A Comparative Study of the Energetics of Avian Reproduction

by

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This thesis is presented for the degree of Doctor of Philosophy

The University of Adelaide

Department of Zoology
University of Adelaide
1994

Summary

The growth and development of precocial king quail (='chinese painted quail'; *Coturnix chinensis*) and altricial cockatiel (*Nymphicus hollandicus*) is examined during embryonic and posthatching periods up until fledging.

Both species lay relatively small eggs (4.9 and 5.9 g respectively), which hatch after 16.5 and 19-21 days respectively. After hatching, the quail is independent of the parents, except for parental brooding, but the cockatiel is totally dependent on the parents for food and brooding. The male quail does not incubate the eggs, whereas the male cockatiel incubates, and both quail and cockatiel parents brood chicks. However, the patterns of parental attentiveness during the brooding period is different between the two species. Quail chicks must forage in order to feed, and return to parents for brooding when body temperature decreases, which is dependent on ambient temperature. In contrast, cockatiel chicks are brooded continuously for 10 days after hatching, then intermittently for 2-3 days, after which the chicks are no longer brooded during the day.

Aims of this thesis

Quail and cockatiel are non-passerines which hatch with a similar body mass (about 4 g). Little information exists for the patterns of growth and development in avian species with small hatchlings other than altricial passerines. The incubation time of all embryos is inversely related to fresh egg mass and the degree of precocity at hatching. Altricial hatchlings are believed to hatch earlier in the developmental sequence at an immature state, whereas precocial hatchlings are mature. As fresh egg mass decreases the developmental time for embryonic growth and maturation decreases, and because maturation occurs late in the incubation period, it is suggested that there is a minimum incubation period for precocial hatchlings. This question is examined in this study by comparing the embryonic development of metabolism of king quail with larger precocial hatchlings.

Posthatching growth rates increase with decreasing asymptotic body mass and decrease with increasing degree of precocity at hatching. The early onset of homeothermy in precocial hatchlings is thought to limit the available energy that can be allocated to converting chemical potential energy to living tissues, and therefore resulting in lower relative growth rates at any given body mass. However, possible limitations of foraging time and ambient temperature on the relative growth rates of small precocial hatchlings have not been considered in other studies. Foraging time of precocial hatchlings is likely to decrease with body mass, because of unfavourable heat production to heat loss ratios. Growth may be further limited by low ambient temperatures due to increased thermogenic costs whilst foraging. This study examines if the relative growth rate of king quail is lower than allometric predictions because of the limiting factors of

foraging time and low ambient temperatures.

The relative growth rates of parrots are lower than those of open-nesting altricial land birds. This is thought to be related to the absence of the selective pressures of predation on cavity-nesting parrots. However, part of the explanation may be that parrots develop homeothermy earlier in their posthatching development than other altricial land birds. Therefore the relationship between relative growth rate and the timing of homeothermy in cockatiel is examined to consider if this alternative explanation for the low growth rates of parrots exists.

Findings

Egg composition and energy invested in eggs

Quails eggs are a smaller fraction of adult body mass, and total investment in clutches is less than in other galliform birds. However, the composition of egg contents and water content is similar to predictions based on fresh egg mass. The energy density of quail egg contents is within the reported range of other precocial eggs. Cockatiel eggs are a similar fraction of adult body mass to the predictions for parrots of the same mass, but total investment in clutches is less than predicted. The fraction of yolk in cockatiel eggs is similar to other parrots, but is higher than other altricial birds. Water content of cockatiel eggs is also similar to predictions. The energy density of cockatiel egg contents is similar to other altricial and semi-altricial eggs. On the basis of hatchling developmental type quail eggs are similar to larger precocial eggs, but cockatiel eggs contain more yolk and therefore more energy than other altricial eggs.

Embryonic respiration and development

The oxygen consumption rate of quail embryos increases exponentially throughout incubation, without the typical plateau of the precocial pattern of development. The oxygen consumption rate of cockatiel embryos also increases exponentially as typical of altricial development. The pre-internal pipping rate of oxygen consumption is similar to predictions based on fresh egg mass of all hatchling types. The water vapour conductance of cockatiel eggs is similar to predictions, but is significantly higher than predicted for quail eggs based on fresh egg mass. The estimated partial pressures of O_2 and CO_2 in the aircells of quail eggs reach 100 and 37 torr respectively at internal pipping. In cockatiel eggs the partial pressures reach 120 and 30 torr respectively at internal pipping, but reverse shortly after to 130 and 15 torr due to star-fracturing of eggshell before external pipping commences.

Growth of quail and cockatiel embryos increases exponentially throughout incubation, but in the quail growth slows late in the incubation period without ever

reaching a plateau. The total energy used by both embryos during incubation is a similar fraction of the total available energy in eggs. The energy contents of internal yolk and yolk-free quail hatchlings is identical to predicted values based on fresh egg contents. The energy content of internal yolk and cockatiel hatchlings is similar to that of quail, but the energy remaining in the internal yolk is greater than predicted for altricial eggs.

Based on fresh egg mass and energy content of eggs, the incubation period of quail is shorter than predicted for a precocial bird and the incubation period of cockatiel is longer than predicted for an altricial bird. However, the incubation period of cockatiel is similar to predictions for parrots, which are characteristically longer than other altricial birds. It is concluded that embryos of quail and cockatiel develop in a manner similar to all other species. Despite the earlier than predicted hatching of quail embryos, there is no obvious indication of reduced maturity in the small precocial hatchlings. It is possible that the relatively poor muscle coordination of hatchlings and weak thermogenic responses reflects some degree of muscle immaturity at hatchling.

Hatchling metabolism and degree of precocity

The mean resting metabolic rates at thermoneutrality of quail and cockatiel hatchlings are higher than allometric predictions for all hatchling types. Quail resting metabolism is 60% higher, and that of the cockatiel is about 50% higher, than predictions for galliforms and parrots respectively. The higher resting metabolism of both species reflects a higher degree of homeothermy at hatching than expected, but this capacity is nevertheless low, due to the small hatchling masses. In response to short-term gradual cooling, oxygen consumption rates of hatchling quail and cockatiel are elevated initially in some individuals, but not in others. In all hatchlings the oxygen consumption rate is at least maintained at resting levels during cooling, and does not decline with ambient temperature as typical of passerine hatchlings. Thus it is concluded that quail are variable in their thermogenic responses to cold after hatching, unlike larger precocial hatchlings, and cockatiel resting metabolism reflects a higher degree of precocity than previously recognised.

Posthatching growth of chicks

The relative growth rates of quail at ambient temperatures > 30 °C during the first 20 days after hatching was almost double the growth rates of quail at 15-20 °C. The highest growth rates of quail are lower than predicted by previous allometric relationships between growth rate and asymptotic mass for precocial land birds. The relative growth rate of cockatiel during summer is similar to allometric predictions for parrots, but is significantly lower than other altricial land birds. Similarly the growth rate of cockatiel hatched in winter is significantly lower than those hatched in summer.

Development of homeothermy in chicks

Hatchlings and chicks less than 10 days of age in both quail and cockatiel are poikilothermic, but between 10-13 days of age chicks of both species are able to maintain high body temperature (33-40 °C) at constant levels dependent on their body mass at ambient temperatures above 20 °C, but not at colder temperatures. With increases in body mass, chicks of both species are eventually able to regulate body temperature at adult levels. It is concluded that cockatiel chicks develop homeothermic abilities earlier in their nestling period than any other altricial species reported so far, and that the timing of homeothermy is not coordinated with the acquisition of plumage as has been suggested for altricial passerines.

The resting metabolism of quail chicks at thermoneutrality increases to a maximum of double the hatchling resting metabolism after small increases in body mass (at 5-7 g), and then declines to adult levels as body mass increases. Peak metabolic rate of quail chicks during cold exposure is identical to resting metabolism initially, but increases to double resting metabolism at 7-10 g body mass, and then declines in parallel to resting metabolism as body mass increases. The resting metabolism of cockatiel chicks increases at 2-3 days of age, and is maximal at a body mass of 13 g, and then declines to adult levels as body mass increases. Peak metabolic rate of cockatiel chicks is higher than resting metabolic rate when body mass is 20 g at the end of the brooding period, and is maintained at maximal levels throughout the nestling period, until the feathers are unsheathed prior to fledging. Thus the resting metabolic rate exceeds that of an adult bird of the same mass early in the development of both species. This pattern is typical of precocial development. However, the early development of thermogenic responses in cockatiel is unlike the pattern of development in altricial passerine nestlings.

Metabolism of chicks and adults during brooding

Brooded quail chicks maintain oxygen consumption rates at rates similar to that of unbrooded chicks at thermoneutrality at ambient temperatures between 10-37 °C. Quail chicks are brooded intermittently during the day until 17-18 days of age when they generally become homeothermic. It is concluded that periods of brooding represent an energy saving to quail chicks, but chicks expend energy during activity and thermoregulation whilst foraging. The oxygen consumption rates of adult quail whilst brooding 1-5 chicks at ambient temperatures above thermoneutrality are not significantly different from non-brooding quail. However, at ambient temperatures below thermoneutrality, the oxygen consumption rates of brooding quail are significantly elevated above non-brooding rates. Oxygen consumption rates remain elevated at night, which indicates that the circadian rhythm of metabolism is temporarily suppressed. The

time quail spend brooding chicks decreases when chicks are 5 days old, but brooding continues intermittently until chicks reach 17-20 days of age.

Brooded cockatiel chicks (less than 8-9 days of age) maintain oxygen consumption rates at half the thermoneutral rates of unbrooded chicks when ambient temperature is between 10-37 °C. At 9-13 days of age, cockatiel chicks are 20-30g body mass and are no longer brooded effectively by parents, and oxygen consumption rates of brooded chicks increases as T_a decreases, but remain lower than unbrooded chicks of the same age. Brood huddling during parental absences in combination with their thermogenic powers allows chicks to achieve effective homeothermy. Continuous brooding also represents an energy saving to cockatiel chicks, but as chick body mass approaches 20 g the energetic savings to the chick diminishes. At the end of the brooding period cockatiel chicks incur significant thermoregulatory costs dependent on ambient temperature. Thermoregulatory costs for cockatiel chicks are higher during winter than summer due to low daily ambient temperatures, and as a result cockatiel growth rates are lower. The oxygen consumption rates of adult cockatiel brooding 1-4 chicks increases as ambient temperature decreases, but is not significantly higher than non-brooding cockatiel at any ambient temperature. It is suggested here that brooding oxygen consumption rate is not elevated because a large thermal gradient in body temperature exists between the adult and chick, and the chick is essentially naked, which makes parental heat transfer more efficient. Therefore it is concluded that the brooding period is an energetic burden to parent quail when ambient temperature decreases below thermoneutrality, but it is not an energetic burden to brooding cockatiel.

Conclusions

Embryonic Development

The results of this study indicate that the embryonic development of king quail is similar to larger precocial birds, except that the incubation period of king quail is shorter than predicted. Two correlates with the shorter incubation are that embryonic metabolism never becomes constrained by shell gas conductance, nor does embryo growth reach a plateau before hatching. The cockatiel embryo development is like the typical altricial pattern, but embryos achieve a higher degree of homeothermy at hatching than other altricial passerines.

Growth of small precocial birds

After hatching, quail chicks rapidly increase their thermogenic powers with little increase in body mass, which is similar to the precocial pattern of development. The amount of time chicks spend foraging is a function of the cooling rate and the degree of

homeothermy at hatching. Quail hatchlings are a smaller than expected fraction of adult mass, and have higher than expected hatchling resting metabolic rates which increases their degree of homeothermy at hatching, thereby reducing brooding time. However, king quail hatchlings' degree of homeothermy is lower than other galliform species in general, and as a result the relative growth rate of quail is lower than predicted for precocial land birds of similar asymptotic body mass, because whilst chicks are brooded they can not forage.

Growth of parrots

On the other hand, the thermogenic powers of cockatiel chicks increases disproportionately as body mass increases early in their posthatching development, which is more like the precocial pattern of development. But the relative growth rates of cockatiel are lower than predicted for altricial land birds of similar asymptotic body mass. The lower growth rate is attributed to the early achievement of homeothermy in comparison to passerines, but unlike the precocial quail, cockatiel benefit from parental feeding, reduced activity and continuous brooding to achieve a growth rate intermediate between precocial and altricial birds.

Declaration

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference had been made in the text.

I give consent for this copy of my thesis, when deposited in the University Library being available for photocopying and loan.

Signed

Date 17/2/95

Acknowledgments

I would like to thank Assoc. Professor Roger S. Seymour for his supervision throughout this study, and particularly his meticulous criticisms and insights. I am also grateful to the many fellow postgraduates and Dr. David Paton for comments on my work. Fran Sheldon and Assoc. Professor Keith Walker were of great help with statistical advice and assistance with SYSTAT. I thank also Nick Pearson and Rachel Palmer for their help and perseverance in preparing this thesis.

Both Roger Seymour and Assoc. Professor Russell Baudinette greatly improved the clarity of the first manuscript from this study. I would similarly like to thank Dr. David Paton for the loan of video-recording equipment, Phil Kempster and Terry MacKenzie for much labour and technical assistance during this study. Much of the comparisons of quail posthatching development would not have been possible without the generous loan of data from Professor Marvin Bernstein.

This work was conducted whilst I was a recipient of a University of Adelaide Postgraduate Scholarship. I am also grateful to the University of Adelaide for a minor round University Research Grant of $700, and the Mark Mitchell Foundation for a Grant of $2000 towards research (ref: DLC; 104238).

All experimental work was conducted at the University of Adelaide, North Terrace Campus, with the approval of the Animal Ethics Committee (S/29/90).

Publications from this study

Pearson JT. Oxygen consumption rates of adults and chicks during brooding in the King quail (*Coturnix chinensis*). J Comp Physiol B (in press).

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CHAPTER 1

Literature Review and Aims of this Study

The Altricial-Precocial Continuum of Avian Development

During the breeding cycle birds invest energy in eggs, maintain incubation temperature close to that of the incubating bird, and rear the chicks after hatching. Parental effort during each phase of the breeding cycle varies between groups of birds. Two main strategies are recognised in birds, *altricial* and *precocial*. The strategy of precocial birds is to invest more effort in the egg and incubation to produce mature and mobile hatchlings, which are relatively independent of the parents. The strategy of altricial birds is to invest less energy in eggs and incubation and more energy in rearing the immature and immobile hatchlings, which are totally dependent on the parents.

Margaret Nice (1962) formulated criteria for categorising the maturity of avian hatchlings, based on behavioural and morphological characters which reflect the relative independence of chicks from their parents. The diversity of hatchling developmental types has since been the subject of much attention in the literature (Ar and Yom-Tov 1978; Ricklefs 1983; Ar et al. 1987; Bucher 1986, 1987; Sotherland and Rahn 1987; Vleck and Vleck 1987).

Her criteria for hatchling developmental types include condition of eyes (open or closed), down (present or absent), mobility (mobile or confined to the nest), mode of feeding (self or parental) and the degree of parental care required after hatching (Nice 1962). At the extremes of the developmental spectrum are precocial (most mature) and altricial (least mature) hatchlings. However, hatchling maturity is a continuous variable and is represented by eight discrete conditions for convenience only. The categories of hatchling developmental type in this study follow those of Nice (1962) in order of decreasing precocity: Precocial (1-4), Semi-precocial, Semi-altricial (1-2) and Altricial.

A brief outline of the taxonomic distribution of developmental types according to Nice (1962) is provided here for reference (Table 1). From this table, it is apparent that avian orders are represented by a narrow range of hatchling developmental types. For example, species within Charadriiformes vary between precocial and semi-precocial hatchlings. Most orders are less variable in their hatchling condition, as typified by the many families of passerines, all of which are altricial. Therefore comparisons of hatchling maturity may be confounded by phylogenetic associations.

The relative maturity of hatchlings is of significance to studies of the reproductive strategies of birds because the different hatchling states have evolved in response to environmental pressures (Ar and Yom-Tov 1978). Precocial land birds leave the nest soon after hatching and feed independently of their parents, and they must be capable of escaping from predators. Therefore precocial hatchlings must be capable of regulating body temperature to some extent at lower ambient temperatures. Until they are able to

fly, altricial land birds remain in the nest where they benefit from significant nest insulation, continuous parental brooding during the initial nestling period, and feeding by their parents. Thus altricial nestlings do not need to be capable of regulating body temperature at hatching, nor do they need locomotory abilities. However, between these extremes are species classified as semi-precocial and semi-altricial, which lack the mobility of precocial land birds, but have better thermoregulatory abilities than altricial and even some precocial birds (Bucher 1986).

The most commonly used system of classification of Nice (1962) is not able to provide a quantitative measure of the relative physiological maturity of hatchlings (Bucher 1986). Bucher compared Nice's classification to an index based on measurements of intensity of energy metabolism of hatchlings for 12 orders of birds. It was concluded that some taxonomic groups are more precocial metabolically than indicated by a category based upon behavioural and morphological criteria. Other orders such as Psittaciformes are considered to be some of the most altricial species according to either physiological or morphological criteria (Bucher 1986). The metabolic intensity of the hatchlings of two altricial parrot species, *Agapornis roseicollis* and *Enicognathus ferruginous*, are only 30% of the adult birds. However, *Agapornis roseicollis* chicks develop thermogenic responses relatively early in their nestling periods for altricial species (Bucher and Bartholomew 1986). Other parrot species may similarly achieve a higher degree of physiological maturity at hatching or soon after, despite their apparent morphological immaturity. Therefore this review examines the differences between altricial and precocial birds in their energetic investment in eggs, and the growth and development of metabolism during incubation and the posthatching periods.

Table 1. A general outline of the taxonomic distribution of the Altricial-Precocial Continuum. Examples of each hatchling type were obtained from the literature (Ar et al. 1987; Vleck and Vleck 1987). Sphenisciformes were formerly considered to be semi-altricial 2 in these references, but the classification of semi-precocial (Bucher et al. 1990) is adopted here.

Condition	Order (Family)	Common examples
Precocial 1	Galliformes (Megapodidae)	Brush turkey, malleefowl
Precocial 2	Anseriformes (Anatidae)	Duck, geese
	Galliformes (Tetraonidae)	Grouse
Precocial 3	Galliformes (Phasianidae)	Quail, pheasant
	Struthioformes	Ostrich
	Rheiformes	Rhea
	Casuariiformes	Emu, cassowary
	Charadriiformes (Alcidae)	Murrelet
Precocial 4	Gruiformes (Rallidae)	Rail, coot
	(Turnicidae)	Button-quail
	Podicipediformes	Grebe
Semi-Precocial	Charadriiformes (Laridae)	Gull, tern
	Procellariiformes	Fulmar, diving-petrel
	Sphenisciformes	Penguin
Semi-Altricial 1	Ciconiiformes (Ardeidae)	Heron
	Falconiformes	Eagle, hawk, falcon
Semi-Altricial 2	Strigiformes	Owl
Altricial	Apodiformes (Apodidae)	Swift, hummingbird
	Columbiformes	Pigeon, dove
	Coraciiformes (Alcedinidae)	Kingfisher
	Cuculiformes	Cuckoo
	Passeriformes	Passerine
	Pelecaniformes	Pelecan, gannet
	Psittaciformes	Parrot

The Egg and Development during Incubation

Relationship between fresh egg mass and adult body mass

There is an extensive mass range of eggs laid by birds, from less than 1g for the hummingbird to 1500g for the ostrich. The relationship between fresh egg mass and adult body mass is considerably variable. Most of the variation in egg mass for any given female body mass is attributable to differences between orders (Rahn, Paganelli and Ar 1975). The smallest eggs as a fraction of adult body mass are laid by passerines and other altricial orders, and the largest eggs by precocial and semi-precocial orders. However, the slopes of the relationship between egg mass and adult mass are the same for all families of birds (Rahn, Paganelli and Ar 1975).

Initial investment in eggs

Initial research found that increasing precocity is correlated with higher yolk contents in fresh eggs (Romanoff and Romanoff 1949; Nice 1962). It is now believed that the relative proportion of yolk in fresh egg content is not strictly correlated with developmental type, but rather that the percentage of lipids in the whole egg is correlated with the degree of precocity at hatching (Ricklefs 1977). Further work on semi-altricial and semi-precocial species in particular, confirmed that there is continuous variation in lipids, solids, water, and energetic content (Carey, Rahn and Parisi 1980; Sotherland and Rahn 1987).

Several avian groups such as the semi-precocial Procellariiformes and several altricial species are exceptions to the noted trends in egg composition (Lawrence and Schreiber 1974; Carey, Rahn and Parisi 1980; Sotherland and Rahn 1987). Studies of the egg composition of offshore and pelagic-feeding species within the orders Procellariiformes and Charadriiformes, and other characteristics of their incubation, have placed them in a special category (Whittow 1980; Williams, Siegfried and Cooper 1982; Grant et al. 1982; Warham 1983; Sotherland and Rahn 1987). The brown pelican, *Pelecanus occidentalis*, has a yolk content within the predicted range for an altricial species (Lawrence and Schreiber 1974), but has a significantly elevated energetic content. Parrots also have significantly higher yolk contents than predicted for altricial eggs of similar mass (Bucher 1983). These facts, in conjunction with the described patterns of embryonic development, suggest altriciality is polyphyletic (Bartholomew and Goldstein 1984). Deviations from the trends in egg composition across the altricial-precocial continuum noted by Sotherland and Rahn (1987), may be attributed to

phylogeny and or ecological adaptations, but nevertheless, the relationship between the degree of precocity at hatching and egg energy content is supported by most avian taxa.

Little is known of the energetic investments made by small birds with precocial hatchlings. A relatively large egg might be advantageous for precocial development in small birds because it provides the hatchling with a larger yolk reserve, which it relies on in the first days after hatching, and a larger egg has a longer time to develop and mature (Lack 1968; Visser 1991).

Shell gas conductance and incubation period

The requirements for oxygen and elimination of carbon dioxide are met by diffusion across the porous shell and shell membranes. The same pores that allow exchange of respiratory gases also result in the diffusion of water vapour, and so the gas conductance of the shell and shell membranes is a compromise between the loss of water and adequate respiratory gas exchange (Wangensteen and Rahn 1970-71; Paganelli, Ackerman and Rahn 1978). The gas conductance of eggs is determined by the pore geometry of the eggs (Ar et al. 1974) and the state of hydration of the shell membranes during incubation (Kutchai and Steen 1971; Lomholt 1976). Total diffusive water loss from avian eggs is independent of egg mass and averages 15% of the initial egg mass (Drent 1970; Rahn and Paganelli 1990). It is suggested that the rate of daily water loss of eggs is matched to achieve such a state of hydration at the end of incubation for optimal hatchability (Rahn and Paganelli 1990).

The daily rate of diffusive water loss from bird eggs is then related to egg mass, incubation period (equation 1), water vapour conductance and the water vapour pressure difference between the egg and its nest environment (equation 2).

$\dot{M}_{H_2O} = 150\ (M/I)$ (eq. 1; Rahn and Paganelli 1990)

$\dot{M}_{H_2O} = G_{H_2O}(P_e - P_n)$ (eq. 2; Paganelli 1980)

Where $\dot{M}_{H_2O}$ is the daily water loss of an egg (mg day^{-1}), M is the egg mass (g), I is the incubation period (days), G_{H_2O} is the water vapour conductance of the egg (mg H_2O $day^{-1}torr^{-1}$), P_e is the water vapour pressure inside the eggshell (torr) and P_n is the water vapour pressure of the nest (torr). Thus egg temperature affects the water vapour pressure gradient between the egg and the nest.

Incubation temperature in birds

Avian embryos develop at incubation temperatures less than the body temperatures of adult birds. On average this difference between egg and adult body temperature is 5 °C (McNab 1966; Rahn 1991). The mean incubation temperature of birds over a range of body masses is 36 °C, but the range extends from 31 to 40 °C (Drent 1975; Webb 1987). The ability of birds to maintain egg temperature over a range of ambient temperatures allows embryonic development to continue in the shortest possible time. During parental absences from the nest, embryonic development slows as egg temperature declines at low air temperature, and below an egg temperature of 25-27 °C embryonic development stops in most avian species (Webb 1987).

Development of metabolism in embryonic birds

The oxygen consumption rate ($\dot{V}O_2$) of avian embryos increases as embryos develop, but the pattern of increase in metabolism is different in altricial and precocial birds (Hoyt, Vleck and Vleck 1978; Vleck, Hoyt and Vleck 1979). The $\dot{V}O_2$ of altricial embryos increases exponentially throughout the incubation period, with energy appearing to be utilised preferentially for rapid growth, as many organ systems appear not be fully functional at hatching (Vleck, Hoyt and Vleck 1979; Hoyt and Rahn 1980). The $\dot{V}O_2$ of precocial embryos increases exponentially during the first 60% of their incubation period as the embryos undergo rapid growth, then plateaus or declines after 75% of the incubation period, prior to pipping the inner shell membrane (Rahn, Paganelli and Ar 1974; Hoyt, Vleck and Vleck 1978; Vleck, Hoyt and Vleck 1979; Hoyt and Rahn 1980). The duration of the plateau phase is variable in both precocial and semi-precocial species (Drent 1970; Vleck, Hoyt and Vleck 1979).

The cause of the plateau in $\dot{V}O_2$ during late incubation of precocial embryos is controversial. Some researchers suggest that when embryonic $\dot{V}O_2$ plateaus in precocial embryos, growth is largely completed and therefore the plateau or decline in $\dot{V}O_2$ is equal to the maintenance requirements for embryonic function (Vleck, Hoyt and Vleck 1979; Hoyt 1987; Vleck and Vleck 1987). This plateau may also allow all the embryos within the clutch of precocial species to synchronise their hatch (Vleck, Hoyt and Vleck 1979). Shell gas conductance is primarily adapted to regulate water loss from eggs and has less influence on $\dot{V}O_2$ prior to pipping. However, the partial pressure of oxygen in the aircell of eggs at this time is more variable than expected (Hoyt, Vleck and Vleck 1978; Vleck, Hoyt and Vleck 1979). Other researchers have demonstrated that low shell gas conductances may limit oxygen uptake during late incubation resulting in a plateau in $\dot{V}O_2$ (Wangensteen and Rahn 1970-71; Tazawa et al. 1989b; Ancel and Visschedijk 1993).

At the pre-internal pipping (PIP) stage of incubation, embryonic $\dot{V}O_2$ is significantly related to embryo mass (Vleck, Hoyt and Vleck 1979), and embryonic $\dot{V}O_2$ is 20-35 % of the BMR predicted for adult birds of a similar mass (Vleck, Hoyt and Vleck 1979; Hoyt and Rahn 1980; Paganelli and Rahn 1984). Such low metabolic rates leads Vleck et al. (1979) to conclude that all embryos probably do not have large thermoregulatory costs associated with their maintenance metabolism during their entire embryonic development. The total oxygen consumed by the embryo up until PIP per gram fresh egg mass is similar for all the avian species considered by Hoyt and Rahn (1980), with a mean value of 94 mL O_2 per gram fresh mass.

In the final stages of incubation precocial embryos appear to develop thermoregulatory responses, because they are able to sustain or slightly increase their heat production in response to decreasing egg temperature, but a low predetermined shell gas conductance and high thermal conductance may limit precocial PIP embryos in their capacity to increase $\dot{V}O_2$ to maintain core temperature during cold exposure (Paganelli and Rahn 1984; Whittow and Tazawa 1991; Nichelmann, Lange and Paulick 1994a). This provides additional evidence that the plateau phase of precocial metabolism is due to an oxygen conductance limitation, and not necessarily a diminished growth rate. PIP embryos which are exposed to hypoxia during cooling tests are unable to sustain their $\dot{V}O_2$, but those in pure oxygen can sustain $\dot{V}O_2$ whilst egg temperature decreases (Tazawa et al. 1989b). The impending metabolic demands of hatching can not be met by chorioallantoic gas exchange alone, but with the onset of pulmonary respiration after IP, mass-specific metabolism is elevated to meet the requirements of the hatching event (Paganelli and Rahn 1984). Once pulmonary respiration becomes the dominant form of respiration many precocial embryos are able to slow the decrease in core temperature during cold exposure by increasing $\dot{V}O_2$ (Booth 1987; Tazawa et al. 1988; Tazawa et al. 1989a; Kuroda et al. 1990; Whittow and Tazawa 1991). However, small precocial Japanese quail eggs (less than 10 g) have higher cooling rates than larger chicken and duck eggs (Tazawa, Turner and Paganelli 1988), and therefore may be less able to maintain core temperature during cold exposure. The thermogenic responses of small precocial embryos may not be revealed if prolonged or gradual cooling tests are applied (Tazawa et al. 1988b; Tazawa et al. 1989a), because the power produced by such embryos may not be sufficient to match the heat loss from the egg, even after pulmonary respiration commences. This does not imply that thermogenic responses do not exist, but that the higher rate of heat loss results in a rapid decrease in egg temperature, and as a result the lowest egg temperature at which $\dot{V}O_2$ can be sustained is closer to thermoneutrality. Semi-precocial and altricial embryos do not appear to be able to maintain or increase heat production whilst in the egg (Matsunaga et al. 1989; Kuroda et al. 1990; Mathiu, Whittow and Dawson 1992). However, thermogenic responses are evidently switched-on after hatching in the semi-precocial wedge-tailed shearwater,

Puffinus pacificus (Mathiu, Whittow and Dawson 1992). The thermogenic responses of small precocial embryos to short and long-term gradual cooling remains to be tested.

Embryonic growth

Altricial embryos grow continuously, which is reflected in the exponential increase in $\dot{V}O_2$. Precocial embryos achieve maximum growth rate early in development and then devote more energy to maturation of their tissues. Thus embryonic growth rate peaks relatively earlier in precocial development than in altricial development (Hoyt 1987). Hoyt provides a new model for avian embryonic metabolism, which includes a term for embryonic growth rate reliant on measurements of PIP $\dot{V}O_2$ and total energy used during incubation (TOT). This model enables predictions of various patterns of metabolism in different precocial species dependent on hatchling mass and incubation period, including species with prolonged incubation periods. The improved accuracy of Hoyt's (1987) model, which explained 97-98% of the variation in observed PIP $\dot{V}O_2$ and TOT is due to the consideration of the greater contribution of maintenance energy to the total energy consumed and the assumption in the model that embryonic metabolism patterns are different between precocial and altricial species (Hoyt 1987).

The total oxygen consumed during incubation is provided for at least two functions: growth and maintenance (Hoyt, Vleck and Vleck 1978). Hoyt (1987) suggests that PIP $\dot{V}O_2$ and TOT can be more accurately predicted with a model based on embryo dry mass, rather than fresh mass. A multiple regression model was fitted to $\dot{V}O_2$ dependent on the dry mass and growth rate of embryos throughout the incubation period (equation 3) for five domesticated precocial species.

$$\dot{V}O_2 = A \cdot \text{Mass}^b + C \cdot \text{Growth rate} \qquad \text{(eq. 3)}$$

The average parameters (A, b and C) of this model provide an estimate of the relationship between embryo dry mass and incubation time, and the $\dot{V}O_2$ of embryos throughout incubation for any species. It was then assumed that the increases in mass of precocial and semi-precocial species was described by a logistic function, and that of altricial and semi-altricial species by an exponential function. Hoyt's (1987) model explains most of the variation in PIP $\dot{V}O_2$ and TOT for the 56 species listed in Vleck and Vleck (1987). Therefore this model appears to provide the best predictions for comparisons of the ontogeny of metabolism in small precocial and altricial species. The differences in embryonic growth rate and metabolism during incubation in altricial species suggested that when altricial species are compared using fresh egg mass as the scaling variable, they have lower costs of development, smaller hatchlings, and shorter incubation periods (Hoyt 1987; Vleck and Vleck 1987). Eggs of altricial and semi-altricial species have

significantly lower energy densities than either semi-precocial or precocial species (Carey, Rahn and Parisi 1980), so when energy content is used as a scaling variable rather than fresh egg mass, it appears that altricial and precocial species use a similar percentage of the energetic content of their eggs (Vleck and Vleck 1987), as predicted in the previous model (Hoyt 1987). Based on a pooled data set of 105 species, of all hatchling developmental types, the major difference recorded between altriciality and precociality is the earlier hatching of altricial species in the developmental sequence and differences in the energy invested in their eggs (Vleck and Vleck 1987). Of the total energy available to embryos a variable amount of energy in the form of yolk is transferred untransformed to the internal yolk of the embryo during the paranatal period. The energy which is transferred to the internal yolk is highest in precocial hatchlings and reduced in altricial hatchlings. When the internal yolk energy is subtracted from the total energy available to embryos the fraction of the total energy converted to hatchling tissues is independent of hatchling maturity type (Ar et al. 1987). The cost of converting chemical potential energy to living tissues, including maintenance costs, also appears to be similar for all embryonic birds. However, parrots hatch after a longer incubation period than expected, despite the fact that the physical state of the hatchling appears immature (Bucher 1983). Therefore further investigation of the energy allocated to parrot eggs, the ontogeny of metabolism and embryonic growth rates is required.

Development of Temperature Regulation

Index to physiological maturity at hatching

The relative physiological maturity of all hatchlings can be ranked according to the ratio of chick metabolic intensity to that of the adult, independent of body mass (Bucher 1986). Mass-independent metabolic rate (MIM) is defined as the total basal $\dot{V}O_2$ of an 'average' adult of a species divided by its body mass raised to the exponent 0.67. However, growing chicks cannot be measured under basal conditions, and so MIM is obtained from the $\dot{V}O_2$ of a chick in the thermoneutral zone. The ratio of chick MIM to adult MIM serves as an indication of the physiological maturity of the hatchling and the developing chick (Bucher 1986).

When the chick to adult ratio is considered, the chick is then ranked on its relative similarity (based on physiological maturity only) to the adult. Thus species with higher ratios are more precocial. On this basis, Bucher (1986) believes that the order Psittaciformes is one of the least mature at hatching.

Degree of homeothermy at hatching

The physiological maturity of hatchlings is also related to their ability to thermoregulate. Many adult functions in birds require the maintenance of a stable core temperature. Few hatchlings have sufficient thermoregulatory abilities to maintain adult body temperatures (38-42 °C). The development of temperature regulation in young birds requires improvements in heat production to maintain high T_b. The thermogenic responses of precocial birds are usually developed at hatching or soon after, but altricial birds are thought to delay the onset of thermoregulation until late in the nestling period (Dawson and Evans 1957, 1960; Dunn 1975; Whittow and Tazawa 1991; Olson 1992). The total cost of temperature regulation after hatching is borne by parents of altricial chicks, but less so by parents of precocial chicks.

The degree of homeothermy of hatchlings is positively correlated with hatchling mass and hatchling metabolism, and is also correlated with phylogenetic affiliation (Klaassen and Drent 1991; Visser 1991). A higher degree of homeothermy in larger hatchlings is attributed to a more favourable ratio of heat production to heat loss (Visser 1991; Visser and Ricklefs 1993). Hatchling resting metabolic rates (RMR_h) are significantly related to hatchling mass, but the exponent of this relationship for hatchlings is 0.86, which is higher than the relationship for adult birds. The level of hatchling metabolism is related to the phylogeny, ecology and the physiology of birds and is thought to be adaptive (Klaassen and Drent 1991). The minimal thermal conductance of birds is related to body mass (Aschoff 1981). One consequence of a higher level of resting metabolic rate for a hatchling of a given mass is that the lower critical temperature of thermoneutrality decreases. A larger thermoneutral range allows a hatchling to remain active at lower T_a.

Many waterfowl are capable of true homeothermy within a couple of days of hatching, as exemplified by the eider duckling, *Somateria mollisima*, and greylag goslings, *Anser anser* (Myhre and Steen 1979; Steen and Gabrielsen 1988; Untergasser and Hayward 1972). All members of the order Anseriformes have some of the highest RMR_h, but in contrast most precocial hatchlings of Galliformes are considered to have intermediate levels of metabolism, and the precocial and semi-precocial hatchlings of Charadriiformes even lower levels of metabolism (Eppley 1984; Klaassen and Drent 1991; Visser 1991). Exceptionally the hatchlings of one galliform family, Megapodidae, are typified by hatchlings such as the malleefowl, *Leipoa ocellata*, and the brush turkey, *Alectura lathami*, which have excellent thermoregulatory abilities (Booth 1984, 1985). The two thermoregulatory competent groups of birds mentioned so far appear to be well adapted to extreme environmental situations, for in the circumstances of waterfowl, many species must be able to tolerate the cold challenges associated with taking to the water soon after hatching, when they follow their parents to feeding grounds, whereas

megapodes are totally independent of their parents soon after freeing themselves from their incubation mounds.

Charadriiform hatchlings have the lowest RMR_h of the precocial orders, and therefore a lower degree of homeothermy (Visser 1991; Visser and Ricklefs 1993). Despite the lower RMR_h, many members of the order Charadriiformes have circumpolar distributions. Thus high RMR_h do not appear to be necessary for birds breeding in extreme polar environments, and the low RMR_h of charadriiform hatchlings may be considered an energetic advantage to the chicks (Bech et al. 1984; Visser 1991). Tolerance of mild hypothermia, and in some cases severe hypothermia without impaired motor function, or the use of distress calls by hatchlings is widely reported in charadriiform birds (Myhre and Steen 1979). Tolerance of hypothermia allows normal foraging behaviour at a lower T_b. The maintenance of a lower thermoregulatory set-point for T_b in many precocial and semi-precocial species during development appears to be characteristic of the orders Anseriformes, Galliformes and Charadriiformes, even if for only the briefest period of development in anseriform hatchlings (O'Connor 1975b; Myhre and Steen 1979; Bech et al. 1984; Eppley 1984; Steen et al. 1991)

Galliform hatchlings have a T_b set-point 1-2 °C below adult T_b, but normally tolerate T_b as low as 37 °C during foraging periods at low T_a (Pedersen and Steen 1979). But ptarmigan hatchlings, *Lagopus lagopus*, (14 g) lose physical coordination when their T_b drops below 35 °C under mild cold exposure, and consequently summon parents by distress calls to initiate parental brooding and avoid severe hypothermia (Aulie and Moen 1975; Pedersen and Steen 1979). At the end of the first week, all ptarmigan chicks are generally capable of initiating shivering for heat production, but they still develop slight hypothermia during routine foraging (Aulie and Moen 1975). Even larger galliform hatchlings, such as those of capercaillie, *Tetrao urogallus*, (32g) which breed in subartic forests, have T_b significantly lower than in adults (Hissa et al. 1983). Hatchlings are able to increase their metabolism below thermoneutrality, reaching a maximum of a 250% increase at T_a 14-16 °C, but become mildly hypothermic below T_a 25 °C. Larger chicks tend to surpass smaller chicks in their ability to resist cooling at the same T_a, and so it was reasoned that there is an energetic advantage for small chicks which allow T_b to decline since the thermal gradient between the chick and the environment is reduced (Hissa et al. 1983). However, if T_b decreases significantly, their ability to feed, digest and assimilate food may also be reduced.

Precocial chicks are self-feeding and the time they spend being brooded by parents is unavailable for feeding. As T_a declines the duration of foraging periods similarly declines and the duration of brooding periods increases. Brooding requirements are expected to increase as the mass of precocial hatchlings decreases, which in combination with high thermoregulatory requirements that are a consequence of small mass, may mean that young precocial chicks are energetically constrained during adverse weather conditions (Pedersen and Steen 1979; Bientema and Visser 1989; Visser

1991; Visser and Ricklefs 1993). Small charadriiform chicks which spend less than 30% of the day foraging due to low T_a do not grow (Bientema and Visser 1989; Visser 1991). The development of one the smallest precocial hatchlings (4 g) from the order Galliformes, the king quail (*Coturnix chinensis*) has previously been investigated, but these hatchlings were raised at thermoneutrality throughout their development (Bernstein 1973). Thus the affect of low T_a on growth and development of temperature regulation is not known.

Charadriiform birds lay larger eggs than galliform birds of similar body mass (Rahn et al. 1975), and therefore hatch as a larger fraction of the adult mass (Visser 1991). As adult mass decreases, the hatchling is a larger fraction of the adult mass in Charadriiformes than in Galliformes. The degree of homeothermy in hatchlings is dependent on body mass and to a lesser extent RMR_h and thermal conductance (Visser 1991). The RMR_h of charadriiform hatchlings is lower than galliform hatchlings, and the thermal conductance is higher at any given body mass, and therefore the degree of homeothermy is lower in Charadriiformes. However, the relationship between the degree of homeothermy, foraging time and RMR of small galliform chicks is not known.

Improvement of thermoregulatory abilities

According to allometric relations, mass-specific metabolic rate increases with decreasing body mass (Aschoff and Pohl 1970). The metabolism of homeothermic adult birds increases as T_a decreases below TNZ. Small chicks require greater mass-specific thermogenic powers than adults to thermoregulate below the TNZ. Balmer and Strobusch (1977) believe that the effectiveness of down of chicks decreases with body mass. Indeed the slope of the allometric relationship between thermal conductance and body mass is significantly steeper for hatchlings than for adult birds (b= -0.702 and -0.484 respectively, Visser 1991). For most chicks, improvements in insulation are late in development, and are usually preceded by improvements in thermogenic capacity, which may be improved in three ways (Marsh 1980): 1) Maturation and or further growth of skeletal muscles for shivering thermogenesis, 2) improvement of neural or endocrinal control of muscle coordination, or 3) delay of the onset of endothermy and indirect improvement of thermoregulatory control by reducing the surface area to volume ratio, so that when a chick eventually becomes endothermic at a larger body mass, relatively less heat production is required to maintain T_b.

Precocial chicks are variable in their ability to increase heat production above thermoneutral levels at hatching, but all appear to devote energy preferentially to increasing their thermogenic capacities in the first days after hatching. Growth of skeletal muscles, which are the principal source of heat production, increases the degree of homeothermy in small precocial species such as ptarmigan, *Lagopus lagopus*, and bantam, *Gallus domesticus* (Aulie 1976). In the same period the oxidative enzyme

capacities for heat production increases in the skeletal muscles and liver, which increases the mass-specific thermogenic capacities. Both the shivering activity of pectoral and leg muscles, and neuromuscular control improves in ptarmigan and the semi-altricial cattle egret, *Bubulcus ibis* (Aulie 1976; Hudson, Dawson and Hill 1974). The rapid improvements in thermogenic capacities of some diving ducks, within hours of hatching, are likely to be the result of a combination of the first two ways listed in the preceding paragraph (Grav et al. 1989; Steen et al. 1989). However, one study suggests that rapid biochemical maturation may not be responsible for the transition from ectothermy to endothermy in shearwater hatchlings. Improvements in the ventilatory movements when the thorax is no longer confined by the eggshell are thought to aid the chick's oxygen uptake during cooling (Mathiu, Whittow and Dawson 1992). However, no precocial or semi-precocial species has been demonstrated to delay the onset of endothermy for more than a few days after hatching.

Altricial passerines are not capable of thermoregulation for a large part of their posthatching development, until their body mass increases and their insulation improves (Dawson and Evans 1957, 1960; Yarbrough 1970; Dunn 1975, 1976; Steen et al. 1989; Choi and Bakken 1990; Olson 1992). Typically the RMR of passerine chicks increases isometrically with body mass throughout development. Other altricial hatchlings, such as parrots and pigeons are ectothermic initially, but develop some thermogenic powers soon after hatching (Breitenbach and Baskett 1967; Bucher and Bartholomew 1986). It is uncertain if some hatchlings lack control of their thermoregulatory processes, or if thermoregulatory control of metabolism and or T_b are actively suppressed.

Altricial chicks achieve energetic savings during low T_a from nest insulation and continuous parental brooding early in their development, and later from brood huddling behaviours during parental absences (Royama 1966; Mertens 1969; Dunn 1975, 1976; O'Connor 1975a). For some species increasing brood number reduces net heat loss because of reduced surface to volume ratios (Royama 1966; O'Connor 1975a). Other species, such as the house sparrow, *Passer domesticus*, are able to achieve effective homeothermy only when there combined mass is sufficient to generate enough heat to raise the nest temperature. Thus broods are capable of reaching 'effective' homeothermy before they reach physiological endothermy (Dunn 1975, 1976).

To assess the degree to which unbrooded nestlings may be capable of regulating T_b, a thermoregulatory index was defined by Dunn (1975) (eq. 4). By convention, the T_b of individual brood members, of different ages in different brood sizes, during short term mild cold exposure (T_a 15 or 20 °C) is compared with the thermoregulatory performance of adults at the same T_a. Effectivc homcothermy is defined as the age at which 75% of the adult ability to maintain a stable T_b was reached (Dunn 1975).

$$TI = 100 \frac{(T_{chick} - T_a)}{(T_{adult} - T_a)} \qquad \text{(eq. 4)}$$

Many altricial passerines are capable of achieving effective homeothermy before their feathers even erupt from their skin. Feathers only offer significant insulation when an effective covering is formed (Dunn 1976). In fact it has been suggested that the degree of insulation may decrease during the period of feather eruption because of the increased blood supply to the skin (Bucher and Bartholomew 1986). A similar pattern of improvement in thermoregulation has been described for several species of altricial non-passerines. Nestling kingfishers, *Megaceryle alcyon*, do not achieve physiological endothermy by the 75% convention until they become fully feathered at adult body mass (Hamas 1981). However, naked nestlings at 6-8 days, which are no longer brooded by their parents are able to maintain T_b of 37-40 °C throughout the day, due to the benefits of large broods, brood huddling behaviour and an improved thermal environment in nesting burrows.

Maturation of skeletal muscle and thermogenesis

Marsh (1980) has suggested that the development of skeletal musculature and maturation of muscle tissues might be critical to the ontogeny of a metabolic response via shivering thermogenesis. Oxidative enzymes in the liver and skeletal muscles are the principal sources of heat production in birds. The enzyme capacities of altricial birds increase slowly throughout development, but thermogenesis does not appear to be utilised early in the nestling period (Marsh and Wickler 1982; Olson 1992; Choi et al. 1993). In contrast, precocial chicks appear to develop thermogenic responses rapidly after hatching, and generally increase RMR by increased enzyme activity (Aulie and Grav 1979; Grav et al. 1988). Thus RMR increases continuously with body mass in altricial birds, but increases rapidly and independently of body mass in precocial birds to levels equal to or greater than levels predicted for adult birds of equivalent body mass.

Coordination of physiological and developmental traits

Webb (1993) discusses the importance of coordination of physiological and morphological development in altricial birds. He hypothesises that the development of feathers is required to retain nestling body heat, and should be closely correlated with the acquisition of improved thermogenic capacities and the regulation of body temperature. Young naked chicks have high thermal conductances (Herreid and Kessel 1967), and continually lose heat to the environment during parental absences. Although nests can be of thermal benefit by reducing the surface area of a brood that is exposed to convective and radiative heat losses (Calder 1973; Kern and van Riper 1984). Some researchers believe that parental brooding acts only to reduce heat loss from the brood (Skutch 1962; Jones 1971), but Webb (1993) demonstrates that chicks are continually losing heat during brooding, and that heat input from the brooding parent is more important than

chick thermogenesis in the brooding period for chick temperature regulation. However, feather growth inhibits heat flow from the parent to the nestling, even though it improves heat retention, and thus Webb argues that feather growth is delayed in the developmental sequence until the transition to homeothermy. In passerines the transition is generally achieved at adult body masses, when nestlings have higher heat capacities, adequate insulation to reduce heat loss, and thermogenic capacities sufficient to maintain high T_b. At this point in development, parental attentiveness decreases rapidly to extend foraging time to meet the increased energy requirements of the brood, which now have significant thermoregulatory costs. The coordination of feather growth and acquisition of homeothermy is supported in general by passerine development (Dawson and Evans 1957; Hill and Beaver 1982; Webb and King 1983b; Webb, Porter and McClure 1990; Webb 1993). However, such coordination of development does not appear to apply to all altricial hatchlings. Parrot nestlings develop thermogenic capacities relatively earlier in their development than altricial passerines (Bucher and Bartholomew 1986). The timing of homeothermy and acquisition of feathers in the cockatiel can be used to test the general applicability of Webb's (1993) hypothesis.

Influence of cold acclimation on thermoregulatory abilities

Cold acclimation significantly increases the thermogenic capacities of chicks of precocial species (Aulie and Grav 1979; Barré et al. 1989b; Duchamp and Barré 1993; Duchamp et al. 1993). Intermittent cold exposure results in improvements in oxidative metabolism in both pectoral and leg muscles, and the liver of bantam chicks (Aulie and Grav 1979). It is uncertain to what extent the higher resting and maximal aerobic metabolic rates are due to the relative contributions of non-shivering thermogenesis (NST) and shivering thermogenesis in that study. But in the precocial bantam, leg muscles are the dominant contributor to heat production and form 9.5% of the body mass at 14 days posthatching. Several studies have elucidated more detail about the mechanisms for cold acclimation in precocial muscovy ducklings (Barré et al. 1989a, b; Duchamp and Barré 1993; Duchamp et al. 1993). Their findings indicate that cold acclimation induces NST by increasing the activities of respiratory enzymes, without the need for increased phosphorylative activity associated with muscle activity via shivering thermogenesis. Uncoupled mitochondrial oxidation in skeletal muscle and liver tissues appear to be the mechanism for NST during cold exposure. The release of free-fatty acids by the hormone glucagon uncouples the mitochondria, increasing oxidative metabolism (Barré et al. 1989a). Skeletal muscle in acclimated ducklings may contribute as much heat production by NST as skeletal muscle in non-acclimated ducklings by shivering thermogenesis during cold exposure (Duchamp and Barré 1993). It remains to be tested if the skeletal muscle of other chicks, such as altricial species, are similarly capable of NST, or if the endocrinal stimulation is lacking early in development, which

would suggest that the early development of thermogenic responses is prevented. However, the presence of NST is beyond the scope of this study and is not considered any further.

Relative Growth Rates of Birds

Lack (1968) defines growth rate as the inverse of the time taken to fledging in birds, but growth in body mass per unit time is a better definition of growth rate than the attainment of flight (Ricklefs 1968, 1973). In comparative studies of avian growth rates, curve fitting techniques are used to describe the increase in body mass or length of body parameters (Ricklefs 1967).

Three types of growth models are commonly fitted to body mass measurements: the logistic equation, Gompertz equation and the von Bertalanffy equation (Ricklefs 1967). The Gompertz equation is the most commonly used in comparative studies (eq. 5). The form of all equations is sigmoid shaped, and detailed descriptions of each technique are given elsewhere (see Ricklefs 1967, 1983). Three parameters are fitted to the growth equation,

$$\text{Mass (g)} = A \cdot e^{(-e(-K(t-wi)))} \qquad \text{(eq. 5)}$$

where A is the asymptotic mass (g), K is the constant directly proportional to the rate of growth (day^{-1}), and w_i is the inflection point (days) at which the relative growth rate is highest. Therefore growth rate increases up to an inflection point after which it decreases.

The shape of growth curves of body mass is not related to the hatchling developmental type. Although growth rates are correlated with adult body mass, nestling period, food availability and hatchling precocity (Ricklefs 1968, 1973, 1979a). The selective pressure of predation on nestlings of open-nesting altricial land birds is thought to select for rapid growth in comparison to hole-nesting species (Lack 1968; Ricklefs 1973). Growth rates are also correlated with brood size, because the more mouths that must be fed, the less any individual brood member is likely to get. Offshore and pelagic feeding seabirds which lay single egg clutches and many tropical landbirds which lay relatively small clutches, both have lower than expected growth rates.

Growth rate is highly correlated with the development of flight capabilities. The highest growth rates are in altricial species which take their first flight later in their development (Ricklefs 1973). Altricial passerines grow at three to four times the rate of a precocial species of similar asymptotic mass (Ricklefs 1973, 1979a, 1983). These differences suggest that the allocation of energy in young birds differs between hatchling developmental types.

The evolution of reproductive strategies in birds is related to growth rate and the timing of mature functions during development (Ricklefs 1973; Ar and Yom-Tov 1978). The risk of predation, food availability and quality, and sibling competition indirectly influence growth rates of birds (Lack 1968; Drent and Daan 1980; Ricklefs 1983). Direct selection is attributed to limitations imposed on growth rates by physiological constraints such as the relative maturity of tissues, assimilation efficiencies and differential growth of organs (Ricklefs 1969, 1979a; Lilja 1983; Lilja et al. 1985; Konarzewski et al. 1989). Thus differences in growth rates of birds are dependent on the partitioning of metabolisable energy between different functions.

Allocation of energy by chicks

The total metabolisable energy (TME) available to chicks is thought to be allocated as described in the energy allocation hypothesis (Dawson and Evans 1957, 1960; Ricklefs et al. 1980), which is simplified here as:

$$TME = M + B + SDA + P + T + A \qquad \text{(eq. 6)}$$

where M is the minimum maintenance costs of supporting tissue function, B is the cost of biosynthesis, SDA is the specific dynamic action of processing and assimilating food, P is the energy in accumulated in tissue, T is the energy expended in thermoregulation and A is the energy expended during activity. All hatchlings allocate energy to these functions, but there are large differences in the amount of energy allocated to thermoregulation and activity in different hatchling types.

Small passerines such as *Spizella pusilla*, *S. passerina* and *Pooecetes g. gramineus* have some of the highest growth rates of birds (Dawson and Evans 1957, 1960). Altricial chicks are able to allocate more energy towards growth and development in comparison to similarly sized precocial chicks due to their lack of locomotory costs and a delayed acquisition of endothermy. They also benefit from brood huddling behaviour and nest insulation (Dawson and Evans 1957, 1960; Olson 1991, 1992). Thus the hypothesis predicts that energy which would otherwise be required to maintain homeothermy at small body masses is available for growth. Other studies have directly measured the aerobic metabolism or examined heat transfer of huddling nestlings and small adult birds, and suggest that nestling-nestling contact results in energetic savings proportional to brood size (Mertens 1969; Webb and King 1983; Brown and Foster 1992).

Another passerine, the red-winged blackbird, *Agelaius phoeniceus*, fledges after only 10 days (Olson 1992). Growth rates and relative growth efficiencies (allocation to new tissues) are highest in the first four days after hatching, before their thermoregulatory capabilities have improved to levels predicted for adults of the same

body mass at 6-7 days. In *A. phoeniceus* the highest growth rates precede the onset of endothermy, at which point the maintenance costs and operating costs of thermogenic tissues require a more substantial proportion of available energy (Olson 1992).

In contrast, chicks of precocial species feed themselves and must meet their own thermoregulatory requirements when they are not brooded by parents during foraging periods (Milanoff and Lindén 1989). Two thirds of the assimilated energy in developing capercaillie, *Tetrao urogallus*, chicks is consumed by thermoregulation and activity. Additionally, in capercaillie there are sex-related differences in the development of body composition (Milanoff and Lindén 1989). Male chicks have faster growth rates and longer growth periods, and must forage for a greater proportion of the day to obtain sufficient food, and thus their thermoregulatory costs are also higher than female chicks. It seems likely that the growth rates and allocation of energy may be influenced by environmental factors, to different degrees across the altricial-precocial continuum. The degree of activity required to obtain food, the efficiency with which food is obtained, the regularity and quality of food obtained (or provided) are likely to influence the pattern of energy allocation in developing birds (Milanoff and Lindén 1989).

Costs of temperature regulation during brooding

The difference in growth rates of birds between altricial and precocial species reflects both differences in energy allocation by the chicks and the relative contributions of the parent to the cost of temperature regulation. Reducing brood heat loss by parental brooding and brood huddling during parental absences, and the construction of a suitable nest with adequate insulation appear to be important for altricial development (Webb and King 1983b; Webb 1993). In contrast, precocial strategies appear to rely on chick thermogenesis and neonatal insulation to maintain high chick T_b, supplemented by parental heat input during brooding periods.

Only one study has examined the importance and effectiveness of heat transfer between parent and nestlings for a small altricial bird (Webb 1993). Nestling thermogenesis is less important than heat input from the parent during brooding periods, but nestling thermogenesis becomes important during parental absences, when contact between the nestlings results in heat exchange between brood members (Webb and King 1983; Webb 1993). Precocial birds lack the benefits of nest insulation to reduce heat loss during brooding because they leave the nest soon after hatching. Therefore it is uncertain if chick thermogenesis is minimal during brooding bouts for precocial birds.

Parental contributions to temperature regulation during brooding are thought to be important for the maintenance of high chick T_b in both altricial and precocial birds (Visser 1991; Visser and Ricklefs 1993; Webb 1993). However, it is not known if the heat transfer between an adult bird and its brood requires additional energy expenditure from the adult above the resting metabolic rate. Many small incubating adults have increased

energy expenditures below thermoneutrality (Biebach 1979, 1981, 1986; Vleck 1981; Drent, Tinbergen and Biebach 1985; Weathers 1985; Williams 1991). It remains to be tested if heat transfer during brooding also requires extra energy expenditure from small birds.

Aims of this Study

The growth of two non-passerine species during incubation and posthatching periods is examined and related to the development of metabolism and temperature regulation to gain insight into the effect of small hatchling mass on relative growth rates and total development time. The precocial king quail, *Coturnix chinensis*, (Galliformes) is compared with an altricial parrot, the cockatiel, *Nymphicus hollandicus*, (Psittaciformes). The following aims are addressed in this study.

- The relative energetic investments in eggs are determined for king quail and cockatiel. Egg composition of both are compared with the allometric predictions for precocial and altricial species of Sotherland and Rahn (1987). Cockatiel eggs and the eggs of other parrot species are compared with altricial eggs in general to determine if there are any significant differences in egg composition as suggested by Bucher (1983). Cockatiel and king quail hatchlings are of similar mass, but the cockatiel egg is larger. The energy invested in the eggs of both species and the energy allocated to hatchlings is determined to compare the cost of development.

- The ontogeny of metabolism is measured as the rates of oxygen consumption throughout incubation, and by integration of these rates an additional estimate of the cost of development is obtained. Embryonic growth rates are determined from fresh and dry embryo mass during incubation. The patterns of metabolism and embryonic growth in king quail and cockatiel are then compared with allometric predictions for precocial and altricial species respectively. It is predicted that small precocial embryos have less time to mature within the egg because of the shorter incubation period, and therefore oxygen consumption rates may never become oxygen conductance limited during late incubation as suggested for larger embryos (Tazawa et al. 1988b).

- The achievement of homeothermy in birds is dependent on the level of hatchling resting metabolic rates, timing of thermogenic responses, hatchling body mass and thermal conductance of the chick. Parrots have longer than expected incubation and posthatching (nestling) periods than altricial passerines, which Lack (1968) attributes to

the absence of selective pressures of predation for rapid growth in cavity nesting parrots in comparison to open-nesting altricial birds. An alternative explanation is considered by comparing the development of homeothermy in the cockatiel with the king quail and with available allometric relationships for precocial and altricial birds in the literature (Visser 1991).

- Bucher and Bartholomew (1986) demonstrated that a small parrot, *Agapornis roseicollis*, increased heat production above resting levels in response to decreasing ambient temperatures at an early age in their nestling period. Webb (1993) has hypothesised that the development of homeothermy in altricial birds must be closely correlated with the development of insulation to retain body heat. This study provides an opportunity to test the suggestion that physiological and morphological traits in birds are coordinated.

- The allocation of energy to the increase of resting metabolism and thermoregulation early in the development of precocial birds is thought to limit the energy available for synthesis of new tissues (Milanoff and Lindén 1989; Dunn 1980; Lindén 1981; Olson 1992). After the onset of thermogenic responses in birds, the cost of thermoregulation in individual chicks increases with decreasing hatchling mass and increases with exposure to decreasing ambient temperatures. In this study the influence of ambient temperature on the growth of king quail and cockatiel is examined to determine if the growth rates of small precocial chicks is limited by their brooding requirements. Cockatiel are brooded continuously after hatching and fed by their parents. Therefore it is expected that their growth rates should be higher than precocial birds.

CHAPTER 2

General Materials and Methods

2.1. Definition of terms in this study

Terminology in studies of avian thermoregulation and energetics has changed considerably in recent years with the realisation that many terms in wide usage are precise or are inapplicable in certain situations. In the context of this study, the terms need to be precisely defined.

For the purposes of this study I have chosen to define temperature regulation in the following ways, which conform to the definitions of terms for thermal physiology set out in Anon. (1987) Pflügers Archives **410**: 567-587.

Ectotherm : An organism which at rest produces insignificant amounts of internal heat towards the maintenance of body temperature, and does not demonstrate active physiological regulation of body temperature. Consequently, body temperature (T_b) is little higher than the ambient temperature (T_a). Typically, such organisms have poor heat retention mechanisms.

The defintion of ectothermy given here specifically refers to the absence of physiological regulation of body temperature, but does not preclude behaviours which may regulate the body temperature of the organism. For example, altricial hatchlings are generally considered to be ectothermic, since T_b of individual brood members is only 1-2 °C higher than T_a, but brood huddling behaviour increases the T_b of each brood member and reduces heat loss from the brood by reducing the total surface area of chick available to heat loss by convection and conduction, and thus higher body temperatures may be achieved (Dunn 1975, 1976; Webb and King 1983).

Endotherm : An organism which produces sufficient internal heat to actively regulate body temperature at a high level (generally 36-40 °C in birds) when T_a is less than T_b. Such organisms are also generally well insulated to mimimise heat loss. Endotherms which regulate T_b within arbitarily defined limits (± 2 °C) by controlling heat production and thermal conductance are defined as **homeotherms**. Endotherms and ectotherms which do not regulate T_b, and have variable T_b over a range of T_a are defined as **poikilotherms**.

Despite the presence of heat retention mechanisms such as down in many hatchlings of different developmental types, the effectiveness of this insulation decreases with body mass (Herreid and Kessel 1967; Balmer and Strobusch 1976). Some larger waterfowl and megapode hatchlings can be considered homeothermic endotherms according to the definitions used here (Untergasser and Hayward 1972; Booth 1984, 1985), but most chicks experience variable T_b when not brooded by parents and therefore are poikilothermic.

Oxygen consumption rate ($\dot{V}O_2$): Mass-specific rate of oxygen consumption of an organism (mL O_2 $g^{-1}h^{-1}$), unless otherwise stated (oxygen consumption rate per animal).

Metabolic rates (MR) : Several terms are currently used to denote the metabolism of an organism, but sometimes the conditions under which such measurements were made are unclear. All metabolic rates in this study refer to the measured oxygen consumption rate of a organism. Throughout this study the following definitions will be adopted:

Standard Metabolic Rate * *(SMR)* - $\dot{V}O_2$ of non-breeding and non-growing birds under the standard conditions of postaborption and resting in the dark within the TNZ.

Resting Metabolic Rate (RMR) - minimal $\dot{V}O_2$ of resting birds at any T_a. Unlike SMR, RMR may be applied to growing birds.

Peak Metabolic Rate (PMR) - maximal $\dot{V}O_2$ of birds during cold exposure in metabolic chambers.

The relationship between mass-specific metabolic rate and ambient temperature (T_a) for a hypothetical bird is given in figure 1. This figure illustrates some of the terms defined in this study. MR within the thermoneutral zone is termed SMR only when measured under standard conditions, or thermoneutral RMR when these conditions are not met.

Thermoneutral zone (TNZ) : For endothermic organisms, TNZ is the ambient temperature range over which an organism does not change its metabolism in order to maintain a stable body temperature. In this study the term TNZ will also be applied to hatchlings, although the thermoneutral range may be very restricted (1-2 °C). The lower and upper limits of thermoneutrality are referred to as lower and upper critical temperature (**LCT** and **UCT** respectively).

Hypothermic temperature (T_{hypo}) : Ambient temperature below which young birds are unable to increase $\dot{V}O_2$ any further and T_b declines with decreasing T_a. PMR may be sustained below T_{hypo} but as T_a decreases further a point is reached when $\dot{V}O_2$ starts to decrease with T_a.

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* It should be noted that the definition of SMR given here, differs from the glossary (Pflügers Arch.) in that the standard conditions do not assume the animal is necessarily awake during measurements.

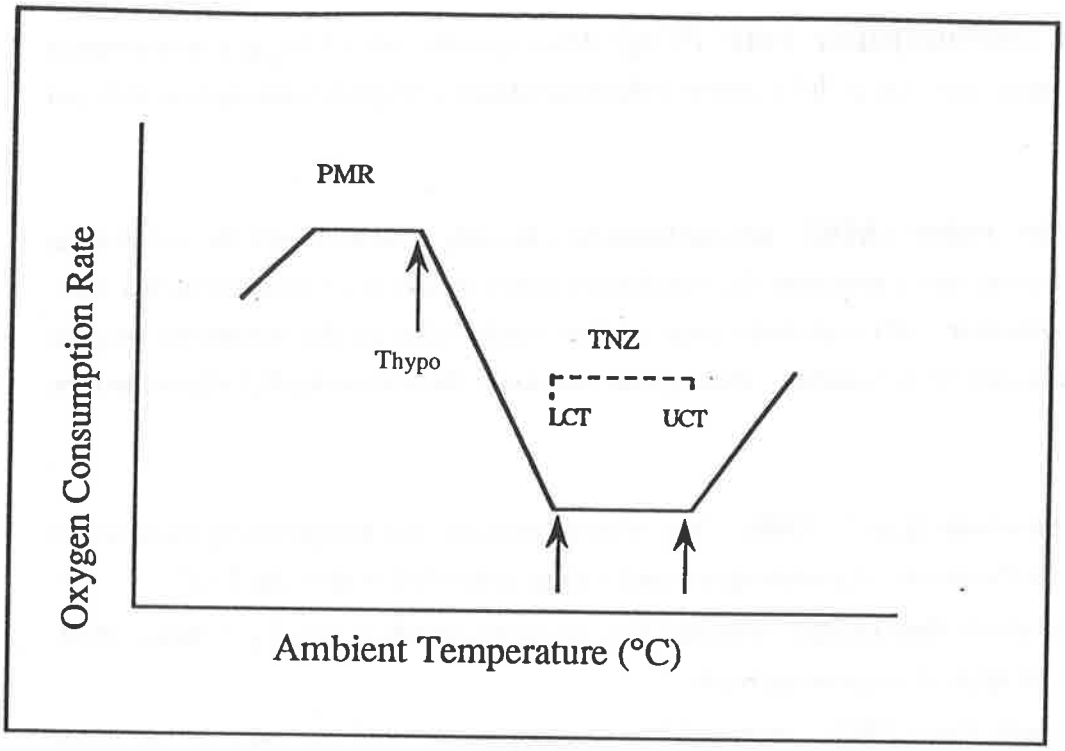

Figure 1. Relationship between $\dot{V}O_2$ and T_a for a hypothetical bird. Labelled terms in figure refer to definitions given in text.

Wet Thermal Conductance (C_{wet}) : rate of heat loss from a body to the environment by evaporative and non-evaporative routes combined per unit of temperature difference between T_b and T_a. C_{wet} is calculated from heat production (W) or measured as $\dot{V}O_2$ of the body and the thermal gradient between the body and the environment as described by Scholander et al. (1950) (mL O_2 $g^{-1}°C^{-1}h^{-1}$ or W g^{-1} $°C^{-1}$).

$$C_{wet} = \frac{\dot{V}O_2}{(T_b - T_a)}$$

Temperature Coefficient (Q_{10}) : The ratio of a physiological process at a particular temperature to the rate at a temperature 10 °C lower, when the logarithm of the rate is an approximately linear function of temperature. Routinely T_2 is greater than T_1.

$$\log Q_{10} = \frac{10}{T1 - T2} \cdot \log \frac{R1}{R2}$$

where R_1 is $\dot{V}O_2$ at T_1, and R_2 is $\dot{V}O_2$ at T_2

Thermoregulatory Index (TI) : The proportion of adult thermoregulatory abilities (%) achieved by a developing young of the same species, as defined by Dunn (1975).

$$TI = 100 \frac{(T_B - T_a)}{(T_b - T_a)}$$

where $(T_B - T_a)$ represents the gradient between adult body temperature and ambient temperature, and $(T_b - T_a)$ represents the gradient between the chick's body temperature and ambient temperature.

Mass Independent Metabolism (MIM) : Mass-independent metabolism has been advocated in several major reviews (Brody 1945; Heusner 1985; Bucher 1986), and is used in this study. It represents a value of metabolic intensity which is essentially independent of body mass (mL O_2 $h^{-1}g^{-0.67}$).

MIM = $\dot{V}O_2$ in TNZ (mL O_2 h^{-1}) $\div$ $M_b^{0.67}$

where M_b is the body mass of a bird

Evaporative Water Loss rates (EWL) : Mass-specific rate of loss of water from a bird by evaporation (mg H_2O $g^{-1}h^{-1}$). Furthermore evaporative heat loss (**EHL**) is calculated from EWL using an energetic equivalent of 2.427 J of heat dissipated per mg H_2O evaporated from a bird at 35 °C (Schmidt-Nielsen 1975).

Heat Production (HP) : The amount of heat produced by a bird using an energetic equivalent of 20.08 J per mL of oxygen consumed (Schmidt-Nielsen 1975).

The following subscripts were used to denote the circadian level of activity of birds during a measurement:

α - active phase (day)

ρ - rest phase (night)

2.2. Housing of experimental birds

Cockatiels and king quail were housed together in five outdoor aviaries of the Zoology Department, Adelaide University at Adelaide, South Australia (Appendix 1). Thirty cockatiels and twenty King quail were initially purchased from a local bird dealer (Camsal Aviaries, South Australia). In the first year of this study (1990), only king quail occupied the aviaries. After the first year, three to five pair of cockatiels and one or two male and four female king quail were housed in each of the aviaries.

All aviaries were provided with 'small parrot mix' seed and water *ad libitum* and bird diets were supplemented with lettuce and mealworm larvae (*Tenebrio* sp.) during the breeding season. Similarly cuttlefish skeletons were provided as a source of minerals for all birds. All birds were wormed on a regular basis with Happavet Bird Wormer (Aust.) added to drinking water.

Nestboxes of plywood, with a layer of potting mix in the bottom of the box, were provided throughout the year for cockatiels in all the aviaries (Appendix 2). Leaf litter and pieces of dry vegetation were placed on the floor in the corners of the aviaries to provide breeding refuges for quail.

2.3. Measurements of adult birds and growth of embryos and chicks

Body measurements were made of the following parameters in embryos, chicks and adult birds using plastic vernier calipers (± 0.1 mm): head length (HL); head width (HW); culmen (C); shoulder to tail (ST); hand (Ha); tarsus (Ta); and middle-toe (To) (fig. 2) However, HL was considered to be unreliable in cockatiel because of the kinetic movements of the bill. Body mass (BM) was measured on a Sartorius Balance 1265MP. Older chicks and adult birds were placed in cotton bags to quiten birds during measurements, and the mass of the bag was subtracted from the total.

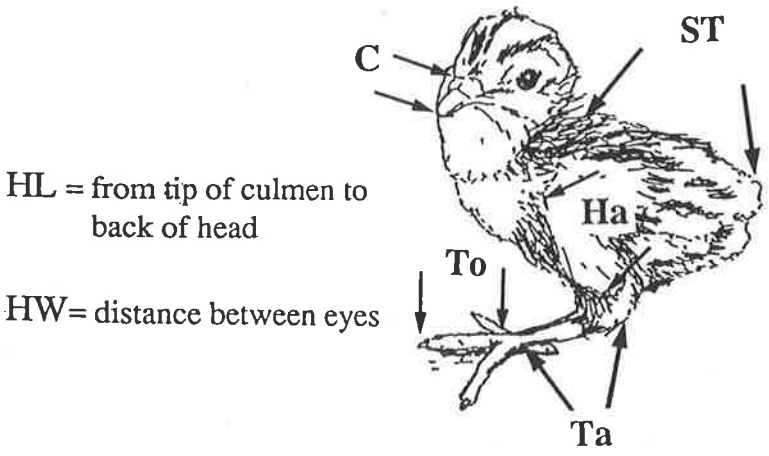

Figure 2. Body parameters measured on embryos, chicks and adult birds (see text).

2.4. Techniques for thermoregulatory studies

Throughout this study the same techniques for measuring $\dot{V}O_2$ and evaporative water loss were used for embryos, chicks and adult birds. Modifications to the techniques and equipment are detailed in each relevant chapter. $\dot{V}O_2$ was measured continuously with a paramagnetic oxygen analyser (Model OA184, Taylor Servomex, England) in an open-flow respirometry system. When adult birds were used for measurements dry air was passed through calibrated flowmeters (SA-18 Fischer & Porter, Hatboro, Pennsylvania) at a flow rate of 800-1000 mL min^{-1} before entering the metabolism chamber (1L plexiglass chamber for king quail and 4.7L PVC chamber for cockatiels). Flow rates of 200-400 mL min^{-1} were used for embryos and hatchlings, and intermediate flow rates between that of hatchlings and adult birds were used for growing chicks. Smaller metabolism chambers were used as appropriate for measurements with embryos and chicks. Measurements were performed under fluorescent light in a constant temperature cabinet during the α phase, but without the light on during the ρ phase. Excurrent air was passed through columns of Drierite (Koch-Light Laboratories, England), soda lime and Drierite, for water vapour and CO_2 removal, respectively, and then was subsampled by the downstream oxygen analyser. $\dot{V}O_2$ was calculated according to equation (2) of Hill (1972), corrected to STPD, and is expressed in units of mL O_2 $g^{-1}h^{-1}$. All $\dot{V}O_2$ determinations were performed in a temperature controlled cabinet ($\pm$ 0.5 °C).

Birds were placed in metabolism chambers 30 min prior to commencing measurements, which was always sufficient time for the birds to settle down. Minimal stable $\dot{V}O_2$ was calculated over a 5-10 min interval at the end of each period of exposure to each T_a. The birds were weighed before and after each $\dot{V}O_2$ measurement to the nearest 0.001g with a Sartorius 1265MP Balance. Core temperature was measured before and after $\dot{V}O_2$ determinations by inserting a precalibrated 36 ga. copper-constantan thermocouple to a depth of 1cm into the cloaca of adult birds, and reading from a digital thermometer (Fluke Model 52). A 40 ga. thermocouple was used for hatchlings and small chicks, and was only inserted to a depth of 0.5 cm. Minimal wet thermal conductance (C_{wet}) was calculated according using the mean recorded T_b of birds in each phase of the day.

$\dot{V}O_2$ measurements of adult birds were obtained from healthy birds with no obvious injuries or substantial loss of feathers. All measurements were limited to a maximum of 2.5 h during the day, and upto 4 h during any night.

It is important to realise that hatchlings were not considered to be postabsorptive because of the presence of an internal yolk supply which lasted 3-4 days after hatching. Cockatiel chicks were never measured under postabsorptive conditions, because previous studies of altricial chicks have all been made on fed nestlings. Therefore cockatiel chicks

were not compared with postabsorptive adults. However, for analysis of patterns of development of metabolism chicks of all ages were compared with fledglings, which were also fed. In contrast, quail chicks, other than hatchlings, were measured in a postabsorptive state, because other studies of precocial chicks have been made on postabsorptive birds.

2.5. Nest and egg temperatures

Several quail and cockatiel nests were monitored for nest, egg and air temperatures during incubation. Thermocouple eggs were made by inserting the end of a 36 ga. copper-constantan thermocouple into a fresh egg via a small hole in the shell and super-gluing it in place. The thermocouple lied just below the upper surface of the egg when the egg was anchored to the floor of the nest. One thermocouple egg was placed in each nest or nest box in addition to the existing clutch and one thermocouple was implanted into the surface of the nesting material (quail) or attached to the inside of a nesting box (cockatiel) above the reach of adults. A third thermocouple was used to monitor air temperature (in shade) in the proximity of a nest or nesting box. A Squirrel Datalogger 1203 (Grant Instruments, Cambridge U.K.) was used for recording temperatures at 10 min intervals continuously over several days and then the data were subsequently downloaded to a personal computer. Generally all measurements were made from the start of incubation through until the clutch started to hatch.

Absences from the nest were inferred from the difference between the thermocouple egg and air temperature. During an absence egg temperature dropped from a stable value (above 30 °C) exponentially towards air temperature. The rate of decline was used to determine if the adult had left the nest or had simply changed posture on the nest or raised it's body to shuffle the eggs. Nest attentiveness, mean period-on and mean period-off (min) were calculated in every case. Similarly mean egg temperature was determined for the whole of the incubation period and each hour of each day of incubation.

2.6. Bomb calorimetry

The energy content of egg contents, embryonic tissues and chicks were analysed using a ballistic bomb calorimeter (Gallenkamp, U.K.). All samples were weighed using a Mettler AE 163 Balance to the nearest 0.0001 g. Analyses were calibrated against known masses of benzoic acid using an energetic equivalent of 26.442 kJ per gram dry mass. Corrections were made for sample material lost during preparation. All energy contents reported here are ash-free energy content.

Samples were oven-dried to constant mass at 70 °C, and stored in an airtight container with silica gel until ready to be combusted. Egg samples and large embryos or

hatchlings were then ground up finely with a mortar and pestle to a homogeneous mix. However, small embryos (<0.3 g dry mass) were not ground up, and instead were combusted intact. Ground samples were pressed loosely into pellets weighing between 0.1 and 0.4 g.

The ballistic bomb calorimeter was a operated within a constant temperature cabinet (± 0.5 °C). The output was Rikadenki chart recorder set in 0-10 mV range, and a chart speed of 12 cm h^{-1}. Samples were combusted in the following procedure:

1) The sample was weighed directly in the calorimeter crucible, which was tared immediately prior.

2) The calorimeter was assembled with a cotton fuse leading from the platinum wire fuse to the sample pellet (direct contact).

3) The calorimeter was filled with O_2 at a pressure of 3000 kPa (30 atm), and then briefly opened to the atmosphere to allow air (mixture of gases) from the calorimeter to escape. The calorimeter was then repressurised with O_2 to fill the volume with pure O_2 only.

4) The chart recorder was activated, and the calorimeter block was covered with a polystyrene box to exclude air currents, the constant temperature cabinet was closed and the calorimeter was allowed to come into thermal equilibrium.

5) When the trace of the chart recorder was stable (no deflection), the bomb was fired to ignite the sample.

6) The calorimeter was left undisturbed until the deflection peaked and then begun to decline. The chart recorder was stopped, the calorimeter opened and the crucible removed. The height of the deflection was read off the chart recorder and recorded.

7) The calorimeter was then cooled with ice water and dried before the next sample was combusted.

8) The crucible was then reweighed to determine ash content, then cleaned prior to the next sample.

The calorimeter was calibrated using samples of benzoic acid (0.1-0.2 g) which were pressed into pellets. Three or four samples of benzoic acid were combusted on any day that samples were analysed, and the mean deflection used to determine sample energy contents. All sample deflections were corrected for the energy content of the cotton fuse used to ignite the sample. This was done by the same procedure as the combustion of a sample, except the crucible did not contain any sample pellet.

2.7. Statistical analysis

In the presentation of these results, the number of species, individual birds, or eggs is reported (n) and the total number of measurements made (N). Typically the relations between $\dot{V}_{O_2}$ and T_a were based on repeated measurements (N), but all other relationships were based on individual measurements (n). All the results collected during this study were analysed using SYSTAT statistical packages (Wilkinson 1990), with the

exception of biphasic regression analysis (Yeager and Ultsch 1989), and plots of results were obtained with SYGRAPH. Analyses were performed on untransformed data unless otherwise stated in the results. Mean values are presented with one standard deviation (± SD) unless otherwise stated. Differences between mean values were evaluated by t-tests. The significance of differences was accepted at the 5% level. Relations between variables were analysed by least squares linear regression analysis (MGLH) or non-linear regression analysis (NONLIN) where appropriate. Linear regressions were plotted with 95% confidence intervals of regression means if significant relationships existed, and the standard error of the regression coefficient (s_b) is presented with the regression statistics. When no significant differences were found between slopes of regressions for each group a modified student's t-test was used to test for significant differences between elevations as recommended by Zar (1984). Repeated measures of $\dot{V}O_2$ were not taken into account when comparing the slopes and intercepts between treatments initially, therefore the statistical robustness of the regression analysis was examined using ANOVA with repeated measures.

CHAPTER 3

Energetics and Gas Exchange during Embryonic Development

Most of the variability in egg mass between species of birds is explained by differences in adult body mass, and further variation is explained phylogeny (Lack 1968; Rahn, Paganelli and Ar 1975). Precocial birds lay larger eggs than altricial birds (Lack 1968; Vleck and Vleck 1987). However, all hatchling birds are between 60-75% of their initial egg mass (Ar et al. 1987). It is of interest to compare how embryos allocate energy during their development, but most precocial birds are larger than altricial species, and therefore lay larger eggs, which makes comparisons of evolutionary strategies difficult (Ar and Yom-Tov 1978).

The aim of this study is to compare the evolutionary strategies of a precocial and altricial species which produce hatchlings of similar mass. The king quail is one of the smallest precocial hatchlings at 3-4 g (Bernstein 1973), of which nothing is known of its embryonic development. The cockatiel is a medium-sized parrot with an altricial hatchling of similar mass at 3.5-4.5 g. Parrots are thought to represent an altricial lineage which is likely to have a separate origin from that of passerines (Bucher 1983; Bucher and Bartholomew 1986). Therefore these species provide an opportunity to compare precocial and altricial development in non-passerine species. In this chapter the relative investment of female birds in their eggs and hatchlings is compared in Section 3.1. Then the development of respiratory gas exchange and the cost of development are determined in Section 3.2. Finally, the patterns of embryonic growth are determined in Section 3.3. Hatchlings of the same mass also provide a starting point for comparisons of the development of temperature regulation and posthatching growth in subsequent chapters.

Section 3.1. Investment in Eggs and Hatchlings

Introduction

Lack (1968) considers a larger egg to be advantageous because it produces a larger hatchling with a larger yolk reserve, or possibly a longer incubation period allows the embryo to hatch with a higher degree of mature functions. Such characteristics are advantageous for precocial species, which are independent of their parents at hatching, except for parental brooding (Nice 1962; Ar and Yom-Tov 1978; Visser 1991). But nest-bound altricial hatchlings are dependent on their parents to a greater extent for food, protection and brooding. It is thought that nest predation may be a strong selective pressure acting to reduce egg size in altricial species (Ar and Yom-Tov 1978; Vleck and Vleck 1987). A smaller egg has a shorter incubation period, which would reduce the total developmental time in the nest and the probability of predation. If eggs should be lost or taken from the nest, then the cost of replacing smaller eggs would be lower.

Birds allocate variable amounts of energy and water to their eggs at any given egg mass. Both the relative yolk content and energy content of eggs increases with the degree of precocity at hatching (Carey, Rahn and Parisi 1980; Ar et al. 1987; Sotherland and Rahn 1987; Vleck and Vleck 1987). Relative yolk content is between 15-35% in altricial eggs and 25-60% in precocial species, and the energy content is on average 4.98 kJ g^{-1} and 8.53 kJ g^{-1} in altricial and precocial species respectively (Ar et al. 1987). As egg mass decreases total energy content and solids content decrease, and conversely the water content increases (Ar et al. 1987; Sotherland and Rahn 1987). At hatching the embryo has a water content similar to that of the initial egg contents, because water lost by diffusion equals the water gained by the embryo's metabolism (Ar and Rahn 1980; Sotherland and Rahn 1987). The initial water fraction of egg contents and hatchlings is significantly higher in altricial species than precocial species (Ricklefs 1977; Ar and Rahn 1980; Vleck, Vleck and Seymour 1984; Sotherland and Rahn 1987). However, most altricial species lay smaller eggs than precocial species (Rahn, Paganelli and Ar 1975), and according to allometric predictions, smaller eggs have higher water fractions (Sotherland and Rahn 1987). It is expected that the smallest precocial eggs also have higher water fractions in their egg contents and consequently higher hatchling water contents than most larger precocial species.

The water content of hatchling tissues is correlated with the functional maturity of those tissues (Ricklefs 1979a, b). Therefore hatchlings from small precocial eggs are expected to be relatively immature in comparison to those from larger eggs because of their higher water contents, although a causal relationship is not implied.

The eggs of several parrot species have more yolk solids than predicted for altricial species with the same egg masses, although the relative yolk fractions are similar to other altricial species (Bucher 1983). The energy density of egg contents of one species, *Agapornis roseicollis*, is reported as 5.31 kJ g^{-1} (Bucher 1983), which is more like the higher energy density of semi-altricial species than altricial species (Ar et al. 1987). However, the initial egg and hatchling water fractions, 81 and 84% respectively (Bucher 1983), are the same as other altricial species (Sotherland and Rahn 1987). It is uncertain if these differences are characteristic of the order Psittaciformes, and if parrot egg composition supports an independent evolutionary line of birds from other altricial groups. More research into egg composition, embryonic and posthatching development of parrots is required.

The aims of this section are to determine the relative parental investment in eggs and clutches, egg composition and energy content, and the energy converted into hatchling tissues and yolk reserves in both the king quail and the cockatiel.

Materials and Methods

Distribution of egg masses

The initial egg mass (M_e), egg length of long axis (L), diameter at widest point of short axis (D) were measured. This was not possible when clutches remained undiscovered on a few occasions. The mean egg mass and range was determined for both species. A subsample of all the eggs, namely quail eggs laid between 1990-92 and cockatiel eggs laid between 1991-93, were used to determine the relationship between egg mass and egg size. Least squares linear regressions were calculated between M_e and each of the following parameters: L, D and $L(D)^2$ for both species.

Egg composition and energy content

Quail eggs were randomly collected from all aviaries, and from as many females as possible to examine the extent of intraspecies variation. Most eggs were collected in the first year of this study. Each egg was measured for length, width and fresh mass and when possible the female was identified and body mass recorded. Eggs were then opened carefully at the blunt end and the contents gently poured into a small petri dish. The contents were then separated into albumen, yolk and shell fractions. Albumen was sucked up into a blunt hypodermic syringe (20 ga.) to avoid rupturing the yolk membranes. Some albumen was lost by evaporation (water only) and a small fraction remained in the syringe. Therefore a corrected fresh mass of albumen was obtained by subtracting the fresh shell and yolk fractions from the initial egg mass. Fresh mass of each fraction was measured to the nearest 0.0001 g with a Mettler AE163 balance. Egg components were oven dried at 70 °C until a constant mass was obtained, generally 24 h. After measuring dry mass, duplicate albumen and triplicate yolk samples were used for analysis of energy content, which was determined by bomb calorimetry (see Chapter 2). In some cases small quail eggs limited the number of samples to one albumen and three yolk samples.

Cockatiel eggs were collected by randomly removing a single egg from fresh clutches in each nest box before incubation commenced. Identical techniques were then used to measure egg composition and energy content.

Parental investment in eggs and clutches

Whenever possible clutch size, laying order, fresh mass, egg size and female body mass at the time of laying were measured. The relationship between M_e and $L(D)^2$ was used to predict fresh egg mass when initial egg mass measurement was not available. Energetic investment of each female in clutches were calculated based on clutch

measurements and the composition of eggs as determined in this study. Investments in clutches was compared between females of each species and between quail and cockatiel.

Hatchling mass and energy content

The mass of most hatchlings was recorded within 0.5 d of hatching for quail and cockatiel. Quail did not feed during the first day, but cockatiel were fed soon after hatching and only cockatiel hatchlings masses were determined before their first feed. The relationship between hatchling mass (M_h) and M_e was determined for all eggs for which the hatchling could be identified. The fresh and dry mass of a sample of yolk-free hatchlings, and their yolk reserves were measured and their energy contents determined by bomb calorimetry.

Results

Distribution of egg masses

The mean egg mass of all eggs laid in this study, was 4.940 ± 0.612 g (SD) (n=162) for king quail, and 5.761 ± 0.531 g (n=74) for cockatiel eggs. The range of king quail eggs laid was 3.437 to 6.209 g, but 80% of all eggs laid were between 3.5 and 5.5 g (fig.1a). The range of cockatiel eggs was 4.254 to 6.925 g, but 90% of the eggs were between 5.0 and 6.5 g (fig.1b).

A sample of quail and cockatiel eggs was measured for initial egg mass, L and D to determine a predictive relationship for initial egg mass to be used in this study when this measurement was not obtained. Mean fresh mass in this sample was 4.929 ± 0.608 g (n=108) for king quail eggs and 5.899 ± 0.485 g (n=33) for cockatiel eggs. $L(D)^2$ was found to explain more variation in egg mass than either L or D alone (Table 1, p.48).

Egg composition and energy content

Twenty two quail eggs and 13 cockatiel eggs were used to determine egg composition. Mean egg mass of the sample of quail eggs was 4.865 ± 0.602 g, and cockatiel was 5.733 ± 0.325 g. This mean value is similar to the mean of all eggs laid in clutches, and a similar degree of variability in egg mass was found.

The mean content and composition of the sampled quail and cockatiel eggs are given in table 2 (p.48). Log-log linear relationships between fresh egg mass and other variables were determined. For quail eggs, only the fresh components (wet shell, albumen and yolk) and dry components (dry albumen and yolk) demonstrated significant linear relationships. As fresh egg mass increased there was a significant increase in the

fresh mass of albumen and to a lesser degree in fresh mass of yolk (fig. 2a). In contrast, the fresh components of cockatiel eggs were a relatively constant fraction of the egg, with only wet albumen demonstrating a significant relationship with fresh mass for cockatiel eggs (fig. 2b). Increases in quail fresh egg mass were correlated with proportional increases in solids of both yolk and albumen (fig. 3a). Dry albumen content increased disproportionately with fresh egg mass ($b > 1.0$), but the total increase was minor, relative to the increase in dry yolk content ($b < 1.0$). The allometric exponents suggest that increases in quail fresh egg mass were principally increases in albumen solids. Solids in cockatiel eggs (fig. 3b) were independent of fresh egg mass. In general, it can be seen from table 3 (p.50), that cockatiel egg composition was variable and almost completely uncorrelated with fresh egg mass, as indicated by the very low coefficient of determinations in most cases.

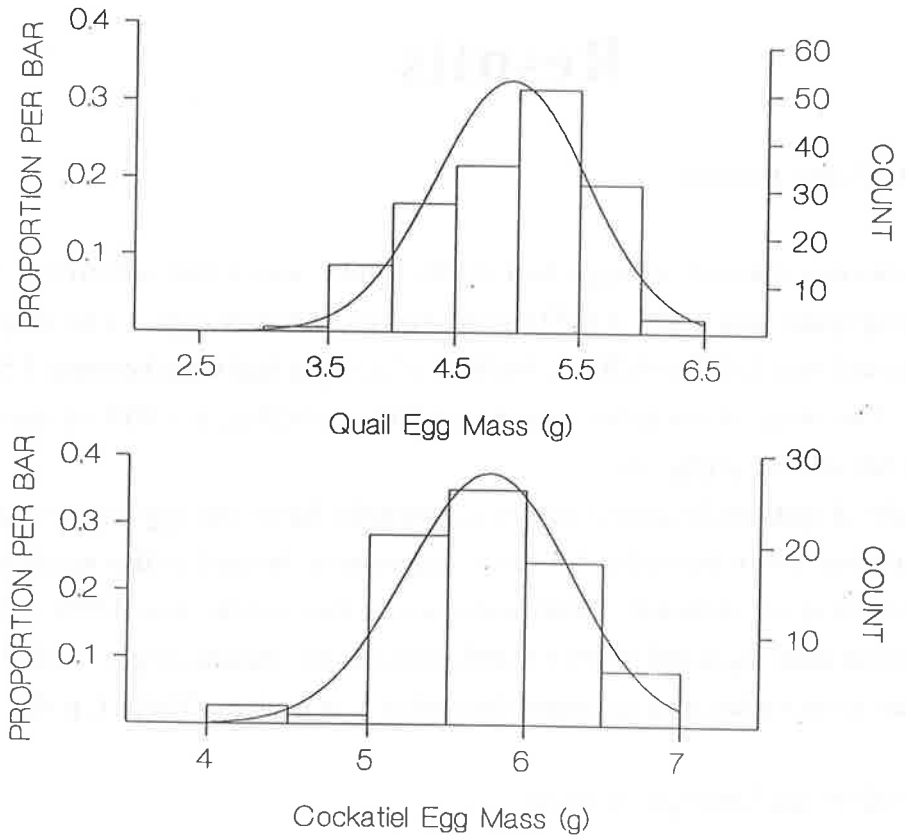

Fig. 1. Frequency distribution of egg masses in this study for king quail (a) and cockatiel (b) (n=162 and 74 respectively). Solid line indicates a normal distribution about the mean egg mass.

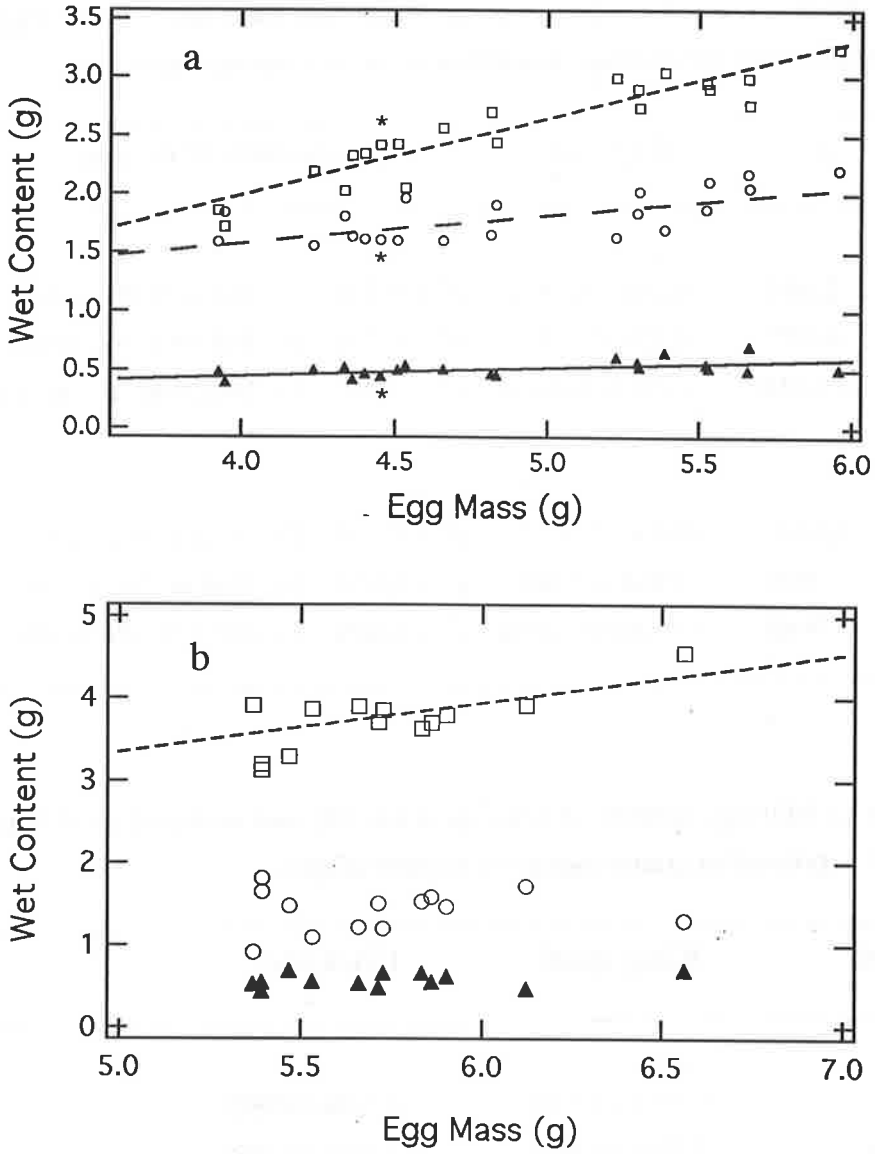

Fig. 2. Relationship between fresh egg content and egg mass for king quail (a) and cockatiel (b). *Triangles and solid line*: shell, *circles and dashed line*: yolk, *squares and fine line*: albumen (g). Star indicates two eggs with overlapping composition. Lines indicate significant relationships (see Table 3). Sample included 22 king quail eggs and 13 cockatiel eggs.

Wet shell content appeared to be relatively invariable with egg mass for both species (fig. 2). As a consequence dry shell did not have a significant linear relationship with egg mass (Table 3, p.50). Water content in each component and the fraction of yolk in contents were also independent of fresh egg mass. The fraction of albumen in egg contents however, demonstrated a barely significant linear relationship with egg mass for quail only.

Table 1. Relationships between egg size and fresh egg mass for samples of king quail and cockatiel eggs. Linear regressions were estimated by least-squares method and are presented in the form y = a + bx, where y is the initial egg mass and x is the egg size variable. Standard error of the regression coefficient (s_b) is presented as $b \pm s_b$.

Variable	*a*	*b* (± s_b)	Regression Statistics
King Quail			
L	-2.361	0.284 (0.043)	$r^2 = 0.724$ F= 281.305 P < 0.001
D	-9.072	0.735 (0.051)	$r^2 = 0.734$ F= 295.984 P < 0.001
L.(D^2)	0.1438	0.0005 (0.001)	$r^2 = 0.965$ F= 2910.650 P < 0.001
Cockatiel			
L	1.631	0.156 (0.057)	$r^2 = 0.197$ F= 13.244 P < 0.001
D	-5.588	0.564 (0.069)	$r^2 = 0.655$ F= 95.806 P < 0.001
L.(D^2)	0.5688	0.0005 (0.001)	$r^2 = 0.875$ F= 352.127 P < 0.001

Table 2. Mean (± SD) egg content of king quail (n=22) and cockatiel (n=13) eggs. Egg variables are expressed in grams content or as percentages.

Variable	King quail	Cockatiel
FRESH MASS		
shell	0.511 (0.073)	0.578 (0.082)
albumen	2.542 (0.416)	3.731 (0.358)
yolk	1.796 (0.213)	1.424 (0.252)
DRY MASS		
shell	0.317 (0.059)	0.355 (0.044)
albumen	0.280 (0.058)	0.476 (0.090)
yolk	0.908 (0.121)	0.599 (0.118)
WATER FRACTION (%)		
shell	37.3 (11.6)	38.3 (3.4)
albumen	88.9 (1.4)	87.2 (2.0)
yolk	49.5 (2.9)	57.9 (5.0)
contents	72.6 (2.4)	79.1 (1.5)
FRACTION OF EGG CONTENTS (%)		
albumen	58.2 (4.0)	72.3 (5.0)
yolk	41.8 (4.0)	27.7 (5.0)

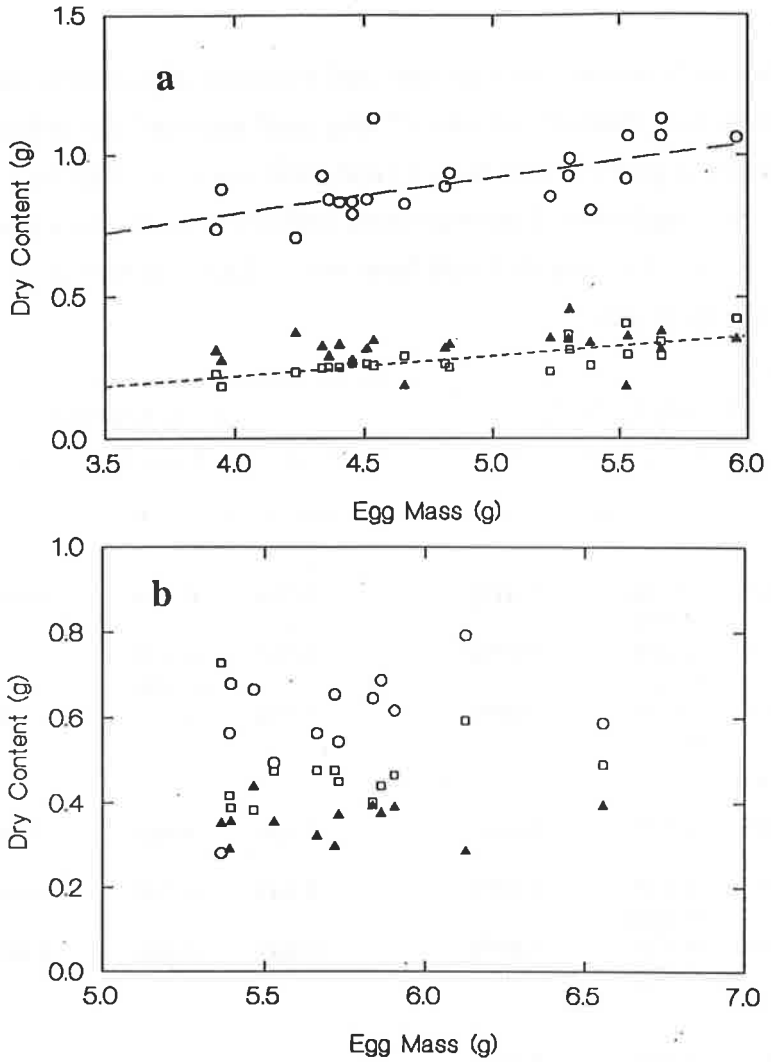

Fig. 3. Relationship between dry egg content and egg mass for king quail (a) and cockatiel (b). *Triangles and solid line*: shell, *circles and dashed line*: yolk, *squares and fine line*: albumen (g). Lines indicate significant relationships (Table 3, p.50). Sample included 22 king quail eggs and 13 cockatiel eggs.

The mean fresh yolk content of quail eggs was 1.796 ± 0.213 g, which was only slightly higher than allometric predictions for an egg mass of 4.865 g (predicted yolk = 1.737 ± 0.035 g) (Sotherland and Rahn 1987). King quail eggs invest their eggs with the expected yolk content for precocial species, and composition is identical to predictions based on the relative yolk content for all birds (Table 4, p.52). The mean fresh yolk content of cockatiel eggs was 1.424 ± 0.252 g, which was higher than predicted for an altricial egg mass of 5.795 g (predicted yolk = 1.223 g), but was within one SEE (Sotherland and Rahn 1987). The relative yolk content of the predicted quail egg was lower than the mean of this study, but the observed yolk content was considerably variable (Table 4, p.52). Across the range of quail eggs sampled here, the relative yolk content varied between 39 and 48% of fresh egg contents (fig.4a). Cockatiel relative yolk content (19-39%) was more variable than the quail egg sample.

Table 3. Linear relations between fresh egg mass and variables of egg composition for king quail and cockatiel eggs. Sample included 22 king quail eggs and 13 cockatiel eggs. Relationships between the dependent variables (Y) and fresh egg mass (M_e) are presented in the form $Y = aM_e^b$. Standard error of the regression coefficient (s_b) is presented as $b \pm s_b$, except where b is not significantly different from zero. Egg variables are expressed in grams content or as percentages.

Variable	KING QUAIL a	b ($\pm s_b$)	r^2	COCKATIEL a	b ($\pm s_b$)	r^2
FRESH MASS						
shell	0.164	0.716 (0.191)	0.413‡	0.286	0.410	0.000
albumen	0.333	1.281 (0.117)	0.858‡	0.782	0.904 (0.354)	0.371‡
yolk	0.644	0.648 (0.151)	0.481‡	0.076	1.637	0.148
DRY MASS						
shell	0.181	0.343	0.041	0.416	-0.085	0.000
albumen	0.039	1.245 (0.215)	0.627‡	0.649	-0.169	0.000
yolk	0.310	0.676 (0.182)	0.407‡	0.007	2.489	0.183
WATER FRACTION (%)						
shell	21.4	0.323	0.015	10.186	0.761	0.117
albumen	89.1	-0.001	0.000	63.680	-0.179	0.048
yolk	51.1	-0.022	0.002	138.68	-0.504	0.069
contents	64.6	0.073	0.073	74.645	0.034	0.000
FRACTION OF EGG CONTENTS (%)						
albumen	39.2	0.250 (0.115)	0.191‡	97.949	-0.163 (0.354)	0.000
yolk	68.5	-0.317	0.176	9.528	0.570	0.000

‡ $P<0.05$

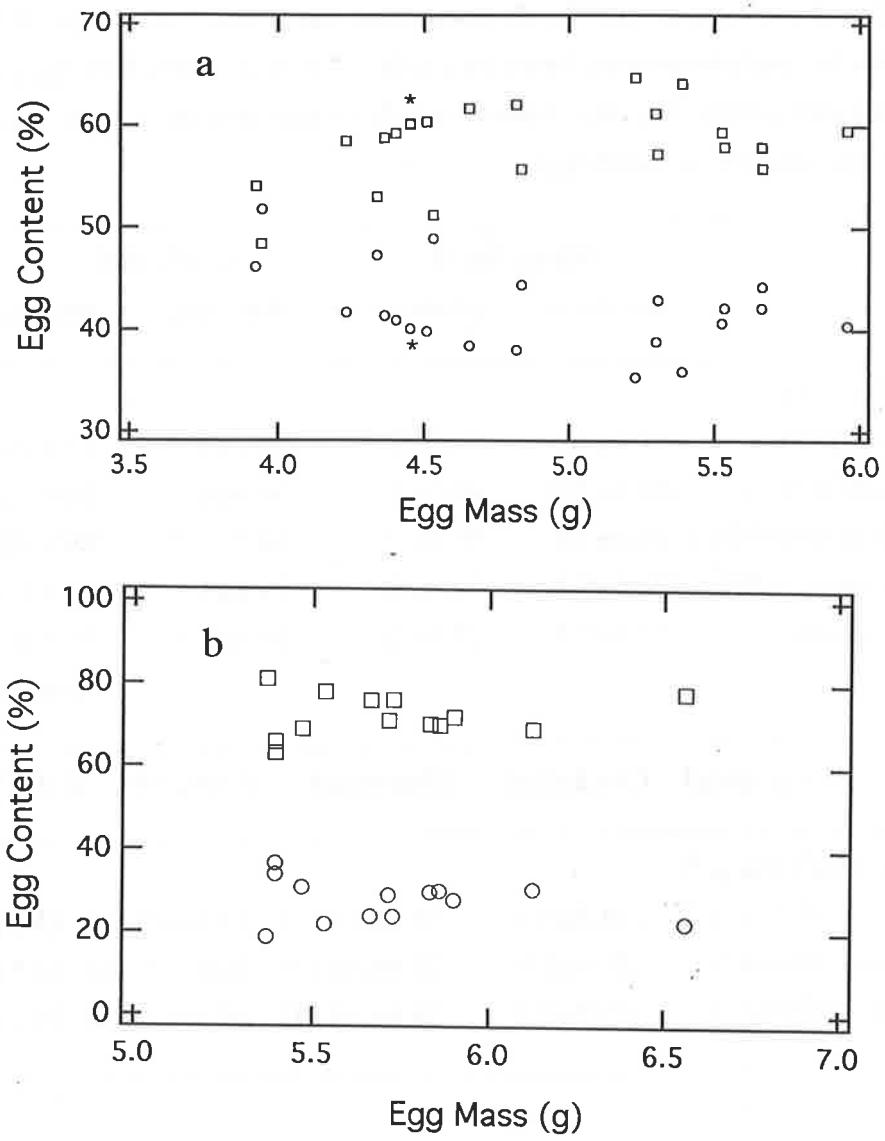

Fig. 4. Relationship between egg mass and yolk fraction (*circles*) and albumen fraction (*squares*) of fresh egg contents for king quail (a) and cockatiel (b). Sample included 22 king quail eggs (star indicates two eggs with overlapping composition) and 13 cockatiel eggs.

The egg shell is generally considered not to contain energy available for embryonic development (Ar et al 1987). Thus energy content and energy densities were examined in relation to dry egg contents and fresh egg contents (table 4). Previously the energy density of total dry solids in eggs was determined for each hatchling maturity type and for all maturity types combined (Ar et al. 1987). The energy densities of egg contents were 8.38 ± 0.86 kJ g^{-1} for quail and cockatiel 5.39 ± 0.73 kJ g^{-1} for cockatiel. The energy densities of quail eggs were not significantly different from a previous comparative study (Ar et al. 1987), but the energy density values of cockatiel eggs were higher than the mean of altricial and semi-altricial species in general.

Table 4. Comparisons of mean egg composition (± SD) and energy content with the previous studies of (1) Ar et al. (1987); (2) Sotherland and Rahn (1987); and (3) Bucher (1983). Allometric predictions were based on a yolk fraction of 41.8% for king quail and 26.2% for cockatiel (Table 2, p.48). Unless otherwise indicated the sample sizes were 22 king quail eggs and 13 cockatiel eggs.

	King quail		Cockatiel	
	this study	predicted	this study	predicted
COMPOSITION (%)				
Yolk fraction (FYC)	41.8±4.0	39.9 (2)	26.2±4.0	23.2±3.0 (3)
Water in yolk (FWY)	49.5±2.9	48.5 (2)	56.9±4.1	54.0 (2)
Water in albumen (FWA)	88.9±1.4	87.8 (2)	87.2±2.1	88.9 (2)
Water in contents (FWC)	72.5±2.4	72.4 (2)	79.2±1.5	79.7 (2)
Solids in contents	27.5±2.4	27.6 (2)	20.8±1.5	20.3 (2)
				19.4±2.0 (3)

	King quail	Cockatiel	Precocial	Altricial	All Types
ENERGY DENSITY (kJ g^{-1})					
Dry yolk	33.2±1.4	29.3±3.1	33.2±1.0 (1)	33.3±0.9 (1)	33.4 (1)
Dry albumen	20.6±1.9	21.0±1.0	22.8±1.8 (1)	21.9±1.6 (1)	22.5 (1)
Total solids	27.6±2.1	25.7±2.2	29.9±1.4 (1)	28.3±1.0 (1)	29.2 (1)

Bucher (1983) suggests that parrot eggs contain the same amount of yolk, but more solids than do altricial species. She reports that the mean solid fraction of 19.4% for three species was higher than altricial and semi-altricial species, 15.7 and 18.3% respectively, reported by Carey, Rahn and Parisi (1980). However, that sample of altricial species was small in comparison to the database of Sotherland and Rahn (1987). The relative yolk content of five species of parrot, including the cockatiel, was not significantly different from that predicted for altricial species (fig. 5a) (ANOVA F= 0.010 N.S.) (Sotherland and Rahn 1987). The relative solid content of the eggs of four parrot species also was not significantly different from that predicted for all avian species on the basis of the relative yolk content of the egg (fig. 5b) (ANOVA F= 0.048 N.S.) (eq. 4, Sotherland and Rahn 1987). Therefore on the basis of this limited sample of parrot species, parrot egg composition is not different from that of altricial birds in general. However, amongst the altricial families presented by Sotherland and Rahn (1987) it is noted that both relative yolk content and solid content appear to be more variable between groups than within, which suggests that phylogeny may explain most of the variation.

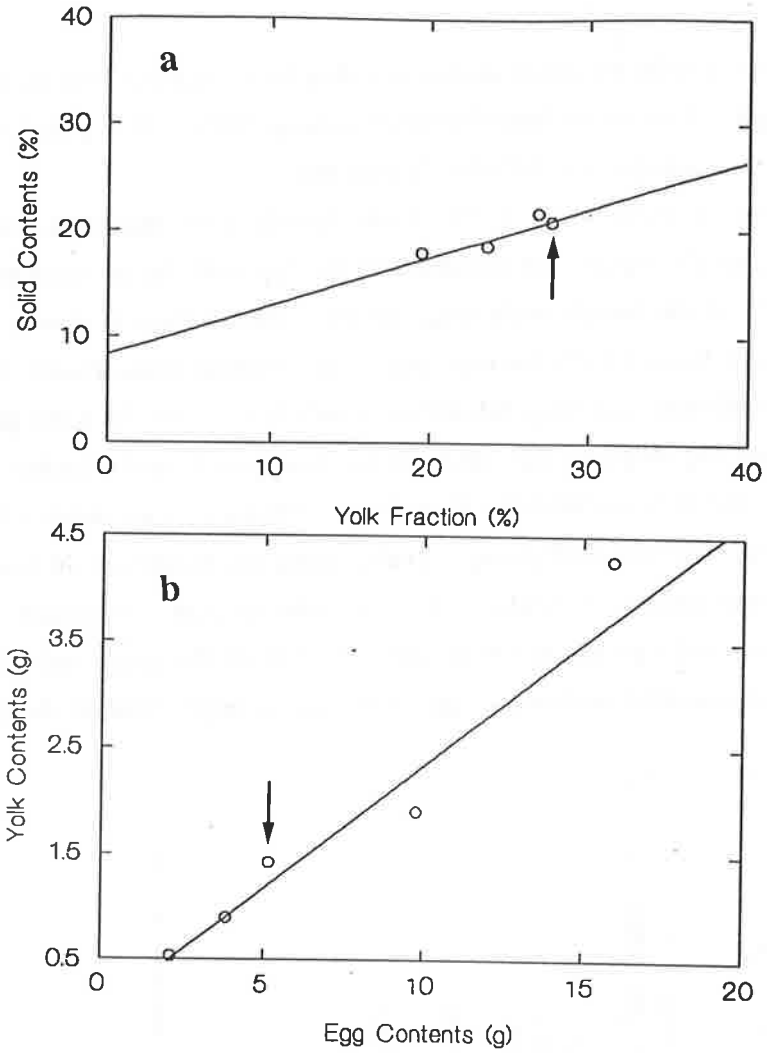

Fig. 5a. The relationship between fresh yolk content of parrot eggs (5 spp.) and egg mass (g). Solid line indicates the regression of Sotherland and Rahn (1987) between yolk content and egg mass for all altricial species (yolk= 0.239 $M_e^{0.99 \pm 0.015}$ (g)). **b.** The relationship between relative solid content of parrot eggs (4 spp.) and relative yolk content (%). Solid line indicates equation 4 of Sotherland and Rahn (1987) between solid content and relative yolk content of altricial species. Data presented are species listed in Bucher (1983) and the cockatiel (indicated by the arrow).

Parental investment in eggs and clutches

Female body mass was measured during the egg-laying period and the relative energetic investment in each clutch was estimated. Female quail body mass was on average 50.4 ± 4.4 g (n=14) and the mean clutch size was 5.9 ± 2.1 eggs (range 4-12) for 34 clutches. The largest clutches of king quail eggs were the result of dump-laying by a second or third female, although one female only usually incubated the clutch (exceptionally two females attempted to incubate the same clutch). Dump-laying was precluded when only one female was present in an aviary at the time of laying; other females were currently incubating eggs; and inspection of cloacal protuberances determined that other females had not recently laid eggs (i.e. no cloacal distention). After

removing clutches known to be the result of dump-laying from analyses, the mean clutch size was 5.3 ± 1.4 eggs. Female cockatiel were on average 93.9 ± 19.9 g and the mean clutch size was 3.2 ± 1.1 eggs (range 2-6) for 23 clutches.

Quail eggs were a mean 9.7 ± 1.6% of the female body mass (not including dump-layed clutches, n=153 eggs). In comparison the typically larger cockatiel eggs were only 6.5 ± 0.81 % of the female body mass (n=74). The coefficient of variation for relative egg mass was 16.8 and 13.0% for king quail and cockatiel respectively. Relative egg mass (egg % of BM) was inversely related to female body mass for king quail and cockatiel (fig. 6-7), but the slope of this relationship was significantly higher in king quail than cockatiel (ANCOVA $F=80.646$ $P<0.001$). Predicted egg masses for king quail and cockatiel were 6.07 and 6.18 g respectively, using the mean female body mass and the allometric relationships presented for each order in Rahn, Paganelli and Ar (1975). The mean observed egg masses were only 80.7 % of the predicted value for king quail, but 95 % for cockatiel with some eggs being a little larger than predicted.

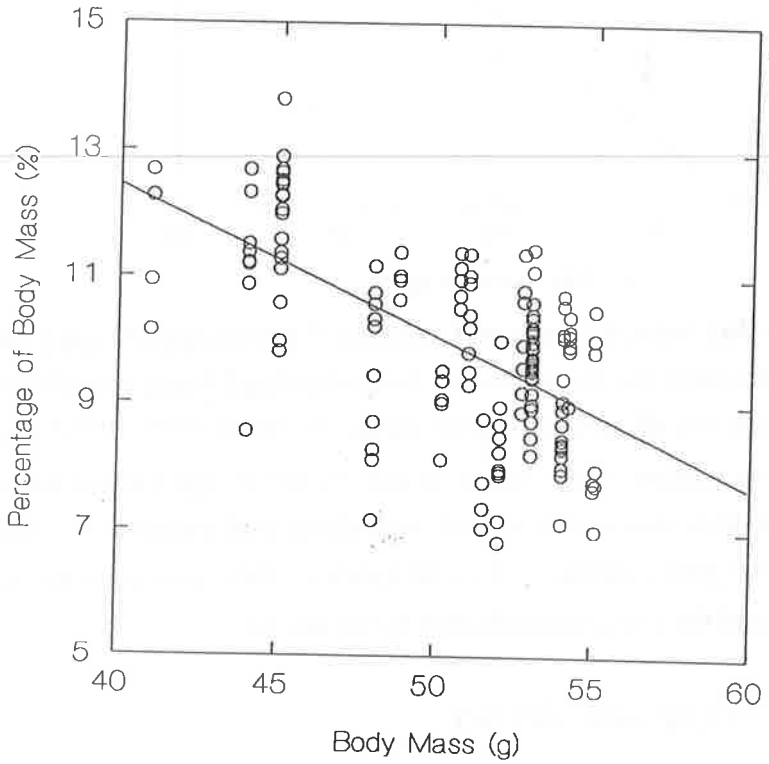

Fig. 6. The relationship between relative egg mass (% of female body mass) and female king quail mass for 34 clutches (n=162 eggs). Solid line indicates a significant relationship (egg%= 22.02 - 0.24 BM, s_b= 0.019 r^2= 0.500 $F_{1,160}$=159.996 $P<0.001$).

Total clutch mass was variable in king quail (mean 25.85 ± 7.47 g), and the relative clutch mass (% of female mass) was not significantly related to female mass (fig. 8). The mean relative clutch mass was 50.4 ± 15.6% of female king quail mass (not including dump-layed clutches). King quail invested significantly less than the predicted

clutch mass for a galliform bird (Phasianidae only) of the same mass, which is 49.3 g or 98% of female mass (Rahn, Paganelli and Ar 1975). The average cockatiel clutch mass was 19.11 ± 5.93 g, and was weakly correlated with female mass, but the relationship was significant (r^2= 0.194 P<0.04) (fig. 9). The mean relative clutch mass was 21.7 ± 7.0% of female mass. From Saunders, Smith and Campbell's (1984) data the following regressions were derived in this study for the relationships between egg mass and female parrot mass (M_b) (eq. 1), and between clutch mass and female mass (eq. 2) for 54 species of Australian parrots.

Egg Mass (g) = $0.228\ M_b^{0.747}$ (eq. 1)
(s_b= 0.019 r^2= 0.967 F= 1547.23 P<0.001)

Clutch Mass (g) = $598\ M_b^{-0.685}$ (eq. 2)
(s_b= 0.050 r^2= 0.785 F= 189.896 P<0.001)

The mean egg mass (5.76 g) found in this study was 85% of the predicted value (eq. 1) for parrots using the mean female mass (94 g). The relative clutch mass predicted using equation 2 (31%) was higher than the mean in this study.

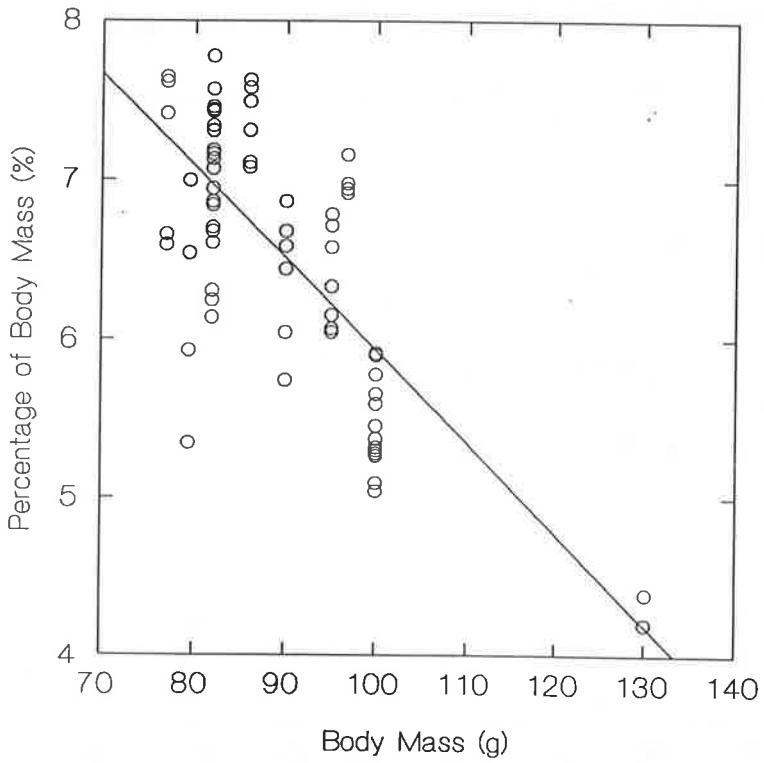

Fig. 7. The relationship between relative egg mass (% of female body mass) and female cockatiel mass for 23 clutches (n=74 eggs). Solid line indicates a significant relationship (egg% = 11.73 - 0.06 BM; s_b= 0.007 r^2= 0.517 $F_{1,72}$=77.169 P<0.001).

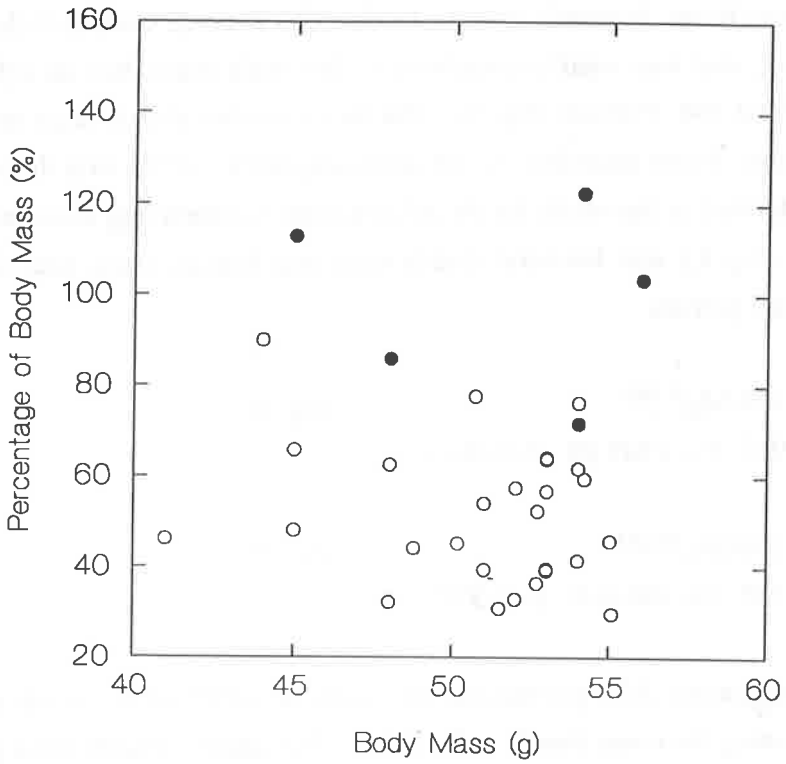

Fig. 8 Relationship between relative clutch mass and female body mass in king quail (34 clutches). Solid symbols indicate dump-laying by two or more quail.

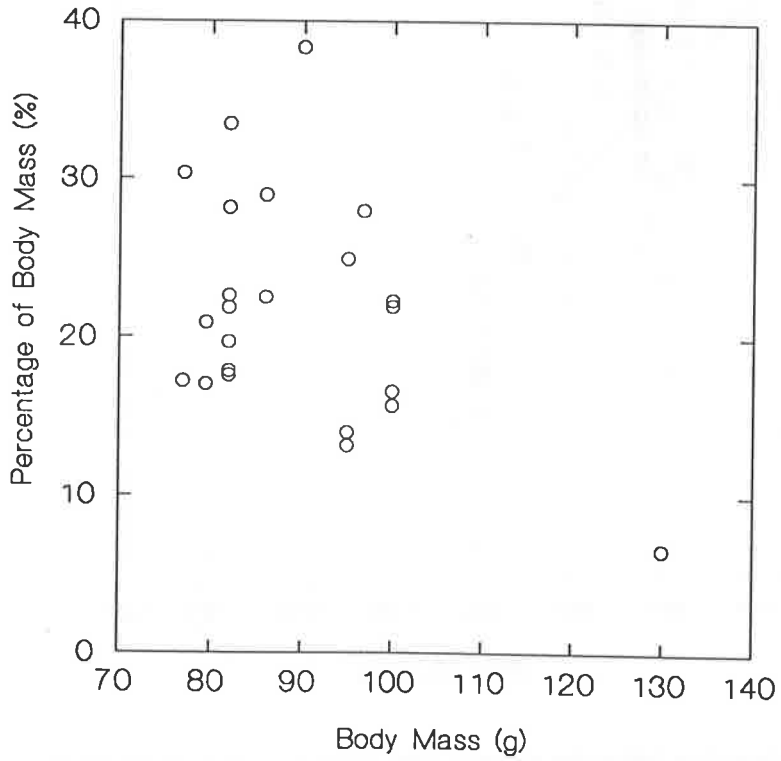

Fig. 9. Relationship between relative clutch mass and female body mass in cockatiel (23 clutches).

Energy invested in eggs

The energy contents of king quail and cockatiel eggs were estimated using the mean energy densities of egg contents, 8.38 and 5.39 kJ g^{-1} respectively. Egg contents were calculated on the basis of initial egg mass, minus the shell content predicted by the allometric (from Table 2) equations on the basis of egg mass. The mean estimated egg energy content was 37.08 ± 4.76 kJ (n=162) and 27.89 ± 2.75 kJ (n=74) for all king quail (mean 4.93 g) and cockatiel eggs (mean 5.90 g), respectively, laid in this study (fig. 1).

Energy in hatchlings and yolk reserves

Hatchling mass was measured in 45 king quail for which the initial egg mass was known, and therefore the initial energy content was predicted. Twelve cockatiel hatchlings were weighed prior to receiving their first feed after hatching. Mean quail hatchling mass was 3.843 ± 0.441 g (n=32) from eggs between 4.27 and 6.94 g (fig. 10). Quail hatchling mass was significantly related to egg mass (r^2= 0.646 P<0.001). However, quail which were slow to hatch or were considered runts (poor coordination and mobility) were smaller than normal hatchlings at 2.976 ± 0.429 g (n=9). The relative quail hatchling mass (% of egg mass) was 72.64 ± 4.09% for normal hatchlings, but the runts were on average a significantly smaller fraction at 60.75 ± 2.18% of the egg (ANOVA F= 69.754 P<0.001) (fig. 11). Relative hatchling mass of normal hatchlings was independent of egg mass (r^2= 0.002 F= 0.06 N.S.). Runt quail hatchlings were not always from the smallest eggs.

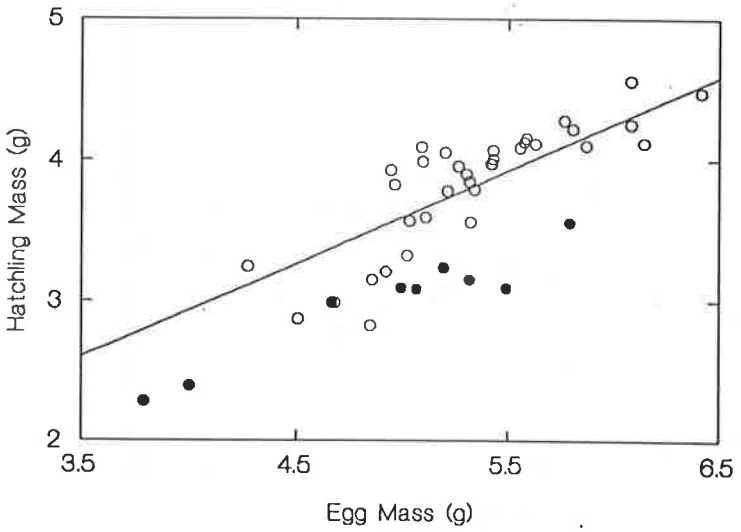

Fig. 10. The relationship between quail hatchling mass and egg mass. *Open circles*: normal hatchlings (n=32); *filled circles*: runt hatchlings (n=9). Solid line indicates a significant relationship between normal hatchling mass and egg mass (chick (g) = 0.290 + 0.661 egg; s_b= 0.084 r^2= 0.646 $F_{1,30}$= 62.160 P<0.001).

Mean cockatiel hatchling mass was 3.818 ± 0.547 g (n=12) from eggs between 4.72 and 6.40 g (fig. 12). Hatchling mass was positively correlated with egg mass (r^2= 0.660 P<0.001), but relative hatchling mass was independent of egg mass (fig. 13). Mean relative hatchling mass was 66.02 ± 5.82% of egg mass.

Yolk-free hatchling mass and yolk reserves were determined for king quail and cockatiel. Included in these samples were externally-pipped embryos and hatchlings which had died during or after hatching, presumably due to chilling. However, three cockatiel hatchlings were killed within 0.25 day of hatching. Yolk-free quail hatchling mass was on average 2.828 ± 0.112 g (n=9), and the mean yolk reserve was 0.419 ± 0.178 g from eggs between 4.26 and 5.30 g. Mean yolk-free cockatiel hatchling mass was 3.351 ± 0.512 g (n=5) and the mean yolk reserve was 0.419 g (n=4, range 0.290-0.586 g) from eggs between 5.44 and 6.52 g. The relative yolk-free hatchling mass (% of egg mass) of king quail decreased significantly from 70% to 50% of the initial egg mass as egg mass increased from 4.26 to 5.30 g (fig. 14). The relative yolk reserve mass (% of egg mass) was not significantly related to egg mass (r^2= 0.386 $F_{1,7}$= 4.402 N.S.), but the remainder of the egg, which included eggshell, extraembryonic membranes and total water lost from the egg during incubation increased significantly with egg mass (fig. 14). This suggests that as quail egg mass decreases more of the egg energy content is converted to yolk-free hatchling, and that quail have similar proportions of yolk reserve at hatching. The mean relative yolk-free hatchling mass was 58.6 ± 6.4 % of the egg mass for king quail and 62.0% for cockatiel. A similar fraction of egg mass was converted into yolk-free hatchling in 19 species (57.0 ± 6.2%) (D.Vleck, Vleck and Hoyt 1980). The mean yolk reserves were 8.5 ± 3.3% of the egg mass for king quail and 7.1% for cockatiel.

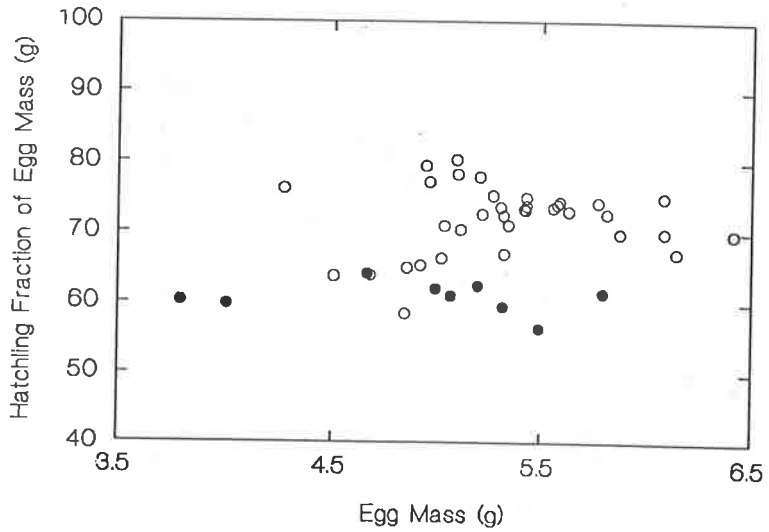

Fig. 11. The relationship between relative quail hatchling mass (% of egg mass) and egg mass. *Open circles*: normal hatchlings (n=32); *filled circles*: runt hatchlings (n=9).

Dry mass of yolk-free quail hatchlings was 0.668 ± 0.059 g (n=9) and 0.577 ± 0.081 g (n=5) respectively, and the dry mass of the yolk reserves was 0.215 ± 0.098 g and 0.137 ± 0.067 g respectively for king quail and cockatiel. The water content of yolk-free quail hatchlings was stable from IP to hatching with a mean of 76.2 ± 1.5% (n=9) (see fig. 14, Section 3.3). Yolk-free cockatiel hatchlings were 82.7 ± 0.9% (n=5) water. The water content of yolk reserves was 53.5 ± 6.7% and 58.7 ± 10.4%, respectively, for king quail and cockatiel. The yolk-free cockatiel hatchling was a little lower than the water content to of another parrot, *Agapornis roseicollis* (85.2%) (Bucher 1983) and altricial species in general (Ricklefs 1977). The whole-hatchlings of king quail and cockatiel were 71.8 ± 2.4% and 80.2 ± 0.7%, respectively, which was similar to the initial water content of their egg contents (72.6 and 79.1%, Table 2 p.48) which is typical of avian embryonic development (Ar and Rahn 1980; Vleck, Vleck and Seymour 1984). The water content of whole-king quail hatchlings was similar to the mean water content of 72.4% reported for precocial species (Ar and Rahn 1980). However, whole-cockatiel hatchling water content is significantly lower than the 95% confidence interval of the mean for altricial species (83.8 ± 2.7%, Ar and Rahn 1980), and is closer to the mean of semi-precocial species (78.1%).

The energy content of yolk-free hatchlings was 16.74 ± 1.60 kJ (n=7) and 14.55 ± 3.00 kJ (n=4) respectively for king quail and cockatiel. The energy density of quail hatchlings, including hatchlings from eggs of unknown size (and therefore unknown energy content), was 23.61 ± 3.79 kJ g^{-1} dry mass (n=15, range 19.08-27.50 kJ g^{-1}). The energy density of quail hatchlings was lower than other precocial species (26.93 ± 1.02 kJ g^{-1}), but there was a some overlap, but was more similar to that of semi-precocial and altricial species (24 kJ g^{-1}) (Ar et al. 1987). The energy density of the four cockatiel hatchlings was 25.22 kJ g^{-1}.

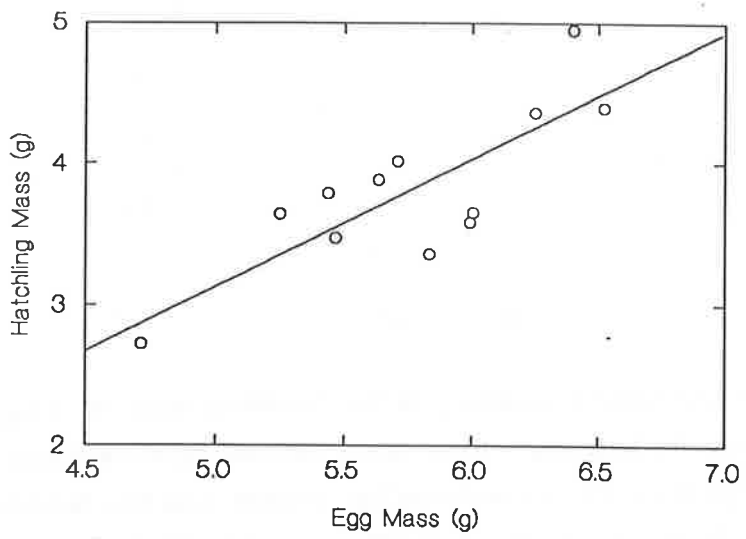

Fig. 12. The relationship between cockatiel hatchling mass and egg mass (n=12). Solid line indicates a significant relationship between hatchling mass and egg mass (chick (g) = -1.388 + 0.903 egg; s_b= 0.205 r^2= 0.660 $F_{1,10}$= 19.402 P<0.001).

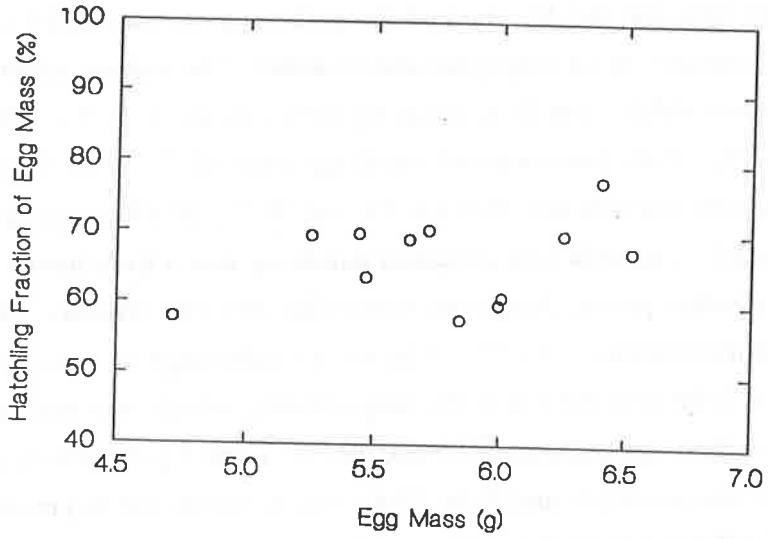

Fig. 13. The relationship between relative cockatiel hatchling mass (% of egg mass) and egg mass (n=12).

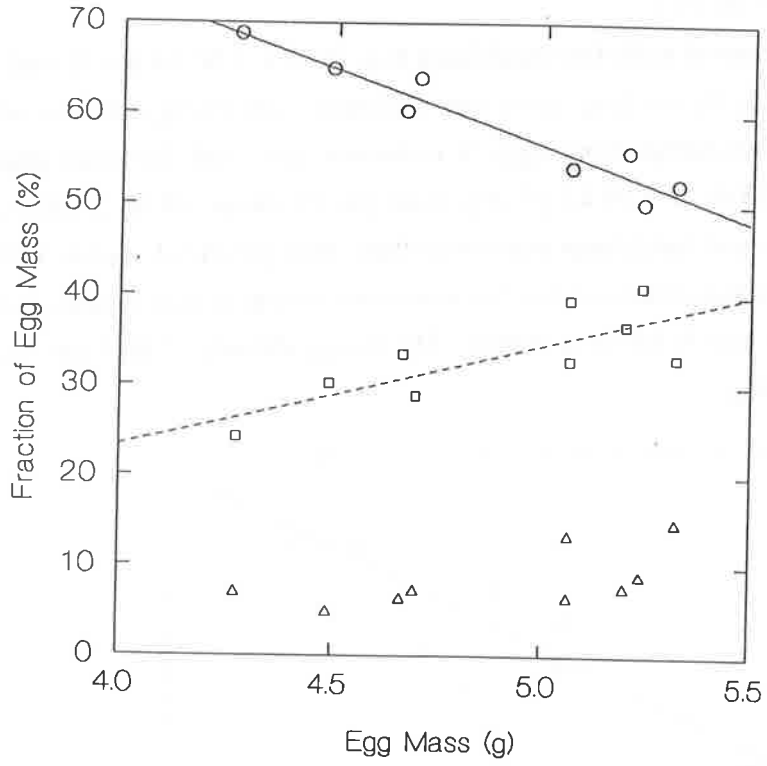

Fig. 14. The relationship between relative yolk-free hatchling mass (% of egg mass), yolk reserve and egg mass for king quail (n=9). Lines indicate significant relationships between fractions and egg mass. *Circles and solid line*: relative yolk-free hatchling mass ($M_{yfh}\% = 140.18 - 16.75\ M_e$; $s_b = 1.860$ $r^2 = 0.921$ $F_{1,7} = 81.143$ $P<0.001$); *squares and dashed line*: egg remainder (water lost, eggshell and extraembryonic membranes) ($M_r\% = -21.27 + 11.16\ M_e$; $s_b = 3.281$ $r^2 = 0.623$ $F_{1,7} = 11.573$ $P<0.02$); *triangles*: relative yolk reserve mass.

Cost of development

The energy content of eggs from which hatchling energy contents were measured were estimated to be on average 35.75 ± 2.95 kJ (n=7) and 28.90 ± 2.53 kJ (n=4), respectively, for king quail and cockatiel. In both instances the eggs were of similar estimated energy content to the mean of all eggs in this study. The sample of yolk-free king quail hatchlings and yolk reserves were on average 49.5 ± 4.7% and 16.6 ± 7.5%, respectively, of the total energy invested in eggs. The sample of yolk-free cockatiel hatchling and yolk reserve were on average 50.0 ± 6.4 % and 16.3%, respectively, of the total energy invested in the eggs. The partitioning of energy in the precocial king quail and altricial cockatiel hatchling was identical to that of semi-precocial and precocial species listed in Sotherland and Rahn (fig. 10 and Table 6, 1987).

The energy invested in the king quail egg, and the energy converted to hatchling tissues and spare yolk was similar to the predictions of Ar et al. (1987). However, on the basis of mean egg mass, Ar et al. (1987) predict a lower energy content of 26.3 kJ for an altricial egg of the same mass. The whole cockatiel hatchling was on average 20 kJ, which is similar to that predicted by Ar et al. (1987), but the yolk-free cockatiel hatchling energy contained less than the predicted 17.2 kJ, and the yolk reserve twice the predicted 2.6 kJ. Therefore, cockatiel converted a similar amount of egg energy to hatchling, but because the eggs are invested with 10% more energy than other altricial eggs, the cost of development was 10% higher than expected. This difference was attributed to the longer incubation period and lower growth rates of parrot embryos.

Discussion

Egg composition and energy content

The species chosen for this study extend comparisons between altricial and precocial species to new limits to test allometric predictions for avian embryonic development. King quail have previously been recognised as close to the physiological limits for minimum hatchling mass of a precocial species (Bernstein 1973; Whittow and Tazawa 1991). Similarly, the inclusion of cockatiel in this comparative study broadens our knowledge of development in non-passerine altricial species.

The average energy density per gram dry mass is low and highly variable in quail and cockatiel eggs, but is not significantly different from that of all hatchling types (Table 4, p.52). Energy density per gram fresh mass in king quail eggs is 8.38 kJ g^{-1} , which is similar to that of other precocial species (Ar et al. 1987). Cockatiel eggs contain 5.39 kJ g^{-1} of egg contents, which is similar to that of another parrot, *Agapornis roseicollis*, and both of which are more similar to semi-altricial species than the lower mean of altricial

species (Ar et al. 1987). It is concluded that both king quail and cockatiel have egg compositions similar to expectations for precocial and altricial species respectively. The variability in cockatiel egg composition is probably due to the small sample size, but may also be influenced by parental age and laying experience.

Intraspecific comparisons of egg composition reveals distinctly different patterns of energy allocation between king quail and cockatiel. Yolk and albumen content of king quail eggs are significantly related to egg mass (fig. 2, Table 3, p.50). Yolk solids in the egg contents increase with quail egg mass according to the allometric exponent (b= 0.68), and albumen solids increase with egg mass at a higher rate (b= 1.25), but there is significant overlap in the confidence intervals of these relationships (Table 3). The allometric exponents of both fresh and dry content of albumen suggest that increases in quail egg mass are mostly increases in water content in the albumen. However, the total water content of quail eggs is independent of egg mass (b= 0.073) (Table 3). The 95% confidence intervals for the allometric exponent for the relationship between yolk solids and egg mass in king quail is not significantly different from b=1, and thus appears to be similar to the relationship reported for domestic Japanese quail, *C. c. japonica* (Martin and Arnold 1991). However, they found that water content scaled isometrically with egg mass, in contrast to king quail which showed no relationship between water content and egg mass. Other studies of precocial species are equivocal about the scaling of yolk content with egg mass, with the American coot, *Fulica americana*, investing proportionately less yolk in lighter eggs (Alisauskas 1986) and *Fulicaatra* reported to be isometric in composition (Horsfall 1984). Mute swan, *Cygnus olor* eggs also contain proportionately less yolk and lipids in smaller eggs (Birkhead 1984).

Cockatiel eggs on the other hand, have a similar proportion of yolk invested in each egg and increases in egg mass are attributed to significant increases in albumen (fig. 2b). However, the scaling of cockatiel egg composition may be also be the result of a small sample size and the small range of egg masses. The scaling of egg composition in several other altricial species has been investigated, but there are no other studies of parrot egg composition which examine the scaling of egg contents. The eggs of the gannet, *Morus bassanus*, increase in albumen, water and non-lipid solids in direct proportion to egg mass, but yolk and lipid contents were independent of egg mass (Ricklefs and Montevecchi 1979). In addition the water content of the albumen increased significantly with egg mass. The yolk content of starling, *Sturnus vulgaris*, eggs were also found to be relatively independent of egg mass, and also highly variable, but albumen content increased significantly with egg mass (Ricklefs 1984). Albumen in cockatiel eggs, increased isometrically with egg mass, but dry albumen was independent of egg mass (fig. 3b), which suggests that it was mostly increases in the water content of albumen that explained the correlation between fresh albumen and egg mass.

Parental investment in eggs and clutches

King quail eggs are on average a small proportion of female body mass (mean 10%), but the typically larger cockatiel eggs are an even smaller fraction of the female body mass (mean 6.5%) (fig. 6-7). In both species relative egg mass (% of female mass) is negatively correlated with female body mass, but female king quail invest significantly more in egg mass at smaller body masses than female cockatiel (ANCOVA $F= 80.646$ $P<0.001$). Quail eggs are in general more variable in egg mass and the relative fraction of female body mass than cockatiel eggs. Only one species in the family Phasianidae (Galliformes) reported by Lack (1968), *Cryptoplectron manipurensis*, lays larger eggs which are 13.7 % of female body mass, and all other species lay eggs which are proportionately smaller than the king quail.

Within Galliformes, it was observed that the trend was for birds to invest more in smaller clutches of larger eggs or larger clutches of smaller eggs (Lack 1968; Rahn, Paganelli and Ar 1975). However, king quail lay smaller eggs than is predicted (6.07 g), using the mean female body mass and the allometric relationships presented for the order in Rahn, Paganelli and Ar (1975). The total clutch investment of king quail, or clutch mass as a % of adult female mass is a mean of 50% (fig. 8), which is also significantly lower than the predicted clutch mass of 49.3 g or 98 % of female body mass for a typical galliform bird of the same mass. Using the predicted egg mass for the same bird, a clutch of 8 eggs is predicted, but the mean in this study is 5.3 ± 1.1 eggs. These allometric predictions for the smaller members of Phasianidae are in poor agreement with real clutch investments. Clutches of up to 12 eggs in this study, as a result of dump-laying, represent a clutch mass greater than female body mass in every case (up to 120%), and is most likely the limit that a female quail can successfully incubate.

The mean Cockatiel egg mass is 5.8 g, which is not significantly different from that predicted (95%) on the basis of female mass for parrots in general (Rahn, Paganelli and Ar 1975). It is only 85% of the value predicted by equation 1 in this study derived from Saunders, Smith and Campbell (1984) for 54 species of Australian parrots. The mean cockatiel clutch mass is 19 g, or 3.2 ± 1.1 eggs, which represents 21% of female body mass (fig. 9). This also less than the 31% predicted by equation 2 for Australian parrots. However, in this study larger cockatiel eggs are generally laid by more experienced breeders. Although it is likely that most of the cockatiel in this study were inexperienced breeders, their age and experience was not known.

Hatchling mass and energy content

The mass of king quail and cockatiel hatchlings is significantly related to egg mass (fig. 10 and 12). Despite the difference in average egg mass between the two species, the hatchlings are a similar mass. On average king quail hatchlings are 3.843 ±

0.441 g (n=32) from eggs between 4.27 and 6.94 g (fig. 10), and cockatiel hatchling are 3.818 ± 0.547 g (n=12) from eggs between 4.72 and 6.40 g (fig. 12). The similarity in hatchling masses is attributed to the lower relative hatchling mass in proportion to egg mass of cockatiel. King quail are on average 73% of the initial egg mass, and cockatiel 66% (fig. 11 and 13).

Quail that are slow hatching (a day late) and runts, which lack muscular coordination, are significantly smaller than other hatchlings (ANOVA $F= 69.754$ $P<0.001$) (fig. 11). Naturally incubated eggs might develop abnormally as result of variable incubation temperatures within a clutch (1-6 °C) (Drent et al. 1970), or low nest attentiveness. But these factors do not influence the embryonic development of artificially incubated eggs, so other factors must have an important influence. In this study these hatchlings usually failed to develop and died.

Yolk-free hatchling mass is 2.8 g and internal yolk reserve is 0.4 g in the king quail or 58.6% and 8.5% of the initial egg mass, and 3.4 g and 0.4 g respectively for yolk-free cockatiel hatchlings and yolk reserves, or 62% and 7.1% of the initial egg mass. King quail and cockatiel hatchlings are a similar fraction of egg mass to other altricial and precocial species (D. Vleck, Vleck and Hoyt 1980). Although the yolk-free hatchling mass of cockatiel determined here is a similar fraction of egg mass, it should be noted that the few individuals measured were from eggs that are larger than the mean of all eggs laid and therefore the hatchling mass is a little higher than the king quail. The relative yolk reserve mass (% of egg mass) of king quail is independent of egg mass, and the mass varies between 0.217 and 0.781 g, but the yolk-free hatchling fraction is inversely related to egg mass (fig. 14). This conclusion is based on a limited number of individuals, but is supported by the larger fraction of yolk in quail egg contents (up to 46% at 4.0 g, fig. 4a) in small quail eggs. Thus more of the energy invested in small quail eggs is converted to hatchling tissues. The calculated fraction of egg mass that remains after subtracting yolk-free hatchling mass and yolk reserve includes eggshell, extraembryonic membranes, excreted waste and total water loss. The remaining fraction of quail eggs increases directly with egg mass (fig. 14). It is concluded that the increase is largely attributable to increased water loss, because the eggshell is a relatively invariable fraction of egg mass.

The water content of whole hatchling king quail (72%) is similar to that of the initial water content of the eggs, and is similar to the mean of other precocial species (Ar and Rahn 1980). The whole cockatiel hatchling water content (80%) is significantly lower than the 95% confidence interval of the mean of other altricial hatchlings (Ar and Rahn 1980). The higher water contents of hatchling tissues of altricial species relative to precocial species (altricial hatchlings 83.8 ± 2.2 % water in comparison to precocial hatchlings 72.2 ± 2.6 %) has previously been demonstrated to be an important index to the relative maturity of embryonic and hatchling tissues (Ricklefs 1977, 1987). It was proposed that cell proliferation is incompatible with cell maturation, and thus the maturity

of developing tissues is reflected in the water content of those tissues (Ricklefs 1977). Konarzewski (1988) similarly supports Ricklefs' hypothesis that physiological constraints limit growth rate, and that it is in fact, easier to examine the influence of changes in body composition than complex ecological factors. Ricklefs (1987) hypothesised that the acquisition of mature function in embryos is correlated with the accumulation of solids in embryonic tissues. His findings suggest that there is evidence for a direct relationship between the rate of increase in solids and the rate of decrease in growth rate of the embryo with respect to increasing embryo mass.

The yolk-free king quail hatchling is 76% water, in contrast to the extremes of megapode hatchlings (calculated as 67 and 62% water for mallee fowl and brush turkey, respectively; Vleck, Vleck and Seymour 1984). The higher water contents of yolk-free king quail hatchlings, in comparison to most larger precocial species, may parallel the rapid growth rates of comparatively small embryos, and thus the high water contents of the hatchling tissues may reflect the immature state of hatchling tissues. The poor thermoregulatory capacities of king quail hatchlings is an indication of physiological immaturity (see Chapter 4). Support for this hypothesis can be found in studies of semi-precocial American coots, *Fulica americana*, which have hatchlings with water indices intermediate between precocial and altricial species (Alisauskas 1986). The allocation of energy was found to decrease, along with yolk content and egg mass, in successive eggs within clutches of coots, and as a result the larger eggs hatched larger chicks with relatively more mature tissues as reflected in their tissue water indices. These first hatched chicks with the lower water indices also displayed greater mobility, which may reflect differences in the degree of precocity of *F. americana* hatchlings (Alisauskas 1986).

Cost of development

King quail invested significantly more energy in their eggs than the larger eggs of cockatiel (mean of all eggs is 36 and 29 kJ, respectively). However, the energy content of yolk-free hatchlings and yolk reserves were little different (yolk-free hatchlings 17 and 15 kJ, yolk reserves 6 and 5 kJ, respectively, for king quail and cockatiel). Despite the difference in egg energy content, the estimated energy converted to hatchling tissues, calculated for individual hatchlings, is on average 50% of the energy in the egg for both species, with 16-17% remaining in the yolk reserve. Therefore the cost of development can be estimated from the difference between energy in the whole hatchling and the initial energy content. Cost of development is 12 kJ for king quail hatchlings and 9 kJ for cockatiel hatchlings. The energy invested in king quail eggs and the amount converted to hatchlings is identical to the allometric predictions of Ar et al. (1987) for precocial species. The whole cockatiel hatchling contains the predicted amount of energy on the basis of egg mass for an altricial species, but there is less energy in the yolk-free

hatchling and twice the amount of energy available in the yolk reserve (Ar et al. 1987). However, the cost of development in the cockatiel is 10% higher than other altricial species, because the cockatiel egg contains 10% more energy than predicted. The higher cost of development may be attributed in part to higher maintenance costs of embryonic metabolism, since the incubation period is significantly longer than expected (see Section 3.2). Nevertheless, it is clear that small precocial embryos have higher cost of development for embryonic development than altricial species as previously suggested by Vleck and Vleck (1987).

The energy density of king quail hatchlings per gram dry mass (24 kJ g^{-1}) is lower than most precocial species (27 kJ g^{-1}), and is more like that of less precocial hatchling types (Ar et al. 1987). Ricklefs (1987) suggests that the accumulation of solids in embryos at the end of incubation parallels the increasing tissue differentiation and maturation. The king quail has a high growth rate throughout the incubation period, which slows down at the end of the incubation period, but does not plateau like larger species (see Section 3.3). Therefore it is likely that the lower energy density of king quail hatchlings (per gram dry mass) is correlated with the relative immaturity, as evidenced by poor thermoregulatory functions (see Section 3.2). Such a correlation is suggested to occur in altricial hatchlings, but not precocial hatchlings (Ricklefs 1987), but unlike larger precocial species, the king quail has one of the shortest incubation periods and is believed to hatch earlier than predicted. The variability in energy density of quail hatchlings is thought to reflect the variability in energy allocation to the eggs.

Section 3.2. Gas Exchange and Metabolism of Embryos

Introduction

The metabolism of all avian embryos increases exponentially over the first 60% of the incubation period (Rahn, Paganelli and Ar 1974; Hoyt, Vleck and Vleck 1978; Vleck, Hoyt and Vleck 1979; Hoyt and Rahn 1980). Metabolism continues to increase exponentially throughout the incubation period of altricial embryos, but it decreases and then plateaus during the last 20% of the incubation period of precocial embryos. It is believed that the metabolism of precocial embryos plateaus during the late stages of incubation because growth is largely completed and growth rate is decreasing, and therefore the plateau in metabolism reflects the maintenance costs of the embryonic tissues (Vleck, Hoyt and Vleck 1979; Hoyt 1987). However, there is increasing evidence that the metabolism of some precocial embryos is limited by the low gas conductance of egg shell (Tazawa et al. 1988b; Kuroda et al. 1990; Whittow and Tazawa 1991; Mathiu, Whittow and Dawson 1992). In several domesticated species, the oxygen conductance of the eggshell barrier appears to limit embryonic oxygen uptake (Tazawa, Mikami and Yoshimoto 1971; Metcalfe et al. 1981; Tullett and Deeming 1982; Burton and Tullett 1983). After precocial embryos pip the eggshell the oxygen conductance limitation is removed and oxygen consumption increases during hatching (Tazawa et al. 1988b; Booth 1987; Whittow and Tazawa 1991). Further studies are required to investigate the relationship between the gas conductance of eggshells, embryonic growth and the ontogeny of oxygen consumption in precocial embryos to resolve this conflict.

All eggs lose about 15% of their initial egg mass by diffusion of water vapour across the eggshell, which is driven by the water vapour pressure difference between the egg and nest air (Drent 1970; Ar and Rahn 1980; Rahn and Paganelli 1990). Both the rate of diffusive water loss ($\dot{M}_{H2O}$) and oxygen consumption rate at PIP are significantly related to egg mass and incubation period (Ar et al. 1974; Rahn, Paganelli and Ar 1974; Ar and Rahn 1978; Hoyt and Rahn 1980; Rahn and Paganelli 1990). Most avian embryos, excluding passerines, appear to have a mass-specific oxygen consumption rate at PIP stage similar to that of the incubating parent bird, despite the embryo being up to 20 times smaller than the adult (Vleck, Hoyt and Vleck 1979; Hoyt and Rahn 1980; Paganelli and Rahn 1984). Vleck et al. (1979) suggest that shell conductance is primarily adapted to regulate water loss and has less influence on PIP $\dot{V}_{O_2}$. However, there is considerable variation in PIP $\dot{V}_{O_2}$ between avian embryos after taking into account egg mass. The allometric relationship for precocial shorebird (Charadriiformes) embryos is significantly higher in intercept than the relationship for avian embryos of all hatchling

types (Visser 1991). Bucher (1983) also reports that PIP $\dot{V}O_2$ is significantly lower in altricial parrot eggs, but it is unclear if these deviations in PIP $\dot{V}O_2$ from predicted values are related to hatchling maturity or phylogeny.

Based on the relationship between PIP $\dot{V}O_2$ and egg mass, Rahn et al. (1974) predicted that the average partial pressures of oxygen (PAO_2) and carbon dioxide ($PACO_2$) in the aircell at PIP would be 104 and 37 torr respectively, for all avian eggs. Lower partial pressures of oxygen and higher partial pressures of carbon dioxide in the aircell are thought to stimulate pipping events (Rahn, Paganelli and Ar 1974; Ackerman et al. 1980; Pettit et al. 1982 a,b; Tullett and Deeming 1982). Measured gas tensions for other avian species confirms the initial prediction that all species experience similar gas tensions at the end of incubation (Rahn and Paganelli 1990; Visser 1991; Ancel and Visschedijk 1993).

Earlier it was suggested that oxygen conductance may limit the oxygen consumption rate and growth of precocial embryos late in the incubation period, but not in altricial species. Most species are variable in their water vapour conductance between individuals (Carey 1986; Rahn, Krogh and Mehlum 1983; Vleck et al. 1983; Bucher and Barnhart 1984). Low conductance eggs of *Agapornis roseicollis* are significantly lower in PAO_2 and higher in $PACO_2$ late in the incubation period, reaching 53 torr and 87 torr respectively. Pipping of *A. roseicollis* embryos is not stimulated at any particular level of PAO_2 or $PACO_2$ (Bucher and Barnhart 1984). During the plateau phase of the incubation period the $\dot{V}O_2$ of precocial guineafowl, *Numida meleagris*, embryos is significantly lower in eggs with lower than average shell gas conductance (Ancel and Visschedijk 1993). The PAO_2 is also significantly lower and $PACO_2$ higher at the end of the incubation period (PIP) in low conductance guineafowl eggs. I suggest here that the $\dot{V}O_2$ of small precocial embryos may not plateau late in incubation because the incubation period is short and less time is available for the embryo to mature. Therefore the $\dot{V}O_2$ of small precocial embryos may not be limited by gas conductance of eggshells.

In preparation for life outside of the egg, precocial embryos might develop thermoregulatory mechanisms at the end of the incubation period (Whittow and Tazawa 1991). Thermogenesis in the egg requires that the embryo increases heat production when egg temperature decreases. The high thermal conductance of eggs and low gas conductance of the shell and shell membranes prevents PIP embryos from increasing oxygen consumption to balance heat loss during cold exposure (Tazawa et al. 1988b; Kuroda et al. 1990). Hatching is an energetically demanding stage of incubation, and the oxygen demand cannot be met by chorioallantoic gas exchange alone (Paganelli and Rahn 1984). However, gradual and prolonged cooling tests reveal that when pulmonary respiration dominates, precocial embryos are able to increase their oxygen consumption rates (Booth 1987; Tazawa et al. 1988b; Tazawa et al. 1989a; Kuroda et al. 1990; Nichelmann, Lange and Paulick 1994). The development of endothermy in large

precocial embryos appears to take place prior to pipping, but in semi-precocial species it takes place only after hatching (Matsunaga et al. 1989; Mathiu, Whittow and Dawson 1992).

As egg mass decreases the thermal conductance of eggs increases (Tazawa, Turner and Paganelli 1986), and therefore small precocial embryos may be less able to maintain core temperature during cooling. Even after the onset of pulmonary respiration, power limitations may not prevent egg cooling. If small precocial embryos can sustain $\dot{V}_{O_2}$ at thermoneutral levels or higher as egg temperature decreases, then it is predicted that the lowest egg temperature at which $\dot{V}_{O_2}$ is sustained will be closer to the incubation temperature in small embryos. In this study the relationship between G_{H_2O}, $\dot{V}_{O_2}$ and partial pressures of oxygen and carbon dioxide in the king quail and cockatiel are examined. Short-term gradual cooling tests, similar to the techniques of Tazawa et al. (1988b), are used to determine if small embryos acquire significant thermogenic powers before they hatch.

Materials and Methods

Water vapour conductance

Water vapour conductance (G_{H_2O}) of eggs was determined by the method of Ar et al. (1974). In brief, fresh eggs were collected and their fresh mass recorded. The eggs were then placed in a plastic desiccator box partially filled with anhydrous silica gel and the lid sealed. The desiccator was maintained at 25 ± 1 °C within a constant temperature cabinet. Once a day, the lid was removed and the mass of each egg was quickly measured and the desiccator sealed again. The first three days of mass losses were ignored because of initial instability. Subsequent daily mass losses were retained if the eggs demonstrated a stable rate of mass loss over at least three days. Mean daily water loss per egg was used to calculate G_{H_2O} for each egg using Fick's Law of Diffusion as follows:

$$\dot{M}_{H_2O} = \Delta P_{H_2O} \cdot G_{H_2O} \qquad \text{(eq. 1)}$$

where $\dot{M}_{H_2O}$ is the daily water loss from the egg (mg H_2O day^{-1}), ΔP_{H_2O} is the difference in partial pressure of water vapour across the shell (torr), and G_{H_2O} is the water vapour conductance (mg H_2O $day^{-1}torr^{-1}$).

Paganelli et al. (1971) have previously demonstrated that the diffusion of water vapour across the shell approximates the diffusion of ideal gases and that the mass loss of eggs is almost entirely due to the diffusion of water through the shell. G_{H_2O} was calculated by dividing the mean mass loss per 24 h by the water vapour pressure

difference (ΔP_{H2O}) across the shell. In the desiccator this difference was assumed to equal the saturation vapour pressure within the egg at 25 °C (24 torr). G_{H2O} was also determined for incubated quail and cockatiel eggs, which were removed from the nest whilst embryo $\dot{V}_{O_2}$ and nest humidities were determined in this study, in which case measurements of G_{H2O} were made whilst the eggs were artificially incubated. G_{H2O} of incubated eggs were corrected to standard temperature (25 °C) (Paganelli, Ackerman and Rahn 1978). The measured conductances of quail and cockatiel eggs at 25 °C were compared with allometric predictions of Ar et al. (equation 3; 1974).

Artificial incubation of eggs

Eggs were collected for artificial incubation in the laboratory. These growing embryos were subsequently used for oxygen consumption measurements and growth studies, including energetic composition of embryos. Bernstein (1973) reported incubation conditions of painted quail ('king' quail) as 40 °C and 90% RH. These conditions were adopted in this study initially, but all fertile eggs failed in early or mid incubation. The necessary incubation conditions were then re-evaluated.

Most avian eggs lose 15 % of their mass prior to external pipping due to diffusion of water vapour across the shell (Ar and Rahn 1980). Using the relation of egg mass to incubation period we can predict the $\dot{M}_{H2O}$ of a typical 5 g quail egg (44 mg H_2O day^{-1}), assuming an incubation period of 17 days according to the equation of Rahn (1974). The predicted water vapour conductance of the same egg was then estimated, using the same value for total water loss (15%), to be 2.08 mg H_2O $day^{-1}torr^{-1}$. Then ΔP_{H2O} is 21 torr and the partial pressure of water vapour outside the shell needed to be 30.0 torr. King quail eggs were then incubated at a relative humidity of 58-59 % and at 38.5 ± 0.5 °C (based on measurements of egg temperature in natural nests with calibrated thermocouple eggs). The same relations between water loss and egg mass were used to determine suitable artificial incubation regimes for cockatiel eggs. Subsequent artificial incubation of cockatiel eggs was performed at 37.2 ± 0.2 °C (measured by thermocouple eggs) and with a relative humidity of 76.9 % (wet bulb 33 °C) in the same forced draught incubator. All reported results refer to embryos raised under these conditions or from natural incubation.

Eggs were placed in a sterile tray lined with cotton-wool with the blunt end pointing uppermost and were incubated for 16.5 to 17 days in a forced draught incubator (Saunders Products Ltd. Australia). All eggs were rotated 180° by hand twice daily up until hatching. Hatchlings were removed from the incubator and returned to the nest.

Oxygen consumption rates during incubation

The oxygen consumption rates ($\dot{V}O_2$) of king quail and cockatiel embryos were measured using open-flow respirometry techniques outlined in Chapter 2. Flow rates of dry air entering the metabolism chambers (0.3 L) were 200-400 mL O_2 min^{-1} for embryos and hatchlings. Measurements were always made at the same time of the day (10:00-14:00 h). A single egg was placed in each chamber 20 min prior to the start of measurements at the respective incubation temperatures of king quail and cockatiel. Up to 3 eggs were measured in separate chambers sequentially. Each egg was measured at incubation temperature for two 5 min periods over a period of 30 min. $\dot{V}O_2$ was determined for king quail and cockatiel embryos from day 4 and 5, respectively, of the incubation period and was expressed in units of mL O_2 day^{-1}.

Gradual cooling tests

Gradual cooling tests were used to determine if late-incubation embryos were capable of thermogenesis or sustaining $\dot{V}O_2$ independent of T_a. The general method of Tazawa et al. (1988b) was employed during cooling tests, but tests were of shorter duration. After the $\dot{V}O_2$ of king quail and cockatiel eggs was measured at incubation temperature, T_a was lowered gradually to 30 °C, which represents a T_a 6-9 °C below incubation temperature. $\dot{V}O_2$ of each egg was measured for one 5 min period after 20-30 min of gradual cooling during short-term cooling tests. On several occasions $\dot{V}O_2$ was measured repeatedly (3-4 times) over 1 h during prolonged cooling tests, by which time T_{egg} had declined almost to 30 °C. Eggs were then returned to the incubator after cooling tests.

Partial pressures of respiratory gases within developing eggs

Both king quail and cockatiel eggs were weighed daily during the incubation period when eggs were artificially incubated. Whenever possible, eggs which were incubated throughout their incubation period were used to determine cumulative water loss during the perinatal (pre-internal pipping) and paranatal (IP to EP) periods, for comparison of water budgets with other species. The measured $\dot{M}_{H2O}$ and G_{H2O} of individual eggs were used to indirectly determine the partial pressures of respiratory gases in the air cells of eggs throughout the incubation period prior to hatching according to Bucher and Barnhart (1984). The G_{H2O} of eggs was converted to G_{O2} and G_{CO2} values by multiplying G_{H2O} by factors of 1.033 and 0.796 respectively (Paganelli et al. 1978). An RQ= 0.71 was assumed for embryonic development, to estimate $\dot{V}_{CO2}$ from measured $\dot{V}O_2$ for individual eggs.

Determination of nest humidities

By comparing the water loss of eggs in the nests and in the incubator, the water vapour gradient in the nest was determined, assuming that egg temperatures were the same as determined with thermocouple eggs. Typically the water loss of two eggs in the nest were recorded for a 24 or 48 h period, then removed and placed in the incubator, and the mass loss of the eggs was monitored over the next 24-48 h. The eggs which were removed from the nest were replaced by other fresh eggs, until the original eggs were returned to the nest.

Results

Incubation period

Using egg mass and female body mass it is possible to predict the incubation periods for each species, based on allometric relationships established in previous studies (Ar and Rahn 1978; Rahn, Paganelli and Ar 1975; Vleck and Vleck 1987; Saunders, Smith and Campbell (1984). In table 1, the mean egg mass and female body mass of king quail and cockatiel were used to compare observed incubation periods with predictions. The incubation periods, egg and female body masses of all 54 species of Australian parrots were presented in Saunders, Smith and Campbell (1984). Significant relationships were found between log-transformed incubation periods and egg mass, and between incubation period and female mass and are presented in table 1 (eq.5: s_b= 0.009 r^2= 0.825 F= 251.59 P<0.001; eq. 6: s_b= 0.013 r^2= 0.809 F= 225.42 P<0.001).

Table 1. Comparison of incubation periods for king quail and cockatiel with allometric expectations based on egg mass (M_e) and female body mass (M_b).

		INCUBATION PERIOD (days)					
	M_e (g)	Observed	Predicted				
	M_b (g)		(eq. 2)	(eq. 3)	(eq. 4)	(eq. 5)	(eq. 6)
King quail	4.9	16.5	16.5	17.5	19.1		
	50						
Cockatiel	5.9	19.0-21.0	17.2	19.4	16.6	20.5	19.9
	94						

eq. 2: $I = 11.64\ M_e^{0.221}$ (Ar and Rahn 1978); eq. 3: $I = 9.105\ M_b^{0.167}$ (Rahn, Paganelli and Ar 1975); eq. 4: precocial $I = 13.49\ M_e^{0.22}$ and altricial $I = 9.933\ M_e^{0.29}$ (Vleck and Vleck 1987); eq. 5: $I = 10.399\ M_b^{0.149}$ and eq. 6: $I = 14.125\ M_e^{0.194}$ from data in Saunders, Smith and Campbell (1984).

The incubation period for king quail was identical to the period predicted by Ar and Rahn (1978) on the basis of fresh egg mass for all hatchling maturity types (eq. 2), but was only 86 % of the period predicted by the equation of Vleck and Vleck (1987) for precocial species (eq. 4). The shorter than predicted incubation period was not dissimilar to the shorter values of other small precocial eggs of galliform and gruiform species in the same study, and was exactly one standard error of the estimate below the predicted value for precocial species. In relation to predictions based on female body mass (eq. 3), king quail incubation was also shorter than expected. Therefore king quail hatch earlier than most precocial species, but the incubation period is not as short as altricial species of the same egg mass.

The incubation period of cockatiel on the basis of fresh egg mass, was longer than predicted by the general equation (2) for all hatchling types (Ar and Rahn 1978) and the equation for altricial species (eq. 4) (Vleck and Vleck 1987), but similar to the expected incubation periods of parrots (eq. 5-6) (Saunders, Smith and Campbell 1984). The observed cockatiel incubation period was also similar to the predicted incubation period on the basis of cockatiel body mass (eq. 3). Bucher (1983) noted that many parrots have significantly longer incubation periods than other altricial species, which is supported by the cockatiel and other parrots (Saunder, Smith and Campbell 1984). Vleck and Vleck (1987) demonstrated that much of the variation in incubation periods between species and hatchling maturity types was explained by differences in the energy invested in eggs by females. In this study, using the mean energy content of eggs, predicted incubation periods for king quail and cockatiel were 18.3 days and 16.6 days, respectively. Using energy content to predict incubation period did not explain why the king quail hatches earlier and the cockatiel later than expected.

Water vapour conductance

A total of 31 quail eggs and 7 cockatiel eggs were used in this experiment to determine G_{H2O} under standard conditions (Ar et al. 1974). In addition G_{H2O} was determined for 26 quail eggs and 14 cockatiel eggs at incubation temperature, and corrected to G_{H2O} at standard conditions (25 °C) by multiplying by a factor $(T_{inc}/298)^{0.5}$ where the incubation temperature is expressed in Kelvin (Paganelli, Ackerman and Rahn 1978). Mean egg mass was 4.864 ± 0.608 g (±SD) and 5.565 ± 0.641 g for quail (n=57) and cockatiel (n=21) respectively, which was similar to the grand mean of all quail eggs, but a little lower than the mean cockatiel egg mass. Water vapour conductance for both groups of eggs were compared with the predicted G_{H2O} (fig. 1-2) (Ar et al. 1974). The mean observed G_{H2O} was 2.10 ± 0.81 mg H_2O $day^{-1}torr^{-1}$ and 2.20 ± 1.02 mg H_2O day^{-1} $torr^{-1}$. The mean predicted G_{H2O} was significantly lower than the observed values for both species (ANOVA quail $F_{1,97}$= 13.203 $P<0.001$; cockatiel $F_{1,40}$= 15.802 $P<0.001$). Ar and Rahn (1978) demonstrated that further

variation in G_{H2O} was explained by egg mass and incubation period combined. The G_{H2O} predicted using the mean egg mass and incubation periods of 16.5 and 19 days for quail and cockatiel were also lower than the observed values (predicted 1.52 and 1.51 mg H_2O $day^{-1}torr^{-1}$ respectively). The G_{H2O} of unincubated quail and cockatiel eggs were variable over the range of egg masses found in this study (fig.1-2). However, the G_{H2O} of incubated quail eggs increased significantly with egg mass above the interspecific allometric expectations of Ar et al. (1974) (fig. 1; intraspecific b= 2.486 ± 0.822 (95% CI) » interspecific b= 0.78 ± 0.05). Larger quail eggs lost proportionately more water during incubation than expected. Martin and Arnold (1991) found that the intraspecific relationship between $\dot{M}_{H2O}$ and egg mass was different from the interspecific relationship for Japanese quail, *Coturnix c. japonica*, eggs during incubation. This trend was also observed in the cockatiel egg, but the confidence interval for the slope of that relationship is not significantly different from the interspecific exponent (fig. 2).

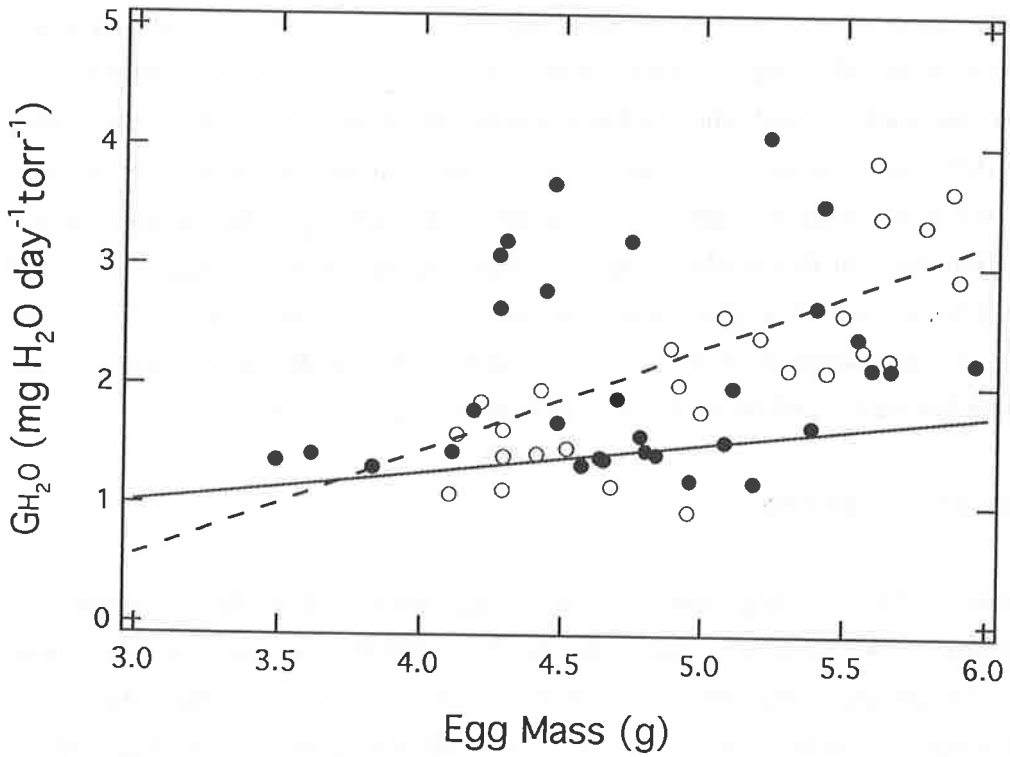

Fig.1. The relationship between G_{H2O} and egg mass for quail eggs. *Solid symbols* indicate G_{H2O} measured under Standard conditions of Ar et al. (1974), and *open symbols* indicate G_{H2O} of incubated eggs corrected to 25 °C. Solid line is the predicted interspecific relationship of Ar et al. (1974). *Dashed line* is a significant intraspecific relationship for quail eggs (log G_{H2O}= -1.430 + 2.486 log M_e; s_b= 0.410 r^2= 0.605 $F_{1,55}$= 36.773 P<0.001).

Before IP, G_{H2O} was a mean of 2.20 mg H_20 $day^{-1}torr^{-1}$ for incubated cockatiel eggs, but during the paranatal period, G_{H2O} increased dramatically before the shells were visibly pipped. Mean $\dot{M}_{H2O}$ of cockatiel eggs prior to IP was 25.55 ± 5.18 mg H_2O day^{-1} (range 17.60-39.50 mg H_2O day^{-1}), and then increased significantly between IP and hatching (ANOVA $F_{1,86}$=120.123 P<0.001) (fig. 3). Although fewer eggs were measured during the paranatal period the G_{H2O} increased by a factor of 2.78 on average (range 1.11-5.81, n=4). The total mass loss of artificially incubated eggs due to diffusion of water vapour was a between 6.2 and 9.0% prior to IP (n=4), and 20.5 to 27.0% (mean 23.1%, n=5) during the entire incubation period (including hatching losses). Typically avian eggs lose 15% of their initial mass as water vapour prior to IP (Rahn and Ar 1974; Drent 1975; Paganelli, Ackerman and Rahn 1978; Ar and Rahn 1980), and a further 3% of their mass on average between EP and hatching (Rahn 1984). Cockatiel eggs incubated in an artificial incubator lost less than 15% of their mass during the perinatal period, and lost most of their water vapour after the eggs star-fractured.

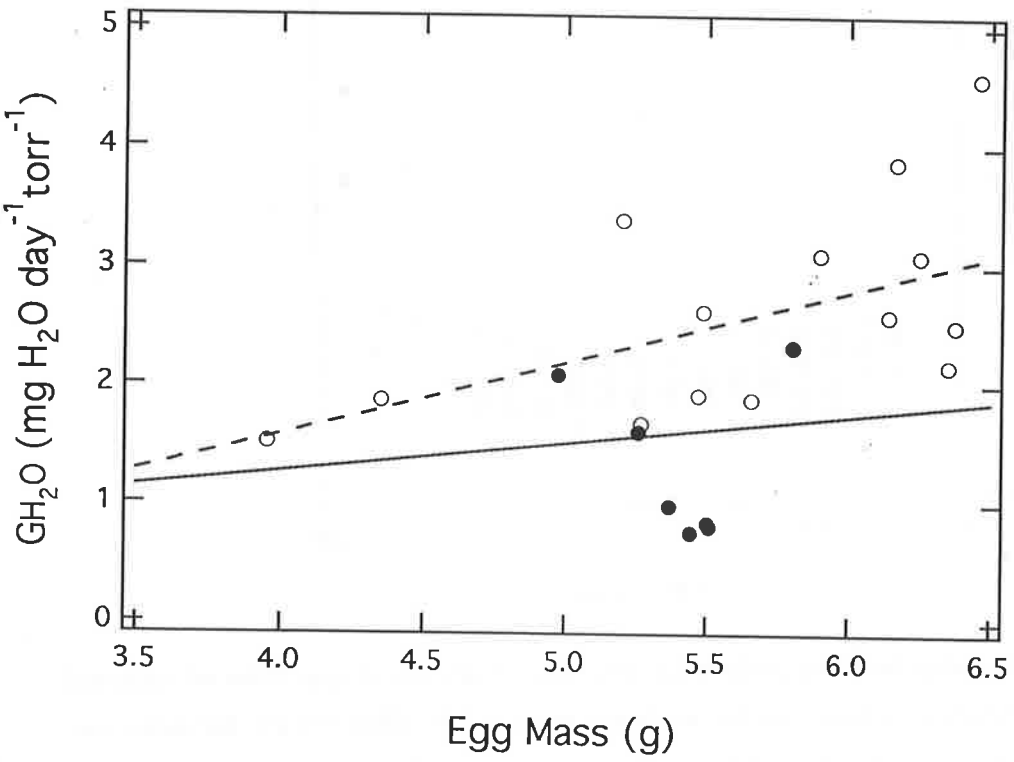

Fig.2. The relationship between G_{H2O} and egg mass for cockatiel eggs. *Solid symbols* indicate G_{H2O} measured under standard conditions of Ar et al. (1974), and *open symbols* indicate G_{H2O} of incubated eggs corrected to 25 °C. Solid line is the predicted interspecific relationship of Ar et al. (1974). *Dashed line* is a significant intraspecific relationship for cockatiel eggs (log G_{H2O}= -0.673 + 1.431 log M_e; s_b= 0.499 r^2= 0.406 $F_{1,12}$= 8.216 P<0.02).

Egg temperature of cockatiel was assumed to be 37 °C based on thermocouple eggs placed in several nest boxes, and king quail was assumed to be 38.5 °C (measured by thermocouple eggs). It was considered unlikely that the egg temperature of the upper surface of quail and cockatiel eggs was significantly higher than the rest of the egg due to the small mass of eggs and therefore measured egg temperature accurately reflected the incubation temperature the embryos experienced (Turner 1987, 1990). The water vapour gradient (ΔP_{H2O}) across the eggshell of eggs in the nest were determined using the Fick diffusion equation, where P_A is the water vapour pressure in the air cell, and P_n is the water vapour pressure of the nest around those eggs.

$$P_A - P_n = \dot{M}_{H2O} \div G_{H2O} \qquad \text{(eq. 6)}$$

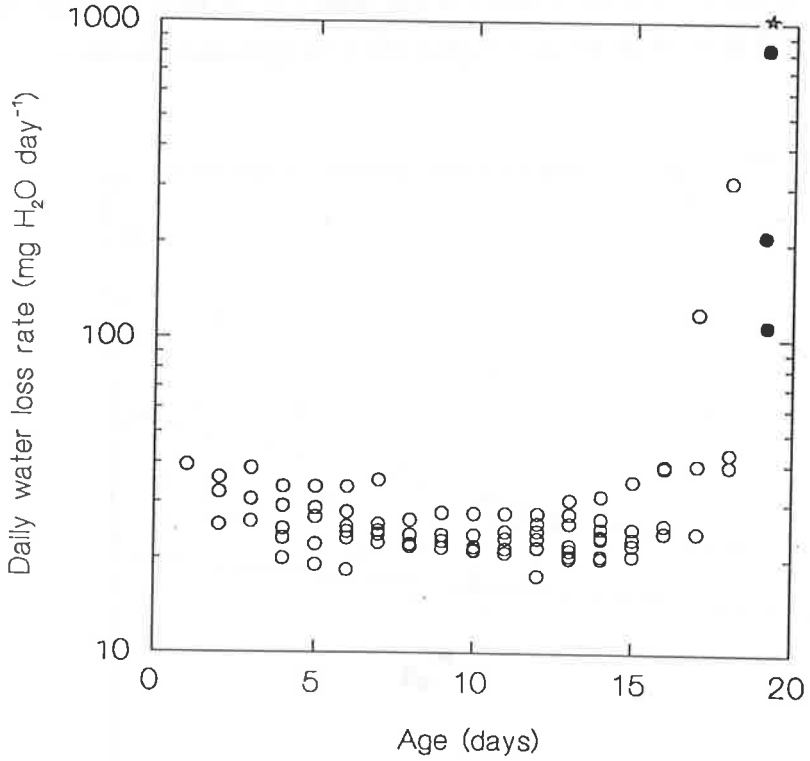

Fig. 3. Relationship between daily water loss rate ($\dot{M}_{H2O}$) and egg mass of cockatiel eggs during incubation. *Open circles*: embryos prior to EP; *filled circles*: EP embryos; *star*: embryo commenced hatching ($\dot{M}_{H2O}$= 3.072 g H_2O day^{-1}, off scale).

The absolute nest humidities of quail and cockatiel are presented in table 2. These calculations assume that the temperature of incubated thermocouple eggs accurately reflects incubation temperatures throughout development. Previously it has been shown that larger eggs increase significantly in egg temperature during late development (Swart, Rahn and de Kock 1987) due to embryonic heat production (Turner 1987). However any significant increases in egg temperature due to embryonic heat contributions seems unlikely for small eggs (Turner 1987, 1990). The mean P_n of king quail nests was 24.8

± 4.2 torr, but within a nest the range of P_n varied between 1 and 10 torr (Table 2). The mean P_n of cockatiel nests was similar at 25.8 torr. The P_n of both species are similar to the means of other birds (Rahn and Paganelli 1990).

Table 2. Estimated absolute nest humidities in king quail and cockatiel nests. The daily rates of water loss ($\dot{M}_{H2O}$) in the nest and an artificial incubator were used to determine water vapour conductance (G_{H2O}) of eggs and the absolute nest humidities (P_n) according to the Fick diffusion equation (eq.6). In some nests $\dot{M}_{H2O}$ and G_{H2O} were determined for more than one egg. Mean P_n was calculated for each nest and the grand mean for all nests.

Nest No. -	Clutch Size	$\dot{M}_{H2O}$ (mg H_2O day^{-1}) nest	incub	G_{H2O} (mg H_2O day^{-1} $torr^{-1}$)	P_n (torr)
KING QUAIL					
nest 1	5	51.9	42.0	2.00	25.1
		38.3	42.5	1.82	27.7
					mean=26.4
nest 2	3	64.6	55.9	2.66	26.7
		72.8	62.2	2.96	26.4
		84.9	73.3	3.49	26.7
					mean=26.6
nest 3	4	63.9	43.1	2.05	19.9
		72.0	49.8	2.37	20.6
		85.2	55.5	2.64	18.8
		26.4	20.2	0.96	23.6
					mean=20.7 ± 2.1
nest 4	4	79.5	77.9	3.71	29.6
		82.9	83.2	3.96	30.1
nest 5	7	59.2	39.9	1.90	19.8
		37.0	24.7	1.18	19.5
		73.0	51.7	2.46	21.3
					mean=20.2
				Mean of 5 nests = 24.8 ± 4.2	
COCKATIEL					
nest 1	3	61.7	30.2	2.67	24.4
nest 2	3	61.4	35.8	3.16	28.1
nest 3	4	108.3	52.9	4.67	24.3
		86.3	44.8	3.96	25.7
				Mean of 3 nests = 25.8	

Oxygen consumption throughout incubation

The oxygen consumption rate ($\dot{V}O_2$) of king quail embryos increased exponentially over the 16.5 day incubation period (fig. 4). Unlike larger precocial species $\dot{V}O_2$ did not appear to plateau prior to IP (day 15) (Hoyt, Vleck and Vleck 1978; Vleck, Hoyt and Vleck 1979). An exponential curve explained more variation in $\dot{V}O_2$ than a sigmoidal curve (sigmoidal function $r^2= 0.724$ $F_{1,109}= 2.629$ N.S.), and the fitted curve is presented as equation 7 for $\dot{V}O_2$ prior to hatching. EP of quail embryos was on day 16 of the incubation period and eggs hatched within 0.5 day.

$$\dot{V}O_2 = e^{1.746 + 0.184\ t} \qquad \text{(eq. 7)}$$

(n=44, $r^2= 0.964$ $F_{1,109}= 26.425$ $P<0.001$)

The mean mass of eggs used for $\dot{V}O_2$ measurements was 5.331 ± 0.582 g, which was higher than the grand mean of eggs in this study. Pre-internal pipping (PIP) was assumed to be the average of $\dot{V}O_2$ on day 14 and 15 (88% of incubation). The PIP $\dot{V}O_2$ was 80.91 mL O_2 day^{-1} was almost identical to the predicted 80.18 ml O_2 day^{-1} of Hoyt (eq. 3, 1987) using the mean egg mass. $\dot{V}O_2$ at IP was a mean of 87.5 ± 14.9 ml O_2 day^{-1} (n=9), and 104.4 ml O_2 day^{-1} (n=2) at EP. During hatching $\dot{V}O_2$ increased to a mean of 135.90 ml O_2 day^{-1} (n=3) in excess of the $\dot{V}O_2$ that is predicted by equation 7 for quail embryos. $\dot{V}O_2$ of two king quail during hatching was 262 mL O_2 day^{-1} and four hatchlings which were free of the eggshell with dry down, up to the age of 0.5 day had a mean $\dot{V}O_2$ of 214.8 mL O_2 day^{-1}.

The $\dot{V}O_2$ of cockatiel embryos increased exponentially throughout the 19 day incubation period (fig. 5). The metabolic pattern was similar to that previously described for six parrot species (Bucher 1983) and altricial species in general (Vleck, Hoyt and Vleck 1979). Incubation treatment was found to have a significant effect on the relationships between $\dot{V}O_2$ and incubation age. The incubation periods of naturally incubated cockatiel eggs was 19.0-21.0 days, but artificially incubated eggs hatched after 19 days.

The $\dot{V}O_2$ of cockatiel embryos was semi-log transformed ($\ln \dot{V}O_2 = a + bt$) and compared between artificially and naturally incubated eggs. The regressions were not significantly different in slope (ANCOVA $F= 1.743$ N.S.), but the intercept of the regression for artificially incubated eggs was higher than naturally incubated eggs, which was equivalent to a reduction in incubation period of 1.7 days. The difference in incubation period recorded was up to two days, with the first laid eggs hatching after 20.5-21.0 days, second eggs 20.0-20.5 days and subsequent eggs 19.0 days. Continuous incubation commenced after the first or second egg. To test if the two day

delay in $\dot{V}O_2$ of naturally incubated eggs was attributable to either nest inattentiveness or low initial incubation temperatures, the incubation period of all cockatiel embryos was assumed to be 19.0 days and all embryo ages were adjusted backwards from the recorded hatching times. The relationship between $\dot{V}O_2$ and day of incubation (eq. 8), where t is the day of incubation, explained more of the variation in embryo metabolism than either relationship for naturally and artificially incubated eggs individually.

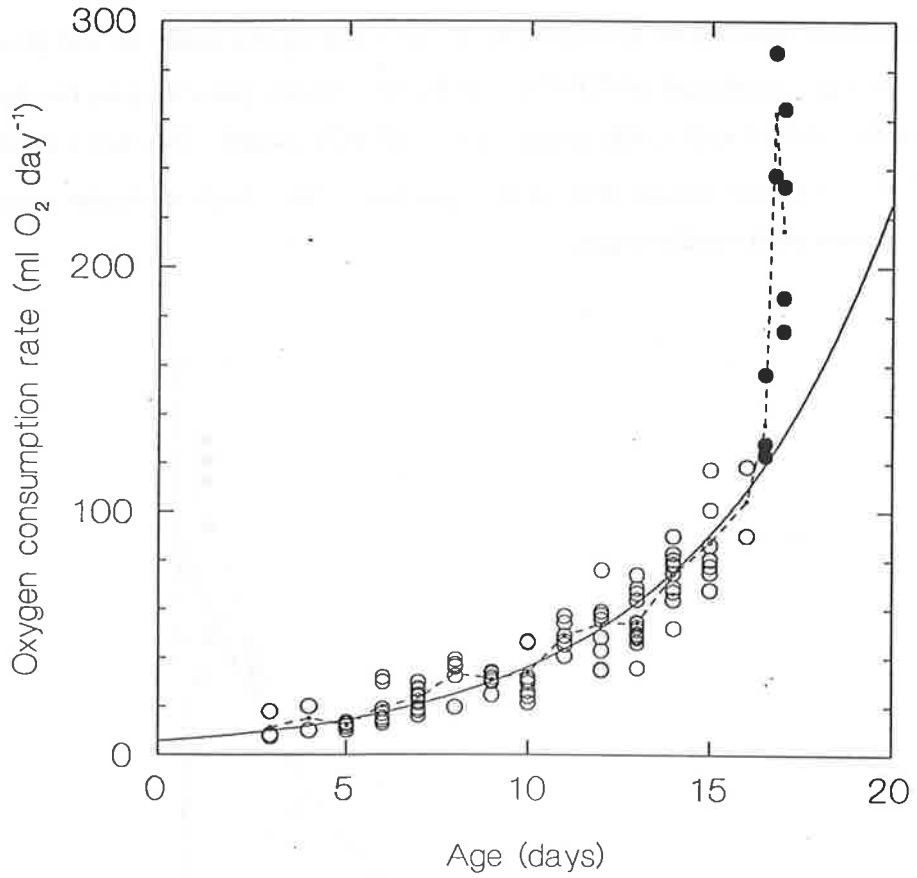

Fig. 4. The relationship between embryonic $\dot{V}O_2$ and days of incubation in king quail (n=44). *Open circles* indicate embryos up to external pipping, and *filled circles* indicate externally pipped and hatching embryos (5) and hatchlings (4). Solid line is an exponential function (eq. 7) and dashed line connects daily mean $\dot{V}O_2$.

$$\dot{V}O_2 = e^{1.385 + 0.182\ t} \qquad \text{(eq. 8)}$$

$(n=19\ r^2 = 0.970\ F_{1,41} = 32.774\ P < 0.001)$

IP of cockatiel eggs was on day 17, EP on day 18 and embryos hatched 1.5 days later. The hatching event was complete 0.25 day after it commenced. The mean egg mass of cockatiel eggs used for $\dot{V}O_2$ measurements was 5.592 ± 0.688 g, which was less than the grand mean of all eggs in this study. The PIP $\dot{V}O_2$ was 80 ml O_2 day^{-1} (day 16.5), which is significantly lower than the 89.3 ml O_2 day^{-1} predicted by Hoyt's (1987)

model of embryonic metabolism (observed:expected of $\dot{V}O_2$ was <95% CI). However, it was assumed in Hoyt's model that PIP was 90% of the incubation period in altricial species, at the same time that cockatiel embryos were considered to have internally pipped. $\dot{V}O_2$ of cockatiel was a mean of 87.32 ml O_2 day^{-1} (n=3) on day 17 at about 90% of the incubation period, which is similar to the predicted value of Hoyt (1987). During the pipping period cockatiel $\dot{V}O_2$ was equivalent to that predicted by the exponential equation (8), in contrast to the smaller parrot species described by Bucher (1983), the $\dot{V}O_2$ of which falls below an exponential curve during the same period prior to hatching. The observed:predicted of PIP $\dot{V}O_2$ for the six species presented in Bucher (1983) ranged between 0.614 and 0.900 using Hoyt's (1987) model. Bucher (1983) noted that the PIP $\dot{V}O_2$ of parrot species with larger eggs were closer to predictions based on egg mass than species with smaller eggs.

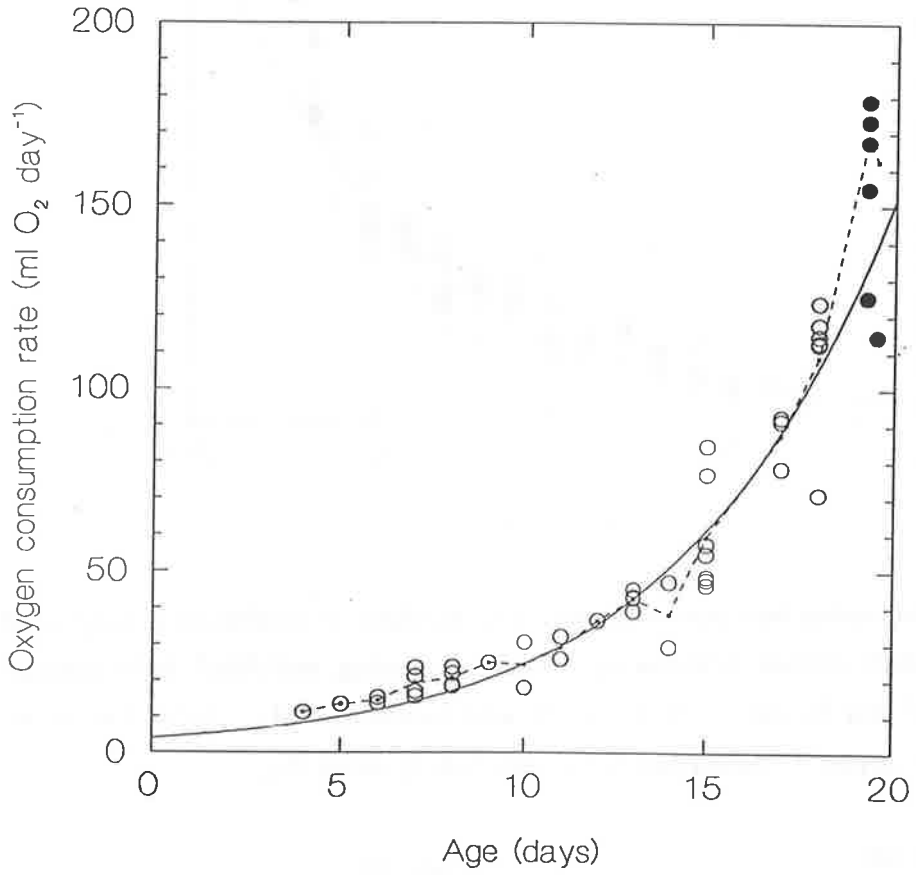

Fig. 5. The relationship between embryonic $\dot{V}O_2$ and days of incubation in cockatiel (n=20). *Open circles* indicate embryos up to external pipping, and *filled circles* indicate hatchlings (6). Solid line is an exponential function (eq. 8) and dashed line connects daily mean $\dot{V}O_2$.

Allometric relationships between PIP $\dot{V}O_2$ and egg mass

In this study the influence of phylogenetic relations on PIP $\dot{V}O_2$ is examined after taking into account egg mass (M_e). The PIP $\dot{V}O_2$ of king quail and cockatiel are included with species compiled in Rahn and Paganelli (1990) and other recent studies, and covered a mass range of 1 to 1450 g (fig. 6).

The relationship between PIP $\dot{V}O_2$ and egg mass was highly significant (eq. 9), and the slope was not changed from the previous allometric relationship (b= 0.734, Rahn and Paganelli 1990). Similarly a significant relationship was obtained between incubation period and egg mass (eq. 10), the slope of which was almost identical to a previously obtained allometric relationship (Ar and Rahn 1974).

$\log \text{PIP } \dot{V}O_2 = 1.363 + 0.742 \log M_e$ (eq. 9)
(s_b= 0.019 r^2= 0.945 $F_{1,85}$= 1459.82 P<0.001)

$\log I = 1.107 + 0.211 \log M_e$ (eq. 10)
(s_b= 0.021 r^2= 0.544 $F_{1,85}$= 101.451 P<0.001)

After taking into account egg mass, the effect of incubation period on PIP $\dot{V}O_2$ was examined in this study. A significant relationship was found between the residuals of equation 9 and equation 10 (eq. 11).

$\text{PIP } \dot{V}O_{2\ resid} = 0.000 - 0.381\ I_{resid}$ (eq. 11)
(s_b= 0.092 r^2= 0.169 $F_{1,85}$= 17.272 P<0.001)

The negative slope of equation 11, which was significantly different from zero (t= -4.156 P<0.001), implies that higher than predicted PIP $\dot{V}O_2$ was correlated with a shorter than expected incubation period (fig. 7). Galliform embryos generally had higher than expected PIP $\dot{V}O_2$ and shorter incubation periods, with the exceptions of the two megapode species. PIP $\dot{V}O_2$ of king quail embryos was equal to the predictions of equation 9, and had a shorter incubation period. Most psittaciform embryos had lower PIP $\dot{V}O_2$ and longer incubation periods than predicted on the basis of egg mass (fig. 7). However, some parrots have shorter incubation periods than other parrots on the basis of egg mass (residuals less negative), including the cockatiel, which has a PIP $\dot{V}O_2$ equivalent to allometric predictions. In general the precocious embryos were found to have higher PIP $\dot{V}O_2$ and shorter incubation periods, and altricial embryos lower PIP $\dot{V}O_2$ and longer incubation periods. Although this correlation may reflect the effect of phylogeny rather than hatchling developmental type.

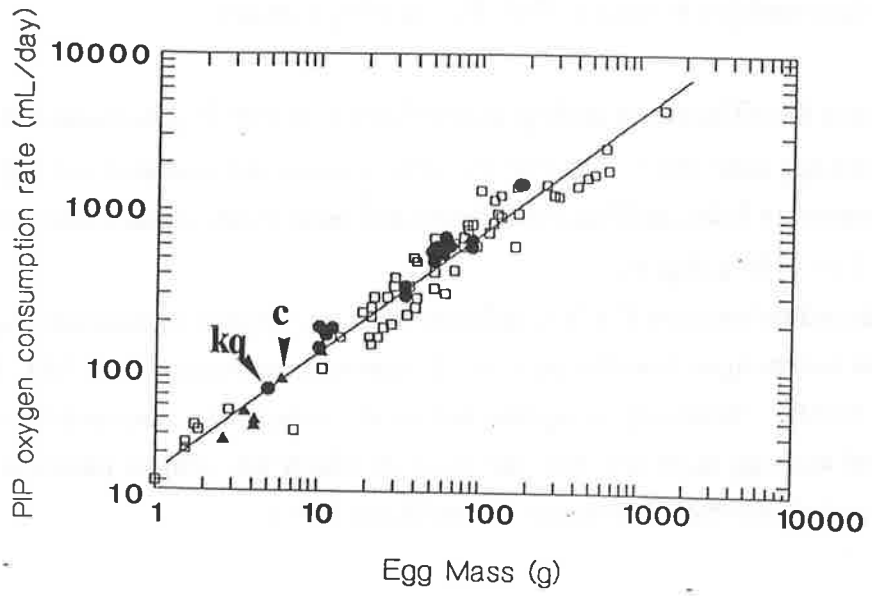

Fig. 6. Relationship between PIP $\dot{V}O_2$ and egg mass (M_e) for 87 species compiled primarily from Rahn and Paganelli (1990), Hoyt and Rahn (1980). Other sources were Booth (1985),Visser (1991), Opt de Hipt and Prinzinger (1992), Ancel and Visschedijk (1993). *Circles*: Galliformes, *triangles*: Psittaciformes, and *squares*: all other orders. Symbols indicate the king quail (kq) and cockatiel (c). Solid line indicates equation 9.

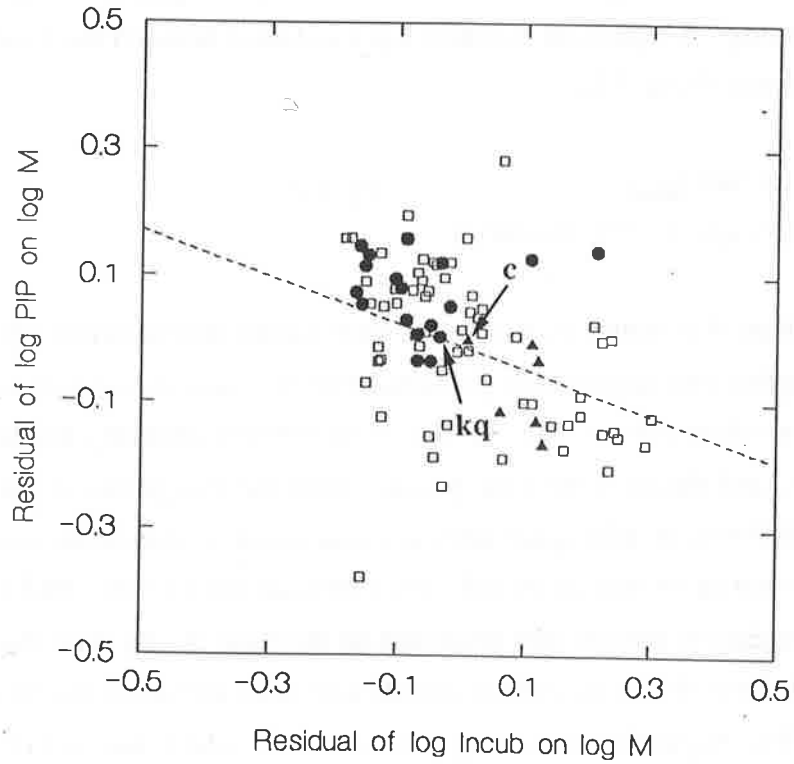

Fig. 7. The relationship between residuals of log-log regressions between PIP $\dot{V}O_2$ and egg mass (eq. 9) and between residuals of incubation period and egg mass (eq. 10). Symbols are the same as figure 6. Dashed line indicates a significant correlation (eq. 11).

Cost of development

The area under the exponential curve (eq. 7) is the total oxygen consumed by the embryo during development, including hatching (TOT). For the king quail, TOT was 654 mL O_2 using equation 7, or 705 mL O_2 under the lines described by the daily $\dot{V}O_2$ means. Hatching $\dot{V}O_2$ was elevated above the exponential equation 7 and as a result TOT was higher on the basis of daily $\dot{V}O_2$ means. Hatching consumed 116 mL O_2 of the total (under daily means), as determined by the difference in mean values of $\dot{V}O_2$ between day 16 and 16.5. Embryonic respiratory quotients in avian eggs have previously been reported as 0.71, indicating that a suitable caloric equivalent for metabolism is 19.64 J mL O_2^{-1} (Vleck and Vleck 1987). Therefore the estimated cost of development in king quail up to EP was 11.12 kJ per egg according to equation 7 and 11.57 kJ per egg according to the mean daily rates respectively and the cost of hatching was 2.29 kJ. The total cost of development to produce a king quail hatchling was on average 13.86 kJ using the daily mean $\dot{V}O_2$. This was marginally higher than the TOT (13.03 kJ) predicted by Vleck and Vleck (1987) for precocial species, using the mean egg mass of 5.33 g, but was within the 95% CI of the mean. However, the predicted value on the basis of mean energy content of 36 kJ was lower (12.38 kJ), but still within one SEE. Hoyt's (1987) model of embryonic metabolism predicted a TOT of 11.51 kJ on the basis of egg mass, which was significantly lower than king quail TOT (» 95% CI of the observed:predicted).

Cockatiel TOT was a mean of 671 mL O_2 under equation 10, and 721 mL O_2 under the lines of the daily $\dot{V}O_2$ means, including 174 mL O_2 during hatching. Therefore TOT was equivalent to 9.75 kJ and 10.74 kJ up until EP according to equation 10 and the daily means, and a further 3.42 kJ was utilised during hatching. The total cost of development to produce cockatiel hatchling was an average of 14.16 kJ using the daily mean $\dot{V}O_2$. The effect of the greater than expected incubation periods of cockatiel, according to allometric predictions (Table 1, p.72), were evident in the higher than expected costs of development. When egg mass and incubation periods of mostly smaller altricial species were used to predict TOT, a 5.9 g cockatiel egg was predicted to use 10.08 and 10.42 kJ (Bucher 1983, equations 4 & 5). Similarly the predicted TOT of parrot eggs according to equation 6 of Bucher (1983), of 12.46 kJ was lower than expected. However the two largest species in Bucher's (1983) sample were also underestimated by this regression. TOT was estimated as 9.35 kJ on the basis of egg mass of altricial species, and 10.11 kJ using the measured energy content (mean 29 kJ) of cockatiel eggs (Vleck and Vleck 1987). The highest estimate of TOT was 12.73 kJ as predicted by Hoyt's (1987) model of embryonic metabolism.

Respiratory gas conductances

$\dot{V}O_2$ and G_{H2O} were measured in the same eggs to obtain partial pressures of O_2 and CO_2 in the aircell of developing king quail and cockatiel eggs. As $\dot{V}O_2$ of king quail and cockatiel embryos increases during incubation, P_{AO_2} decreases and P_{ACO_2} increases exponentially (fig. 8-12), because the gas tension difference across the eggshell is linearly related to the metabolic rate of the embryo (Wangensteen and Rahn 1970/71). Curvilinear relationships were fitted to both species for P_{ACO_2} and P_{AO_2}, except when no significant relationship could be established (fig. 11). The P_{ACO_2} and P_{AO_2} were calculated to be about 40 torr and 110 torr, respectively, immediately before IP in king quail eggs (fig. 8-9), but only 30 torr and 125 torr respectively in cockatiel eggs (fig. 11-12).

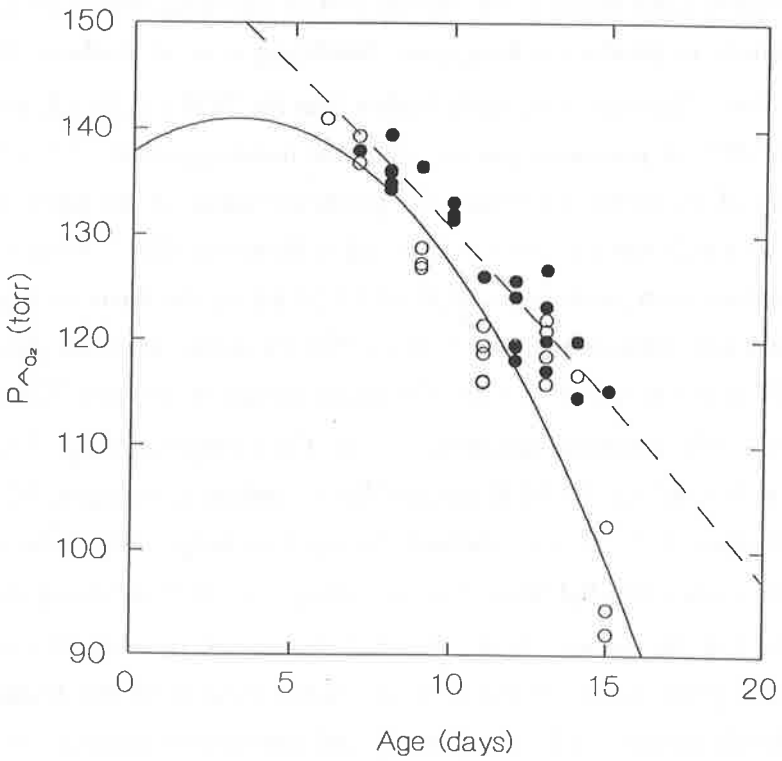

Fig. 8. The relationship between calculated P_{AO_2} and day of incubation in king quail eggs (n=12). *Open symbols and solid line*: eggs with G_{H2O} <2.0 mg H_2O $day^{-1}torr^{-1}$ (regression P_{AO_2} = 137.83 + 1.97 age - 0.31 age^2, r^2= 0.988 $F_{1,20}$= 437.438 P<0.001); *filled symbols and dashed line*: eggs with G_{H2O} >2.0 mg H_2O $day^{-1}torr^{-1}$ (regression P_{AO_2} = 159.36 + 2.68 age - 0.02 age^2, r^2= 0.871 $F_{1,18}$= 261.842 P<0.001).

The average gas tensions in the aircell of most species at PIP are 37 torr and 104 torr respectively, for O_2 and CO_2, and are thought to stimulate IP and the initiation of pulmonary ventilation (Rahn, Paganelli and Ar 1974; Rahn and Paganelli 1990). The

predicted gas tensions in king quail eggs conformed well with other species, but the CO_2 tensions are low and O_2 tensions are high in the cockatiel. To examine the effect of G_{H2O} on $\dot{V}_{O2}$, quail eggs were arbitrarily divided into two groups based on G_{H2O}. Despite the limited number of measurements in this study, king quail eggs with a G_{H2O} <2.0 mg H_2O $day^{-1}torr^{-1}$ have lower $\dot{V}_{O2}$ and P_{AO2}, and higher P_{ACO2} than in eggs with G_{H2O} >2.0 mg H_2O day^{-1} $torr^{-1}$ from mid-incubation to IP (fig. 8-10). The results suggest that gas exchange across the eggshell is affected by a conductance-limitation, even though $\dot{V}_{O2}$ never plateaus. Ancel and Visschedijk (1993) found that the difference in $\dot{V}_{O2}$ is greatest between low and high conductance *Numida meleagris* eggs during the plateau phase, but the effect of a shell conductance limitation on respiration is distinct at 65% of the incubation period, before $\dot{V}_{O2}$ plateaus.

After IP in cockatiel eggs, P_{AO2} appeared to reverse and begin to increase to 120-140 torr, and P_{ACO2} similarly appeared to decline from a maximum value to 10-30 torr. However, small sample sizes prevent comparisons before and after IP. A similar pattern of air cell gas tensions was observed by Bucher and Barnhart (1984) for another parrot, *Agapornis roseicollis* , with the exception that the absolute levels of gas tension in this study were relatively less hypoxic and hypercapnic in comparison.

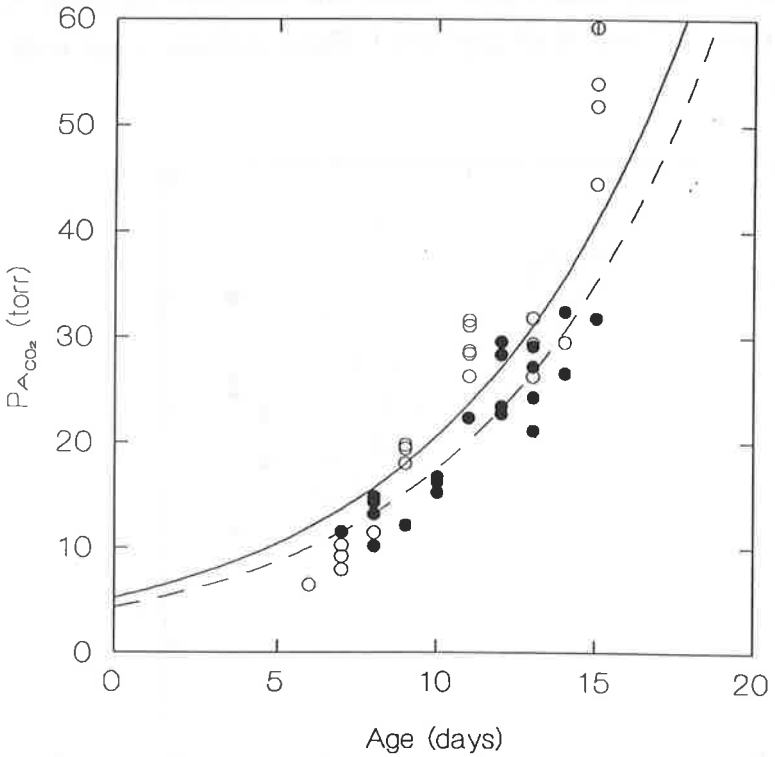

Fig. 9. The relationship between estimated P_{ACO2} and day of incubation in king quail eggs (n=12). *Open symbols and solid line*: eggs with G_{H2O} <2.0 mg H_2O $day^{-1}torr^{-1}$ (regression $P_{ACO2} = e^{(1.654 + 0.137age)}$, r^2= 0.966 $F_{1,20}$= 28.130 P<0.001); *filled symbols and dashed line*: eggs with G_{H2O} >2.0 mg H_2O $day^{-1}torr^{-1}$ (regression $P_{AO2} = e^{(1.462 + 0.140age)}$, r^2= 0.982 $F_{1,18}$= 55.565 P<0.001).

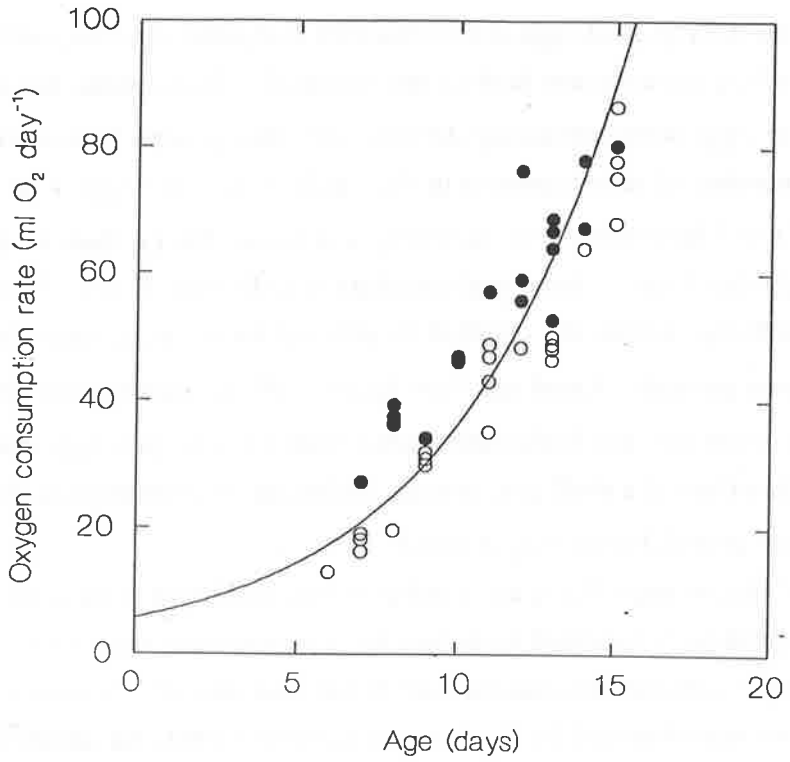

Fig. 10. Relationship between $\dot{V}O_2$ and day of incubation in eggs used to determine gas tensions under the shell of king quail eggs. Solid line indicates equation 7. *Open symbols*: eggs with G_{H2O} <2.0 mg H_2O day^{-1}torr^{-1}; *filled symbols*: eggs with G_{H2O} >2.0 mg H_2O day^{-1}torr^{-1}.

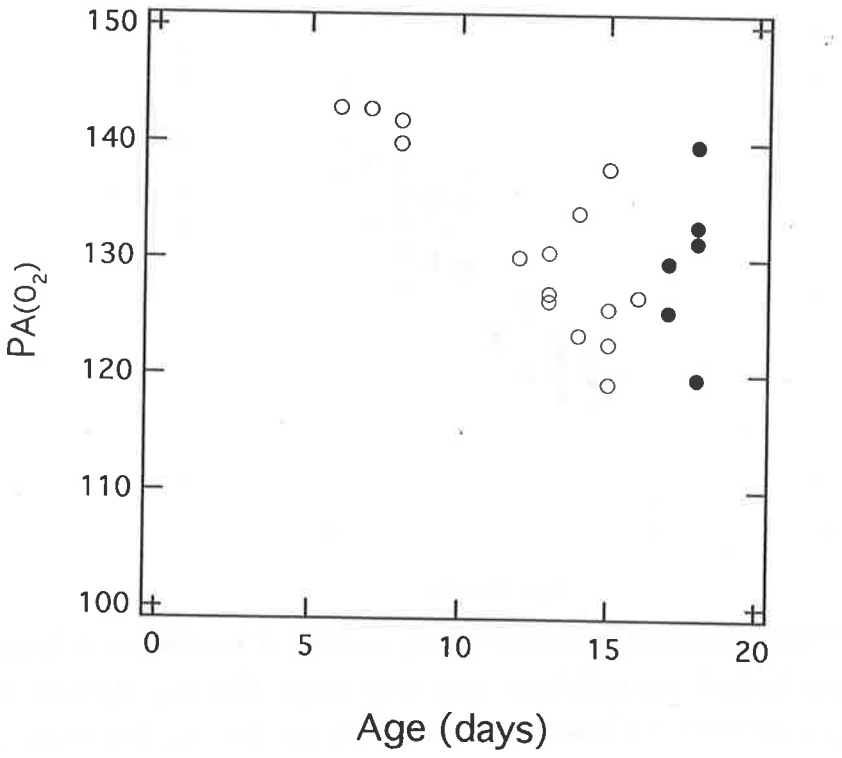

Fig. 11. The relationship between estimated P_{AO2} and day of incubation in cockatiel eggs. *Open symbols*: eggs <17 days; *filled symbols*: eggs >17 days. Variability in gas tensions in eggs <17 days, prevented a significant curvilinear relationship.

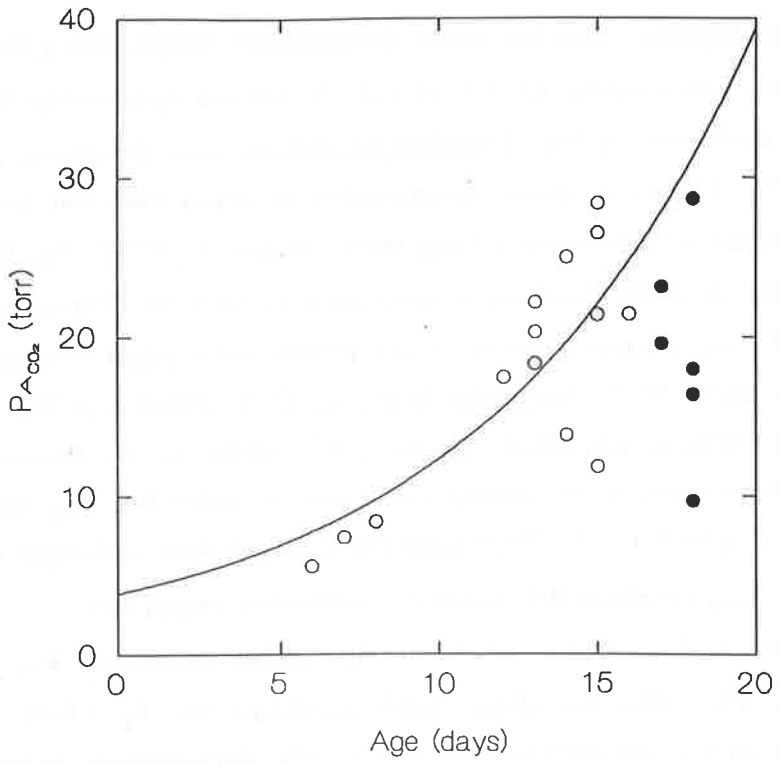

Fig. 12. The relationship between estimated P_{ACO_2} and day of incubation in cockatiel eggs. *Open symbols*: eggs <17 days; *filled symbols*: eggs >17 days. Solid line indicates a significant regression at age <17 days ($P_{ACO_2} = e^{(1.354 + 0.116age)}$, $r^2 = 0.945$ $F_{1,12} = 17.346$ $P<0.001$).

Oxygen consumption rates during gradual cooling

The gradual cooling curve for one non-living quail egg is presented in figure 13. The thermocouple egg was placed in a metabolism chamber at 38 °C, and then T_a lowered gradually to T_a 22 °C. T_{egg} decreased exponentially to one degree above T_a in 60 min (fig. 13). In larger chicken eggs embryonic resting heat production (at incubation temperature) increased with age, and egg temperature was elevated above T_a by a small increment, but the thermal conductance of the living egg was not different from that of a non-living egg (Tazawa et al. 1988b). The T_{egg} of living quail eggs was not determined invasively, but was assumed to be similar to non-living eggs (thermocouple eggs) because embryonic heat production is less significant in small eggs (Tazawa, Turner and Paganelli 1988).

The $\dot{V}O_2$ of four king quail eggs was measured during prolonged gradual cooling (1 h) from T_a 38-40 °C down to T_a 30 °C. During these gradual cooling tests, T_a decreased exponentially from 38-40 °C to 32 °C. These tests were of a shorter duration than previously used by Tazawa et al. (1988b), because the small metabolism chambers of this study cooled more rapidly, and experiments were terminated before T_a in the chamber equilibrated with T_a in the constant temperature cabinet. The $\dot{V}O_2$ of embryos at incubation temperature was variable between eggs, so the $\dot{V}O_2$ of each egg during

prolonged cooling was expressed as a fraction of the incubation temperature (38-40 °C). The $\dot{V}O_2$ of four quail embryos (day 13, 13, 14 and 15) was not significantly elevated above thermoneutral levels, but the $\dot{V}O_2$ of hatchlings (<0.5 day) was elevated in three of the four quail (fig. 14). However, these late-incubation embryos were able to sustain constant $\dot{V}O_2$ independent of T_a between 32 and 38 °C. Below T_a 32 °C, $\dot{V}O_2$ declined rapidly to 50-70% of the thermoneutral level of each egg at T_a 30-31 °C. The temperature coefficients (Q_{10}) of $\dot{V}O_2$ during short-term and prolonged gradual cooling were approximately 1 at T_a above 32 °C, but higher below T_a 32 °C (Table 3, p.90). At the end of the cooling test it was estimated that T_{egg} was 2-3 °C above T_a , but because T_{egg} lags behind T_a throughout much of the cooling test, it was estimated that T_{egg} was 34.5 °C at T_a 32 °C (according to fig. 13). Thus when the embryos were no longer able to sustain constant $\dot{V}O_2$, T_{egg} was about 4 °C below the incubation temperature.

Hatchling quail (<0.5 day) were variable in their ability to increase $\dot{V}O_2$ during gradual cooling (fig. 14). One hatchling clearly increased $\dot{V}O_2$ by 170% above thermoneutral levels at 28 °C. The other hatchlings were only able to sustain increases of 20-30% in $\dot{V}O_2$ above the thermoneutral level of $\dot{V}O_2$ at T_a 28-29 °C. Unlike most larger precocial hatchlings, king quail were equivocal in their thermogenic responses.

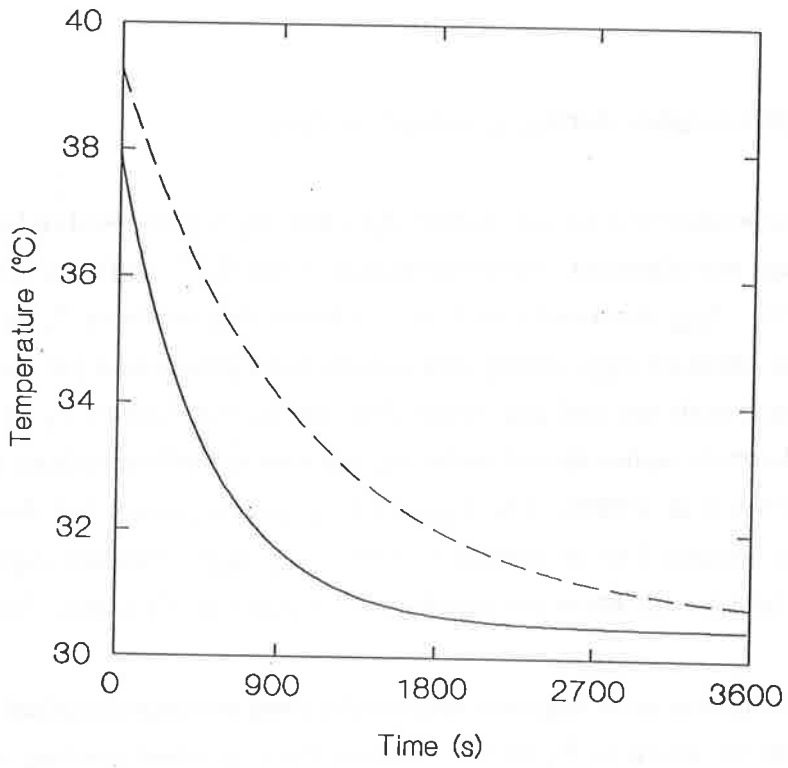

Fig. 13. A representative cooling curve for a non-living king quail egg during gradual cooling to T_a 22 °C. Solid line indicates T_a in metabolism chamber and dashed line is egg temperature.

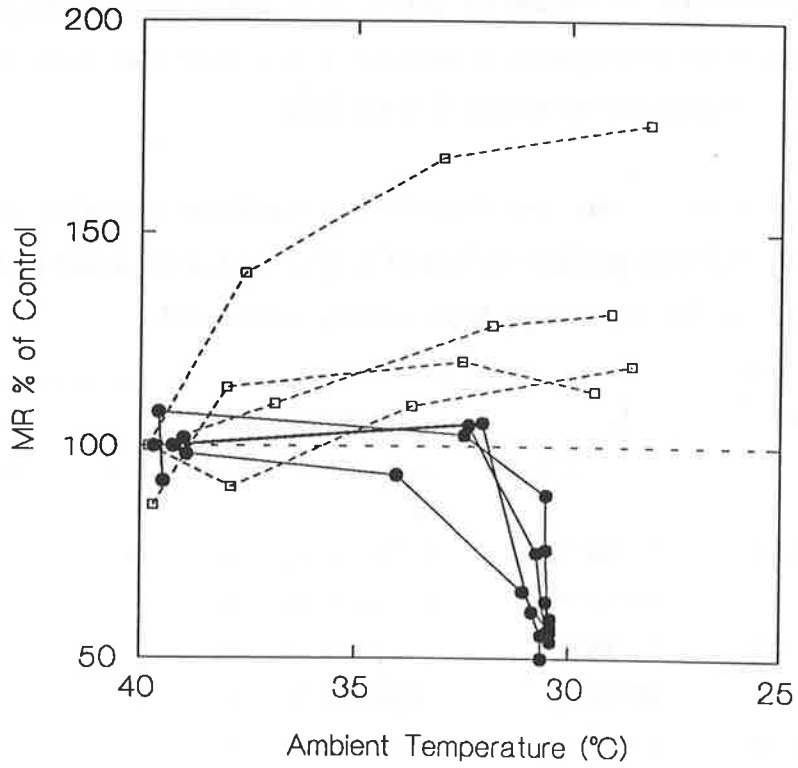

Fig. 14. Oxygen consumption rates of king quail eggs and hatchlings during 'prolonged' gradual cooling (1 h). Rates are expressed as a percentage of $\dot{V}O_2$ at thermoneutrality of individuals. Lines connect individual embryos. *Filled symbols*: quail embryos (day 13, 13, 14 and 15); *open symbols*: hatchlings (<0.5 day) (n=4).

The $\dot{V}O_2$ of a larger number of quail embryos was measured during short-term gradual cooling (<30 min), during which time T_a in the constant temperature cabinet was lowered to 30 °C as in the previously measurements of this study, but the measurements were terminated within 30 min. $\dot{V}O_2$ during short-term cooling tests was expressed as a percentage of the mean $\dot{V}O_2$ at incubation temperature of 38-40 °C (control) for each day of incubation. The relationship between $\dot{V}O_2$ and T_a during short-term cooling tests was determined for quail embryos on day 13, 14 and 15 (fig. 15). At all three ages during late incubation $\dot{V}O_2$ at 38-40 °C was variable between eggs, which was attributed to the large range of egg masses used in these experiments. Individual eggs were also highly variable in $\dot{V}O_2$ at thermoneutrality. During cooling tests the youngest quail embryos (day 13), and those embryos which presumably had internally pipped or in one case had externally pipped, were equally able to maintain constant $\dot{V}O_2$ above T_a 33 °C, but not below 32 °C (fig. 15). There was no indication of thermogenic responses in late term embryos, but $\dot{V}O_2$ of the embryos never decreased within this time period either. It is suggested that most king quail were in the second stage of the development of

homeothermy ('incipient endothermy') according to the scheme of Tazawa et al. (1988b) during the paranatal period (day 14-15) and the period immediately after hatching. The earliest that king quail demonstrated significant increases in $\dot{V}O_2$ in defense of decreasing body temperature was during the transition period of hatching.

Table 3. Mean daily $\dot{V}O_2$ (mL O_2 day^{-1}) of control embryos at thermoneutrality, and the mean Q_{10} of $\dot{V}O_2$ changes during gradual cooling of king quail and cockatiel embryos from figure 14-16. T_a range for $\dot{V}O_2$ change during cooling is indicated.

Age	mean $\dot{V}O_2$	T_a	Q_{10} (±SD)	n
KING QUAIL				
13	54.2	32-38 °C	1.09 ± 0.16	8
		30-32 °C	1.64 ± 0.39	5
14	74.3	32-38 °C	1.01 ± 0.11	9
		30-32 °C	3.69 ± 3.20	4
15 (EP)	87.5	32-38 °C	1.11 ± 0.21	7
COCKATIEL				
15	59.4	31.5-37.5 °C	1.03	3
17 (IP)	87.3	31.5-37.5 °C	1.20	3
18 (EP)	108.7	31.5-37.5 °C	0.93	4

The $\dot{V}O_2$ of cockatiel embryos was measured during short-term gradual cooling (<30 min) only, during which time T_a was lowered gradually to T_a 30 °C. $\dot{V}O_2$ during short-term cooling tests was expressed as a percentage of the mean $\dot{V}O_2$ at incubation temperature of 37-37.5 °C (control) for each day of incubation. The relationship between $\dot{V}O_2$ and T_a during short-term cooling tests was determined for quail embryos on day 15, 17 and 18 (fig. 16). The $\dot{V}O_2$ of all embryos during late incubation at 37-37.5 °C was variable between eggs, which was also attributed to the range of egg masses. Individual eggs were also highly variable in $\dot{V}O_2$ at thermoneutrality. During cooling tests the cockatiel embryos were able to maintain constant $\dot{V}O_2$ independent of T_a between T_a 30-37.5 °C (fig. 16). It is suggested that cockatiel have incipient endothermy according to the scheme of Tazawa et al. (1988b) at the end of the incubation period and immediately after hatching. Several days after hatching increases in $\dot{V}O_2$ in defense of decreasing body temperature were found in unbrooded cockatiel chicks (see Chapter 4).

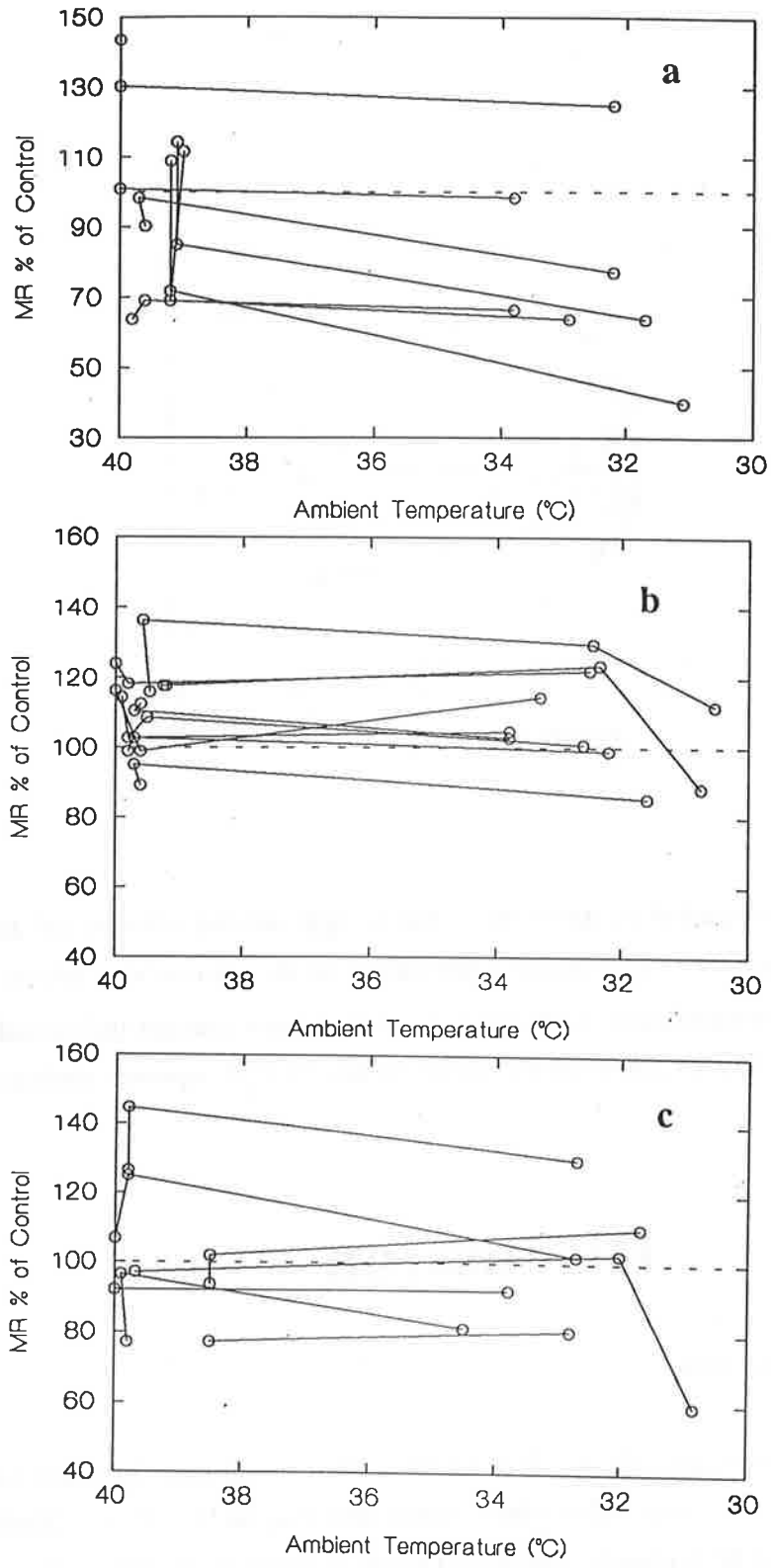

Fig. 15. Oxygen consumption rates of king quail eggs during 'short-term' gradual cooling (<30 min). Rates are expressed as a percentage of the control $\dot{V}O_2$, which is the mean daily $\dot{V}O_2$ at thermoneutrality (see Table 3). Solid lines connect individual data. **a.** embryos day 13 (n=7), **b.** embryos day 14 (n=10), **c.** embryos day 15 (n=6, including one day 16).

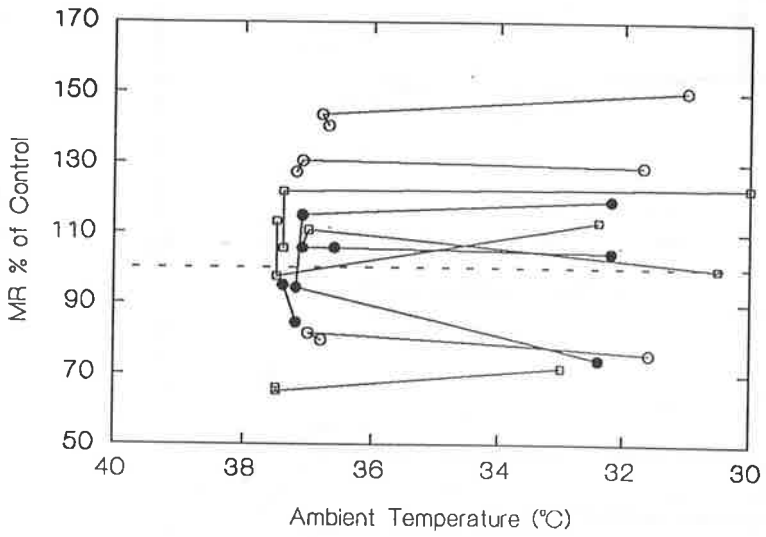

Fig. 16. Oxygen consumption rates of cockatiel eggs during 'short-term' gradual cooling (<30 min). Rates are expressed as a percentage of the control $\dot{V}O_2$, which is the mean daily $\dot{V}O_2$ at thermoneutrality (see Table 3). Solid lines connect individual data. *Open circles*: embryos day 15; *filled circles*: embryos day 17 (IP); *squares*: embryos day 18 (EP).

Discussion

Water vapour conductance

The eggs of all species lose on average 15% of their initial mass by water vapour diffusion (Drent 1970; Ar and Rahn 1980; Rahn and Paganelli 1990). Shell gas conductance appears to be primarily adapted to regulate water loss, rather O_2 uptake (Vleck, Hoyt and Vleck 1979; Ar and Rahn 1980; D. Vleck, Vleck and Hoyt 1980). The incubated eggs of king quail and cockatiel hatched successfully over a 4-fold range in G_{H2O} (figs. 1-2, p.74-75). Carey (1986) also found that red-winged blackbird, *Agelaius phoeniceus*, embryos hatch over a 4.3-fold range in G_{H2O}. Many other studies also report large variations in G_{H2O} of naturally and artificially incubated eggs (Vleck, Hoyt and Vleck 1979; Hoyt, Vleck and Vleck 1979; Rahn, Krogh and Mehlum 1983; Vleck et al. 1983; Bucher and Barnhart 1984). The G_{H2O} of king quail and cockatiel eggs

measured under standard conditions at 25 °C (Ar et al. 1974) are variable at all egg masses, but the G_{H2O} of incubated quail eggs increases significantly with egg mass at a rate that is higher than the interspecific relationship (fig. 1-2). Martin and Arnold (1991) also found that larger Japanese quail eggs lost proportionately more water during incubation than small eggs. This study supports their conclusion that in some species at least, the intraspecific relationship between G_{H2O} and egg mass is significantly higher in slope than the interspecific relationship.

Deviations in the length of the incubation period explain a significant amount of variation in G_{H2O} at any egg mass (Ar and Rahn 1978). Eggs with shorter than expected incubation periods have higher G_{H2O} and vice versa. However, the G_{H2O} of king quail and cockatiel eggs is significantly higher than predicted on the basis of egg mass and incubation period (predict 1.52 and 1.59 mg H_2O $day^{-1}torr^{-1}$ respectively) (Ar and Rahn 1978). Egg water loss is also related to the absolute nest humidity (Paganelli 1980; Rahn and Paganelli 1990). In this study the absolute nest humidity is on average 24.8 torr (range 20-30 torr) in king quail nests, and 25.8 torr (range 24.4-28.1 torr) in cockatiel nest boxes (Table 2, p.77). Rahn and Paganelli (1990) report that the absolute nest humidities for 20 species ranges between 11 and 25 torr. Possibly the high G_{H2O} of king quail and cockatiel eggs are adaptive for the humid nest environments. King quail are generally found in damp swamp and grassland habitats (p. 415, Marchant and Higgins 1993). Similarly the nesting cavities of parrots in tree limbs may be humid because of rotten wood.

The $\dot{M}_{H2O}$ and G_{H2O} of most, but not all, cockatiel eggs increases 2 to 4-fold from internal pipping (IP) (fig. 3, p.76). Increased water loss from cockatiel eggs is attributed to fractures in the eggshell one day prior to external pipping (EP), at approximately the same time that the embryo pips into the aircell. Bucher and Barnhart (1984) found that the eggs of another parrot species, *Agapornis roseicollis*, also increase in G_{H2O} immediately prior to EP. The increase G_{H2O} of *A. roseicollis* was considered to be the result of abrasion of the shell membranes by embryonic movements. However, the inner shell membrane is a minor source of resistance to diffusion compared the outer shell membrane and eggshell, so it seems unlikely that embryonic movements are likely to decrease the resistance of the eggshell and its membranes. Star-fractures are visible on the eggs of petrels (Procellariiformes) prior to IP and are thought to possibly increase the rates of chorioallantoic gas exchange before EP and hatching (Ackerman et al. 1980; Whittow 1980; Pettit et al. 1981, 1982).

Total water lost during incubation in cockatiel eggs is similar to that of other birds, at 23.8% on average of the initial egg mass including water loss during hatching (Rahn 1984). However, water loss prior to IP is less than 15% (cockatiel 6-9%), which is typical of most avian eggs. It is considered that this does not reflect natural incubation water losses of cockatiel eggs. The low rate of water loss prior to IP is likely to be a consequence of high humidities (77%) in the artificial incubator, which was estimated on

the basis of the predicted G_{H2O} of the same egg mass. The G_{H2O} of cockatiel eggs is on average higher than predicted by egg mass (fig. 2). Eggs placed in cockatiel nests to determine nest humidities lost water vapour at approximately double the rate than when the same eggs were artificially incubated. The $\dot{M}_{H2O}$ of one such egg was 61.4 mg H_2O day^{-1} in the nest, and the estimated water lost up to IP is 16.7% of the initial egg mass (17 days × 61.4 mg H_2O day^{-1}), which is similar to most avian eggs. It is considered here that cockatiel embryos are able to tolerate wide variations in G_{H2O} and still achieve the required water loss at hatching by behaviours such as fracturing the eggshell prior to pipping.

Incubation period

The incubation period of king quail (16.5 days) is shorter and the cockatiel (19-21 days) longer than expected on the basis of egg mass according to allometric relationships for precocial and altricial species respectively (Table 1, p.72). Altricial species in general have shorter incubation periods than precocial species (Vleck and Vleck 1987). However, variation in the incubation periods of avian embryos at any given egg mass appears to be strongly influenced by phylogeny, but is not strictly correlated with hatchling maturity. Among the altricial orders, parrots have longer incubation periods than predicted on the basis of egg mass (eq. 5) (Bucher 1983; Saunders, Smith and Campbell 1984), but passerines have shorter incubation periods (Rahn and Ar 1974; Vleck and Vleck 1987). Similarly the incubation periods of precocial anseriform species are characteristically shorter than predicted by egg mass (Ricklefs 1987). It is suggested here that the shorter than predicted incubation period of king quail and the longer than predicted incubation period of cockatiel is an important influence on the ontogeny of $\dot{V}_{O2}$ in these species.

Oxygen consumption throughout incubation

The $\dot{V}_{O2}$ of king quail and cockatiel embryos increases exponentially up to IP at 90% of the incubation periods respectively (fig. 4-5, p.79-80). The pattern of increase in metabolism in both species is similar to that of altricial species (Vleck, Hoyt and Vleck 1979; Bucher 1983). The $\dot{V}_{O2}$ of king quail embryos does not plateau during the last 30% of the incubation period as typical of larger precocial species (Hoyt, Vleck and Vleck 1978; Vleck, Hoyt and Vleck 1979; D. Vleck, Vleck and Hoyt 1980; C. Vleck, Vleck and Hoyt 1980). Visser (1991) found that the $\dot{V}_{O2}$ of two charadriiform species increases almost exponentially throughout incubation, but $\dot{V}_{O2}$ plateaus briefly before pipping in two other species. The shape of the $\dot{V}_{O2}$ curve up to the PIP stage is determined by egg mass and incubation period. The inflection point of curves is later in

the incubation for precocial eggs of small mass and or shorter than predicted incubation periods.

The PIP $\dot{V}O_2$ of king quail embryos is identical to that predicted by Hoyt's (1987) model for precocial species (mean 80.9 ml O_2 day^{-1}). The PIP $\dot{V}O_2$ of cockatiel embryos is the same as that of the king quail, but is significantly lower than predicted for altricial species using the same model (<95% CI of oberved:predicted, Hoyt 1987). All the species of parrot for which the pattern of $\dot{V}O_2$ throughout incubation is known to have significantly lower PIP $\dot{V}O_2$ than other altricial species according to Hoyt's (1987) model. The observed:predicted of PIP $\dot{V}O_2$ of seven parrot species varies between 0.61 and 0.90. Bucher (1983) notes that the rate of increase in $\dot{V}O_2$ is not constant, although close to being exponential in shape, $\dot{V}O_2$ falls below an exponential curve prior to PIP and hatching. Other altricial species, two passerines and a pigeon species, similarly have $\dot{V}O_2$ above the fitted exponential curve in mid-incubation, but unlike parrots, $\dot{V}O_2$ during the paranatal period in these species is equal to or above the curve (Vleck, Hoyt and Vleck 1979). Vleck and Vleck (1987) consider that altricial species hatch earlier in the developmental sequence before $\dot{V}O_2$ is able to plateau. Cockatiel hatch with a higher degree of physiological precocity than other altricial species (see Chapter 4). It is suggested here that the higher degree of metabolic maturity achieved by cockatiel at hatching is the result of a relatively longer incubation period than non-psittaciform altricial species. $\dot{V}O_2$ falls below an exponential curve in smaller parrot species, including *A. roseicollis*, prior to pipping and hatching (Bucher 1983). The lower metabolic intensity of this species during late incubation and early posthatching period is correlated with the acquisition of thermogenic powers earlier than other altricial species, but later than that of the cockatiel (see Chapter 4).

Allometric relationships between PIP $\dot{V}O_2$ and egg mass

The PIP $\dot{V}O_2$ of avian embryos is significantly related to initial egg mass (fig. 6, p.82) (Hoyt and Rahn 1980; Rahn and Paganelli 1990). Bucher (1983) noted that small parrot species have lower than predicted PIP $\dot{V}O_2$, but larger species have higher PIP $\dot{V}O_2$, although parrots in general are lower than expectations. Visser (1991) found that several species of precocial charadriiforms have significantly higher PIP $\dot{V}O_2$ than predicted by Rahn and Paganelli (1990). Incubation period explains a significant amount of the variation in PIP $\dot{V}O_2$ after egg mass is taken into account (fig. 7). Galliform embryos have higher PIP $\dot{V}O_2$ and shorter incubation periods on average than expected on the basis of egg mass. Exceptionally, the two megapode species included have higher PIP $\dot{V}O_2$ and longer incubations periods associated with their unique mode of underground incubation (Vleck, Vleck and Seymour 1984).

Parrot embryos are variable, but generally have longer incubation periods and lower PIP $\dot{V}O_2$ than predicted on the basis of egg mass. The three larger species of parrot, including *Nymphicus hollandicus*, *Enicognathus ferruginous* and *Bulborhynchus lineola* have PIP $\dot{V}O_2$ residuals which are not different from zero, but only the cockatiel has a shorter incubation period than the other parrot species included.

PIP $\dot{V}O_2$ is not strictly correlated with hatchling type, although precocial orders such as Galliformes, Anseriformes, and Charadriiformes (Families Scolopacidae and Charadriidae) have higher PIP $\dot{V}O_2$, and altricial and semi-altricial orders such as Psittaciformes, Ciconiiformes have lower PIP $\dot{V}O_2$. Other orders appear to contradict this trend, such as Passeriformes, which have high PIP $\dot{V}O_2$ for altricial species, and the more precocial groups such as the ratites and Procellariiformes, and the semi-precocial Sphenisciformes have lower PIP $\dot{V}O_2$. Therefore phylogeny is likely to be more important in explaining variation in PIP $\dot{V}O_2$ than hatchling maturity.

Partial pressures of O_2 and CO_2 in the aircell of eggs

As $\dot{V}O_2$ of king quail and cockatiel embryos increases during development, P_{AO_2} decreases and P_{ACO_2} increases exponentially (fig. 8-12, p.84-87). Partial pressures of CO_2 and O_2 reached 40 torr and 110 torr at PIP stage in king quail, but only 30 torr and 125 torr in the cockatiel. However, only a small number of measurements with cockatiel embryos were made immediately before IP, and so gas tensions of CO_2 may be higher and O_2 lower at PIP. The average gas tensions in the aircell of most species at PIP are P_{ACO_2} of 37 and P_{AO_2} of 104 torr, and are thought to stimulate hatching (Rahn, Paganelli and Ar 1974; Rahn and Paganelli 1990). The predicted gas tensions in king quail eggs are comparable to most species, but the P_{ACO_2} is low and P_{AO_2} is high in the cockatiel egg. However, these tensions are not exceptional (Rahn, Paganelli and Ar 1974) and are attributed to the higher than predicted G_{H_2O} of cockatiel eggs. Despite the limited number of measurements in this study, king quail eggs with a G_{H_2O} <2.0 mg H_2O day^{-1} $torr^{-1}$ have lower P_{AO_2} and $\dot{V}O_2$, and higher P_{ACO_2} than in eggs with G_{H_2O} >2.0 mg H_2O $day^{-1}torr^{-1}$ from mid-incubation to IP. The results suggest that gas exchange across the eggshell becomes conductance-limited when the rate of increase in $\dot{V}O_2$ is greatest. Ancel and Visschedijk (1993) found that the difference in $\dot{V}O_2$ is greatest between low and high conductance guineafowl, *Numida meleagris*, eggs during the plateau phase, but the effect of a shell conductance limitation on egg respiration is distinct at 65% of the incubation period, before $\dot{V}O_2$ plateaus. Although the eggs of many altricial and precocial species vary in G_{H_2O} by a factor of up to 4.3-fold (Carey 1986), Bucher and Barnhart (1984) found that $\dot{V}O_2$ is not significantly different between eggs of low, intermediate and high G_{H_2O}. Whittow and Tazawa (1991) also suggest that altricial embryos do not experience a conductance-limitation on $\dot{V}O_2$ during incubation. King

quail embryos do not experience a conductance limitation on $\dot{V}O_2$ during incubation, but in the second-half of the incubation period eggshell conductance does appear to slow the rate of increase in $\dot{V}O_2$ in the same way that it affects *N. meleagris* eggs before $\dot{V}O_2$ plateaus. It is likely that the increasing variability in $\dot{V}O_2$ of other precocial species during late incubation is the result of differences in G_{H2O} (Vleck, Hoyt and Vleck (1979).

The increased G_{H2O} of cockatiel eggs with star-fractures (at IP) in the eggshell results in the reversal in the direction of change of aircell gas tensions during the paranatal period. During this period P_{ACO2} decreases from 30 torr to 10 torr and P_{AO2} increases from 120 torr to 140 torr. Bucher and Barnhart (1984) report the same pattern of reversal of gas tensions in *A. roseicollis* during the paranatal period, but the lower tensions of O_2 and higher tensions of CO_2 are reached prior to the reversal in that species, which is attributed to the lower than predicted gas conductance of the eggshell. In contrast the gas conductance of the cockatiel eggshell is higher than predicted (fig. 2, p.75). The reversal of gas tensions in eggs of *A. roseicollis* prior to internal pipping was attributed to an increase in G_{H2O} associated with embryo movements within the egg. However, the increase G_{H2O} of eggshells of cockatiel eggs was attributed to star-fractures at the same time they were presumed to have IP.

Cost of development

The estimated cost of development (TOT) for king quail embryos is 13.9 kJ. The cost of development of king quail estimated from the difference between energy in the egg and total hatchling energy is 33.9% of egg energy (100 - 49.5 - 16.6 = 33.9%, from Section 3.1, p.61). The TOT estimated from integration of $\dot{V}O_2$ throughout incubation, in this section, is 34.7% of egg energy (13.9 kJ ÷ 40.11 kJ in eggs used for $\dot{V}O_2$). So the two estimates of TOT are comparable. The predicted TOT for a precocial embryo according to Vleck and Vleck (1987) on the basis of egg mass is similar to the estimate obtained here, but it is higher the predicted by Hoyt's (1987) model. The reason for the difference between predicted values is that values predicted by Vleck and Vleck (1987) are based solely on a linear correlation between measured TOT and egg mass for a small number of species, the confidence limits of which were wide. Hoyt's (1987) model is dependent on the assumption that all precocial embryos have a similar pattern of growth which can be estimated from dry hatchling mass and the known incubation period. However, it is suggested in this study that precocial embryos from small eggs hatch earlier in the developmental sequence. As a result the growth curve and $\dot{V}O_2$ appear to be shifted to the left (see Section 3.3 fig. 11, p.113). In comparison king quail are larger than the predicted embryo mass, throughout the incubation period, and consequently embryonic $\dot{V}O_2$ and TOT is higher. For that reason Hoyt's (1987) model is more likely to be sensitive to deviations from the predicted patterns of embryonic growth.

The TOT of cockatiel embryos estimated from integration of $\dot{V}O_2$ is 14.2 kJ, or 50.2% of egg energy (14.2 ÷ 28.3 kJ). TOT estimates based on estimated calorific content of eggs and hatchlings are too variable, considering the small number of samples in this study, and thus are not compared with TOT estimates obtained by integration of $\dot{V}O_2$. The estimated TOT from integration of $\dot{V}O_2$ is significantly higher than predicted by either Vleck and Vleck (1987) or Hoyt (1987). The higher cost of development of the cockatiel and another parrot, *A. roseicollis* (Bucher 1983), is likely to be characteristic of parrots in general. The incubation periods of parrots are significantly longer than other altricial species (Bucher 1983). The embryos of pelagic seabirds also have longer incubation periods and consequently have higher maintenance costs and higher TOT than predicted by egg mass (Vleck and Kenagy 1980). Therefore the predicted TOT according to Vleck and Vleck (1987) is likely to be underestimated for parrot species. Hoyt's model takes into account the longer incubation period of the cockatiel embryo, but the growth curve is shifted to the left of the predicted pattern (see Section 3.3 fig. 12, p.114). The higher TOT of cockatiel is attributed to the larger embryo mass maintained early in the incubation period.

Oxygen consumption rates during gradual cooling

King quail embryos do not significantly increase $\dot{V}O_2$ during short term (<30 min) or prolonged (1 h) gradual cooling (fig. 14, p.89). Embryos between day 13 and 15 (age 79 and 91% of incubation, respectively) are capable of sustaining $\dot{V}O_2$ initially during cooling tests, but $\dot{V}O_2$ decreases with T_a below 32 °C, even in EP embryos. Tazawa et al. (1988b) suggested that the development of endothermy in birds takes place in several stages. The first stage, which is common to all hatchling types throughout most of the incubation period, is characterised by the lack of thermoregulatory control and metabolism is temperature dependent or 'Arrhenius-limited'. However, precocial species make the transition into the second stage, or 'oxygen conductance-limited' stage, before they leave the egg. Although precocial embryos are still poikilothermic, thermoregulatory responses are evident in pre-pipping chicken and duck embryos, which are constrained in the uptake of oxygen by the pre-determined low eggshell conductance (Tazawa et al. 1988b; Tazawa et al. 1989b; Kuroda et al. 1990; Nichelmann, Lange and Paulick 1994). Less precocious species and altricial species do not appear to be conductance-limited, nor are thermogenic responses of embryos evident before hatching (Kuroda et al. 1990; Mathiu, Whittow and Dawson 1992; Mathiu, Dawson and Whittow 1994). After pipping precocial species are no longer limited by chorioallantoic gas exchange and are capable of increasing heat production in defence of body temperature, but are 'power-limited' (stage 3). In contrast altricial species are poikilothermic at

hatching and only become homeothermic later in the nestling period (Whittow and Tazawa 1991; Olson 1992).

Small king quail eggs cool rapidly (fig. 13, p.88), but late-incubation embryos sustain $\dot{V}O_2$ initially as T_{egg} decreases, although no significant increases in $\dot{V}O_2$ occurred. It is considered that king quail embryos do not face an oxygen-conductance limitation which has been suggested to occur in larger precocial species (Tazawa et al. 1988b; Ancel and Visschedijk 1993), because thermoneutral $\dot{V}O_2$ does not plateau at the end of incubation, and eggshell gas conductance is significantly higher than expected (fig. 1, p.74). Since $\dot{V}O_2$ at the end of incubation is less than the conductance limit of the eggshell, $\dot{V}O_2$ should increase in response to decreasing T_{egg} if thermoregulatory control mechanisms are operative. And if the king quail is as precocious as larger chickens and ducks, then thermogenic responses should be evident after internal pipping when oxygen uptake can be increased further. However, it is suggested here that king quail hatch earlier in their developmental sequence, and that hatchlings enter stage 3 of homeothermy during hatching in a few individuals, and in many other individuals only several days after hatching (see Chapter 5).

Booth (1985) considers that the greater thermoregulatory abilities of malleefowl, *Leipoa ocellata*, hatchlings over the related brush turkey, *Alectura lathami*, hatchlings (both about 114 g) is correlated with a significantly longer incubation period. Dietz and van Kampen (1994) now believe that the greater thermoregulatory abilities of guinea fowl, *N. meleagris*, hatchlings over turkey, *Meleagris gallopavo*, hatchlings is similarly related to differences in incubation period. At 2 h after hatch, guinea fowl have higher mass-specific $\dot{V}O_2$ and T_b before and after cooling tests (20 °C) than the larger turkey hatchlings. The thermoregulatory abilities of both species are equal at the end of the first day after hatch. However, the guinea fowl achieves its highest degree of homeothermy within a few hours of hatching, whereas the turkey takes longer to achieve the same abilities. Dietz and van Kampen (1994) attribute the weaker thermoregulatory abilities of turkeys to their shorter than predicted incubation periods.

In this study it was predicted that the ability of precocial embryos to increase heat production at the end of incubation decreases, and the rate of heat loss increases with decreasing egg mass. Therefore the T_a at which thermogenesis can no longer balance heat loss will be closer to the incubation temperature. Although king quail do not increase $\dot{V}O_2$ during gradual cooling, they are able to sustain $\dot{V}O_2$. The estimated T_{egg} at which $\dot{V}O_2$ is no longer sustained and subsequently decreases is 34-35 °C, which is only 4 °C lower than the incubation temperature. In comparison, the domestic fowl is able to sustain or increase $\dot{V}O_2$ down to T_a of 34.5 °C (Tazawa et al. 1988b).

The incubation period of the king quail is shorter than predicted by allometry, and is one of the shortest developmental periods known for a precocial species. Embryonic growth of king quail only starts to plateau when hatching is initiated, and before the

embryo reaches an oxygen-conductance limitation. It was suggested at the start of this section that small precocial embryos may not be as mature at hatching compared to larger species because development time is shorter. It is concluded from these results that on average thermogenic responses are acquired later in the developmental period of king quail relative to the event of hatching.

Section 3.3. Patterns of embryonic growth

Introduction

The ontogeny of growth and metabolism differs between precocial and altricial species. Altricial embryos constantly increase in mass throughout the incubation period, whereas the mass of precocial embryos increases exponentially during the first 60-70 % of the incubation period and then growth rate declines as embryos approach hatchling mass at 80% of the incubation period (Hoyt et al. 1978; Vleck et. al. 1979; C. Vleck et al. 1980; D. Vleck et al. 1980; Bucher 1983; Bucher and Bartholomew 1984; Ricklefs 1987). The metabolic rates of all embryos increases exponentially over the first 60% of the incubation period, and then the rate of increase declines in precocial species (plateau phase) but continues to increase exponentially in altricial species (Hoyt et al. 1978; C. Vleck et al. 1980; D. Vleck et al. 1980; Bucher 1983; Vleck and Vleck 1987; Hoyt 1987). Embryonic metabolism is the sum of both the energy required to synthesise new tissues and the energy required to maintain existing tissue functions.

Some researchers think that the plateau in $\dot{V}O_2$ of precocial species is a consequence of decreases in the relative growth rate and therefore the energy required for growth, which reduces the total oxygen requirements of the embryo (Vleck et al. 1979; C. Vleck, Vleck and Hoyt 1980; D. Vleck, Vleck and Hoyt 1980; Vleck and Vleck 1987). However, others believe that shell gas conductance limits the oxygen uptake of the embryo during late incubation (Wangensteen and Rahn 1970/71; Tullett and Deeming 1982; Burton and Tullett 1983; Visschedijk, Tazawa and Piiper 1985; Ancel and Visschedijk 1993). For eggs which have a wide variation in shell gas conductance, the highest PIP $\dot{V}O_2$ and hatchability is in eggs with intermediate conductance (Visschedijk, Tazawa and Piiper 1985). Both PIP $\dot{V}O_2$ and hatchability decrease at low and high gas conductances. Similarly Ancel and Visschedijk (1993) found that low conductance guinea fowl, *Numida meleagris*, eggs also have lower PIP $\dot{V}O_2$. Low conductance chicken eggs not only have lower PIP $\dot{V}O_2$, but the embryonic growth rate is slower (Burton and Tullet 1983). High conductance eggs also have slower growth rates and

lower hatchling water contents due to excessive water loss (Tullet and Burton 1982; Okuda and Tazawa 1988). Shell porosity appears to be primarily adapted to regulate water loss (Vleck, Hoyt and Vleck 1979; Ar and Rahn 1980; D. Vleck, Vleck and Hoyt 1980). Although, it is suggested by Whittow and Tazawa (1991) that another function of egg shell porosity might be to limit the energy consumption of precocial embryos. If precocial embryos achieved homeothermy within the egg, the parent would need to provision the egg with sufficient energy to develop and regulate body temperature, and this would require a 'prediction' of the thermoregulatory costs the chick will incur.

The incubation period of all avian embryos increases with egg mass (Ar and Rahn 1974). Embryonic growth of precocial species as a fraction of hatchling mass, is close to complete at about 80% of the incubation period (Vleck, Hoyt and Vleck 1979; Hoyt 1987). During late incubation precocial embryos develop thermogenic responses (Steen and Gabrielsen 1988; Tazawa et al. 1989b; Kuroda et al. 1990), and other functions also mature during this period (D. Vleck, Vleck and Hoyt 1980). Therefore it is expected that with decreasing egg mass, incubation period decreases and embryos have less time to mature prior to hatching. Vleck and Vleck (1987) consider that altricial embryos have evolved as the result of an earlier hatching event in the developmental sequence.

Some believe that embryonic growth of precocial species is best described by a sigmoidal curve (logistic function) and altricial species by an exponential curve (C. Vleck, Vleck and Hoyt 1980). Hoyt (1987) has provided a model for embryonic metabolism, to predict $\dot{V}O_2$ at PIP and the total cost of development (TOT), which is based upon the use of logistic and exponential functions to describe embryonic growth rates. The predicted values of PIP $\dot{V}O_2$ and TOT from this model are estimated in section 3.2 for the precocial king quail and altricial cockatiel.

Ricklefs (1987) believes the growth rates of all embryos are similar from a few days of age to shortly before hatching, when the growth rates of precocial species declines, but when the growth rates of altricial species increases. Apart from the beginning and end of incubation, the growth rates of all embryos are best described by parabolic functions as follows,

$$\frac{dM}{dt} = aM^b$$

where b is the rate of decline in relative growth rate with increasing embryo mass (M), and a is the factorial change in growth rate at all ages. Ricklefs (1987) advocates the use of a uniform growth model which is applied to all species for comparative purposes. He is critical of the sigmoidal functions (logisitic and Gompertz equations) being applied to embryonic growth because fitted asymptotes from such equations are up to double the hatchling mass, and are therefore not related to changes in growth rate. Deviations from the parabolic function are usually restricted to the period immediately before hatching in some species (Galliformes and Anseriformes), whereas deviations from sigmoid curves

occur throughout incubation. The constants *a* and *b* obtained from many families of birds are similar for most species, independent of hatchling type (Ricklefs 1987). He notes that values of *a*, *b* or both tend to increase with egg mass in several avian families, and therefore the decrease in growth rate occurs earlier in the development in smaller species (*b* decreases). Departures from expected incubation periods can be explained by comparing the constant *a* and *b* to other species.

Ricklefs (1979a,b) has suggested that cell proliferation or growth is incompatible with tissue differentiation or maturation during the posthatching period. Similarly declining growth rate in precocial embryos is paralleled by increasing tissue differentiation and the accumulation of solids in embryonic tissues (Ricklefs 1987). He demonstrates that the rate of increase in solid matter in the embryo is directly related to the rate of decrease in growth rate (*b*) of the embryo with respect to increasing mass. It is suggested here from Ricklef's work that with decreasing egg mass the constant *b* will decrease, and therefore growth rate will decline earlier in development.

In this section the pattern of growth for both species is determined by measuring wet and dry mass of embryos. The relationship between growth rate and incubation period is then compared with the patterns reported previously (C. Vleck, Vleck and Hoyt 1980; Hoyt 1987; Ricklefs 1987). Several predictions are tested in this study; 1) that precocial embryos from small eggs also hatch earlier in the developmental sequence, and as a result embryonic metabolism does not plateau in late incubation before pipping, and 2) that absolute embryonic growth rates of small precocial species will start to decrease later in the incubation period.

Materials and Methods

King quail and cockatiel eggs which were incubated for at least three days and subsequently abandoned by the parent were used to determine embryo growth. Most embryos were of known age, and the age of remaining embryos was determined by interpolating from the body measurements of embryos of known age. Eggs were measured for length, diameter and mass, then opened at the blunt pole. Embryos which had dried, were infected or abnormally developed were not included. It was noted if embryos had internally-pipped (IP) into the aircell.

All embryos were measured for head length and width, culmen, shoulder to tail, hand, tarsus and middle-toe to 0.1 mm using plastic vernier calipers, except cockatiel head length was not measured (see fig. 2, Chapter 2). Embryonic tissue, yolk and albumen were quickly separated and weighed to the nearest 0.0001 g before being dried at 70 °C to constant mass. Embryo samples were maintained in a desiccator until their energy content was determined by bomb calorimetry.

Wet embryonic mass and growth measurements were then fitted with three growth functions: the Gompertz function (eq. 1), an exponential equation (eq. 2) and a parabolic equation (eq. 3).

$$\text{Mass (g)} = A \cdot e^{(-e(-K_G(t - w_i)))} \qquad \text{(eq. 1)}$$

where A is the fitted asymptotic mass (g), K_G is the constant directly proportional to the rate of growth (day^{-1}), t is the day of incubation, w_i is the inflection point (day).

$$\text{Mass (g)} = e^{(a + bt)} \qquad \text{(eq. 2)}$$

where a is the y-intercept and b is the exponent of the relationship, and t is the day of incubation.

$$\text{Mass (g)} = a^* \cdot (t - i)^{b^*} \qquad \text{(eq. 3)}$$

where a* and b* are fitted constants, t is the day of incubation and *i* is the time lag before the onset of parabolic growth (Ricklefs 1987). Growth rate can then be calculated according to equation 4 as follows,

$$\frac{dM}{dt} = aM^b \qquad \text{(eq. 4)}$$

where *a* is the factorial change in growth rate at all ages, and *b* is the rate of decline in relative growth rate with increasing embryo mass (M).

Results

Embryonic growth in king quail and cockatiel

Wet mass of embryos

Total embryo mass increased constantly with day of incubation, without any significant decrease in growth rate before hatching (fig. 1a). Fitted logistic and Gompertz equations were both highly significant (Table 1, p.107), though the logistic equation overestimated embryo mass in the first half of the incubation period more than the Gompertz equation. The upper range of hatchling masses found exceeded total embryo mass of pipped embryos by as much as 1g. The broader range of hatchling masses

reflects a larger range of egg masses than the sample of eggs which the embryos were removed from. The fitted sigmoidal growth equations, which were based on both embryos and hatchlings, underestimated embryo mass in mid-incubation, and only started to decrease after the day of hatch (fig. 1a).

The yolk-free embryo mass of quail increased with day of incubation in a sigmoidal manner (fig. 1b). A significant relationship was fitted by Gompertz curve (Table 1). The fitted asymptotic embryo mass of 3.71 g exceeded the average yolk-free hatchling mass (2.83 ± 0.12 g, n=9 including EP embryos) by 31%. Growth rate of yolk-free embryo mass visibly decreased after day 11 of incubation, but growth rate did not plateau.

Fewer cockatiel embryos were measured, but total embryo mass increased constantly with day of incubation (fig. 2a). A fitted Gompertz curve was highly significant (Table 2, p.109), but the fitted asymptotic mass greatly exceeded hatchling masses. However, an exponential curve could not be fitted because of the variance in embryo mass at the end of incubation.

Growth of body measurements

The increase in length of all body parameters of king quail embryos was exponential in the first 10 days of incubation, and then the growth rates declined (fig. 3-5). Significant growth equations were fitted to all body paramaters, except head width (Table 1). Fitted growth constants were highest for C, then Ha and Ta (Table 1). The lowest growth constant was for ST. Growth of most parameters was nearly complete by day 10 (60% of incubation), except ST and To, which did not plateau before quail hatched (fig. 3-5).

Growth of body parameters in cockatiel embryos was similar to that of the king quail. Growth of all parameters was nearly complete by day 12 of incubation, except ST (fig. 6-7). Despite the plateau in most body parameters, significant Gompertz curves could not be fitted to Ta, HW and C. Significant exponential curves were fitted to these parameters, but these curves may be an artefact because of the lack of embryo measurements in the first half of the incubation period (Table 2).

Dry mass of embryos

Dry mass of yolk-free quail embryos increased with day of incubation at a slower rate than wet mass, as reflected by the growth constants of fitted growth equations (Table 1), but the pattern of increase in mass was the same (fig. 8). The asymptote of the fitted equation for dry mass also exceeded the dry mass of hatchling quail (0.668 ± 0.059 g, n=9) by 39%. The estimated dry mass of quail hatchling was 0.72 g. Dry mass of cockatiel embryos increased constantly until day 15 of incubation, and then the rate of

increase in dry mass slowed (fig. 9). The dry mass of cockatiel hatchlings was lower than that of king quail (0.61 and 0.67 g respectively), although the hatchling masses were similar.

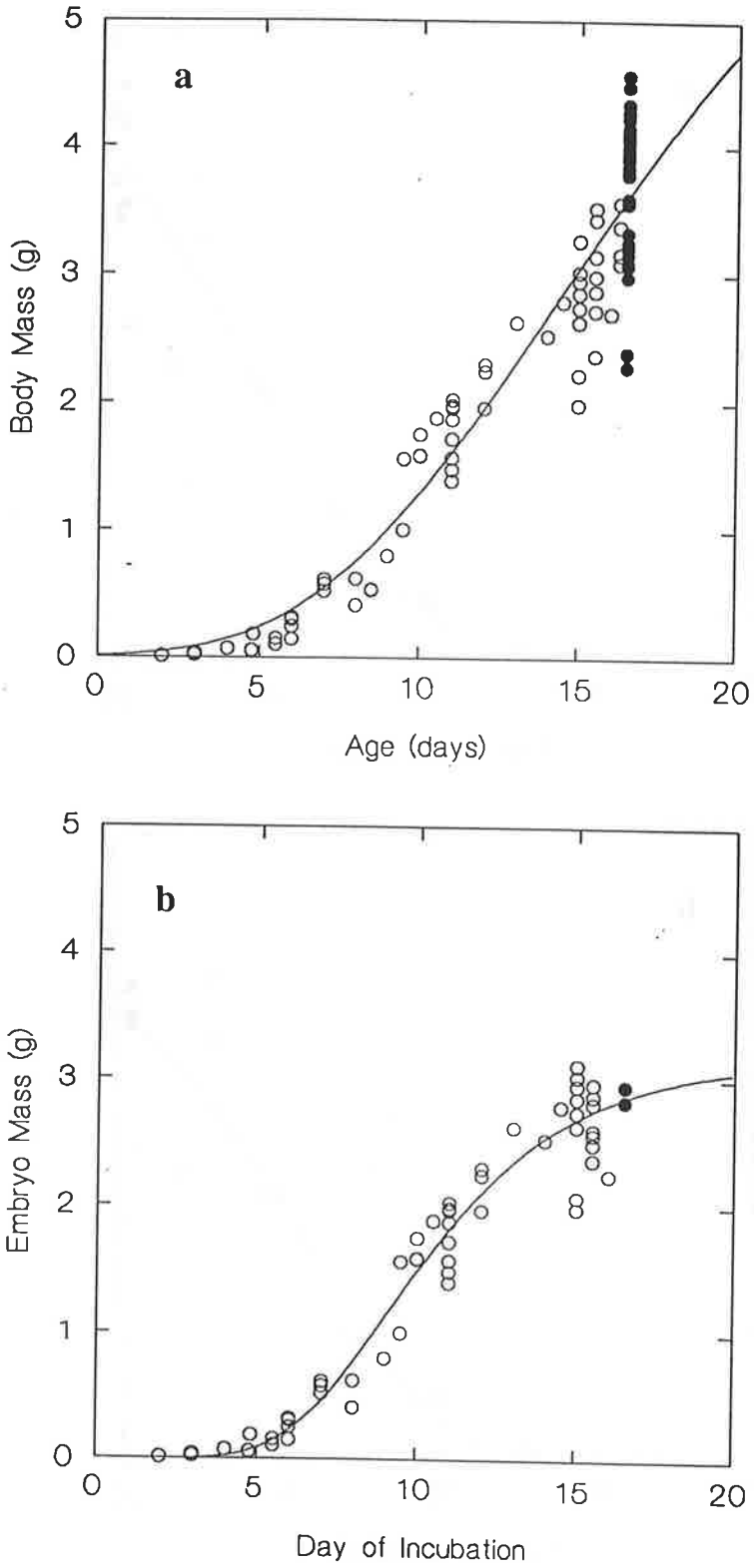

Fig. 1. Relationship between embryo mass and day of incubation of king quail. **a.** total embryo mass (including yolk reserve). **b.** yolk-free embryo mass. Solid lines indicate significant relationships (Table 1). *Open symbols*: embryos (n=71), *filled symbols*: hatchlings (n=26) (Yolk-free mass was only determined for two newly hatched chicks).

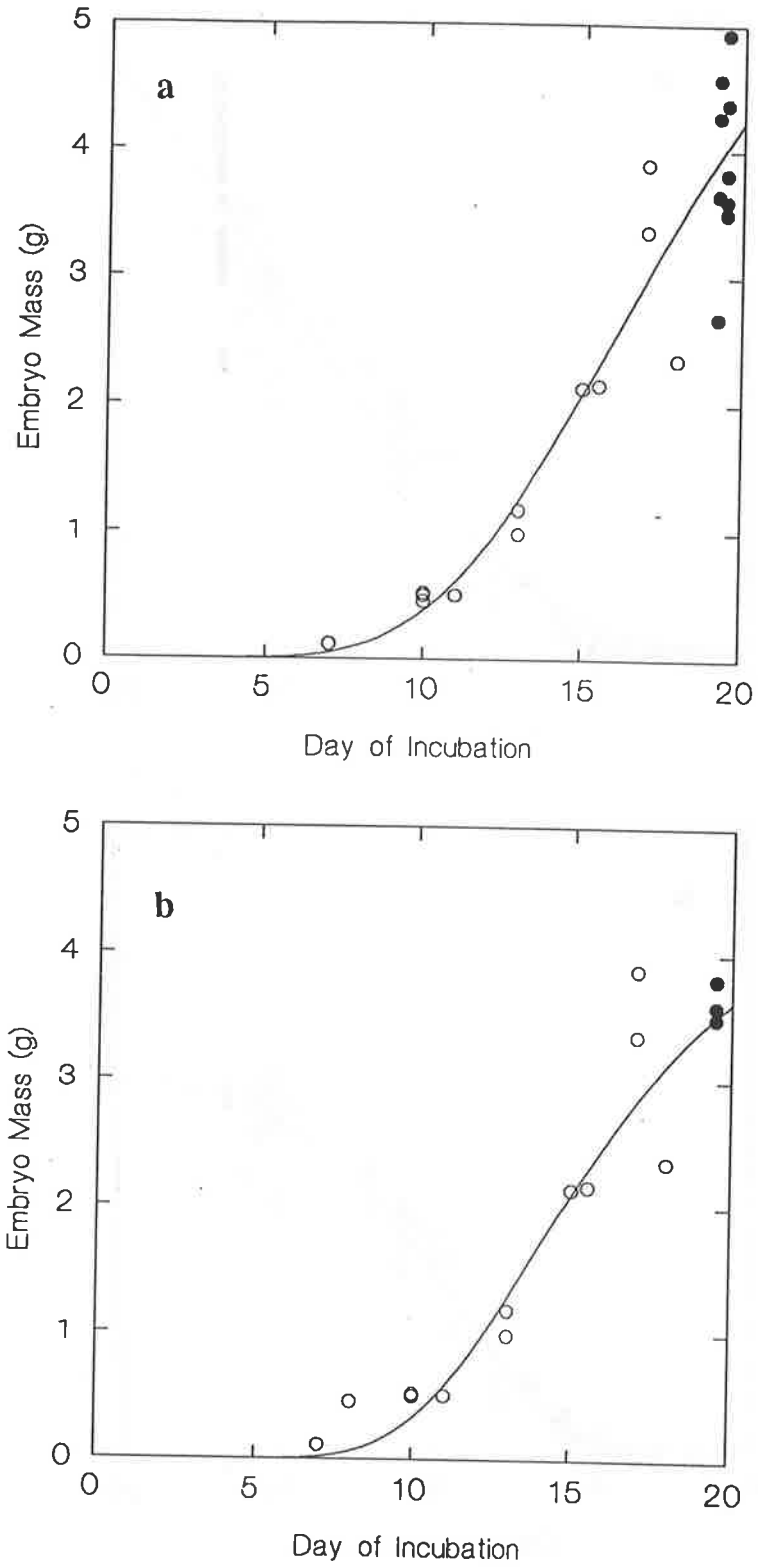

Fig. 2. Relationship between embryo mass and day of incubation of cockatiel. **a.** total embryo mass (including yolk reserve). **b.** yolk-free embryo mass. Solid lines indicate significant relationships (Table 1). *Open symbols*: embryos (n=12), *filled symbols*: hatchlings (n=11).

Table 1. Gompertz functions for the relationships between growth parameters and day of incubation for king quail embryos. Fitted equations are defined in text (eq. 1), and included hatchlings (n=23) except where noted. True embryo mass (g) is the yolk-free embryo mass (wet and dry), and total embryo mass (wet) includes yolk reserve. All body measurements are in mm, K_G is day^{-1} and w_i in days.

Growth Parameter	A	K_G	w_i	r^2	F	P
KING QUAIL						
True Embryo (wet)	3.17	0.309	9.1	0.984	63.375	0.001
True Embryo (dry)	0.93	0.248	11.0	0.969	31.389	0.001
Total Embryo	7.54	0.575	16.3	0.980	50.045	0.001
head length	17.33	0.248	4.9	0.996	228.827	0.001
head width	not possible					
culmen	4.99	0.393	6.3	0.988	79.229	0.001
shoulder-tail	27.25	0.190	6.7	0.994	160.873	0.001
hand	9.04	0.381	6.7	0.990	103.429	0.001
tarsus	12.47	0.350	7.7	0.992	125.418	0.001
middle-toe	12.34	0.299	8.0	0.992	121.891	0.001

Hoyt (1987) provided a model which enables the estimation of PIP $\dot{V}O_2$ and TOT on the basis of initial egg mass. It was assumed in Hoyt's (1987) study that increases in dry mass of precocial species are described by a sigmoidal function, and that of altricial species by an exponential equation. In comparison to the predicted pattern of growth of precocial species, the king quail was significantly larger throughout the incubation period after 30% of the incubation period (fig. 10). The integrated area under the quail growth curve in this study was 34.1% higher than the model. Similarly cockatiel mass was larger than predicted by Hoyt's (1987) model after 40% of the incubation period (fig. 11). The integrated area under the cockatiel growth curve in this study was 56.4% higher than the model. Consequently the predicted TOT using Hoyt's (1987) model were lower than estimated in this study, but this difference was not significant in the king quail (see Section 3.2).

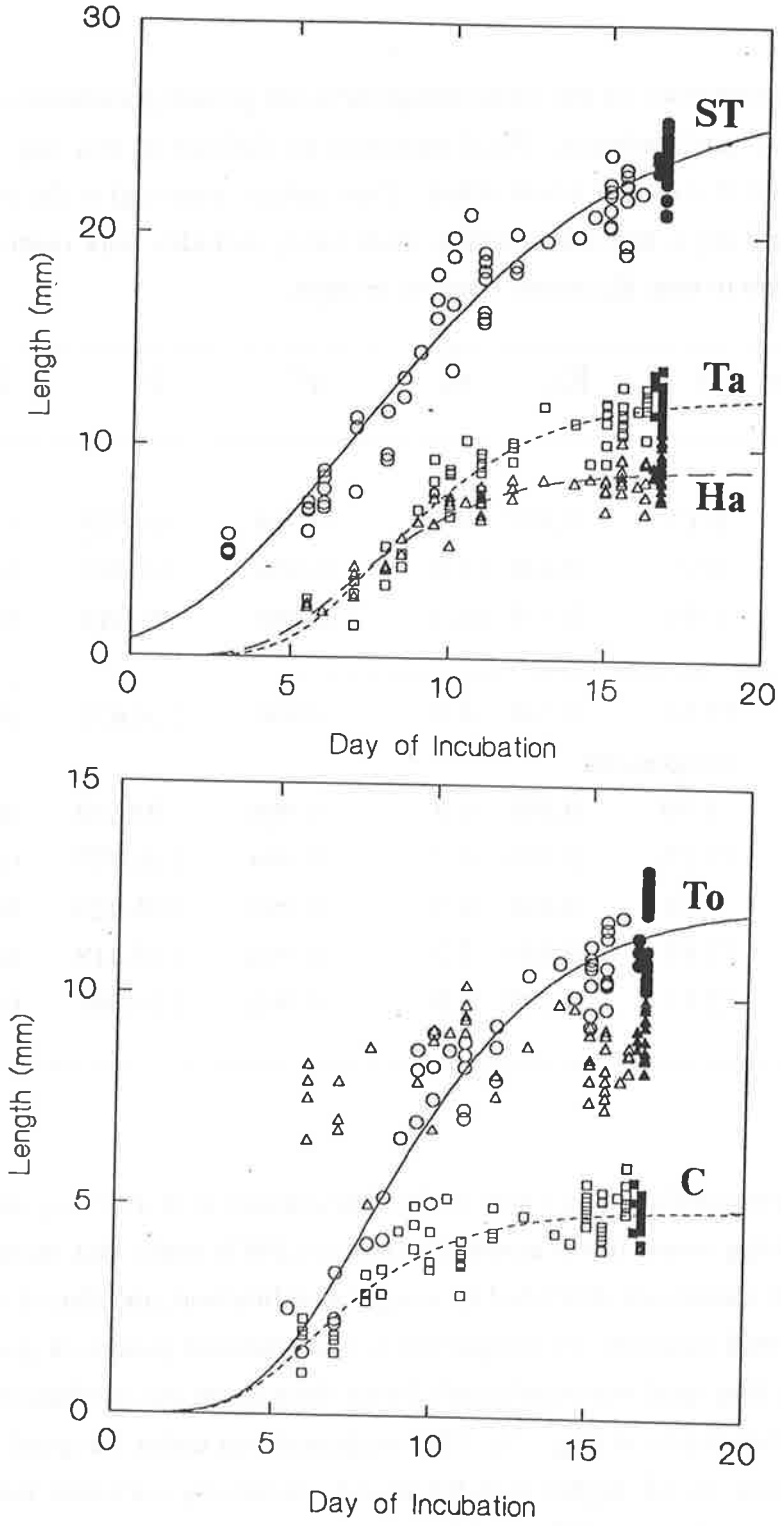

Fig. 3-4. Relationship between body parameters of king quail embryos (*open*, n=61) and hatchlings (*filled*, n=26) and day of incubation. Lines indicate significant relationships listed in Table 1. Symbols in figures refer to body parameters shoulder-tail (ST), hand (Ha), tarsus (Ta), middle-toe (To) and culmen (C).

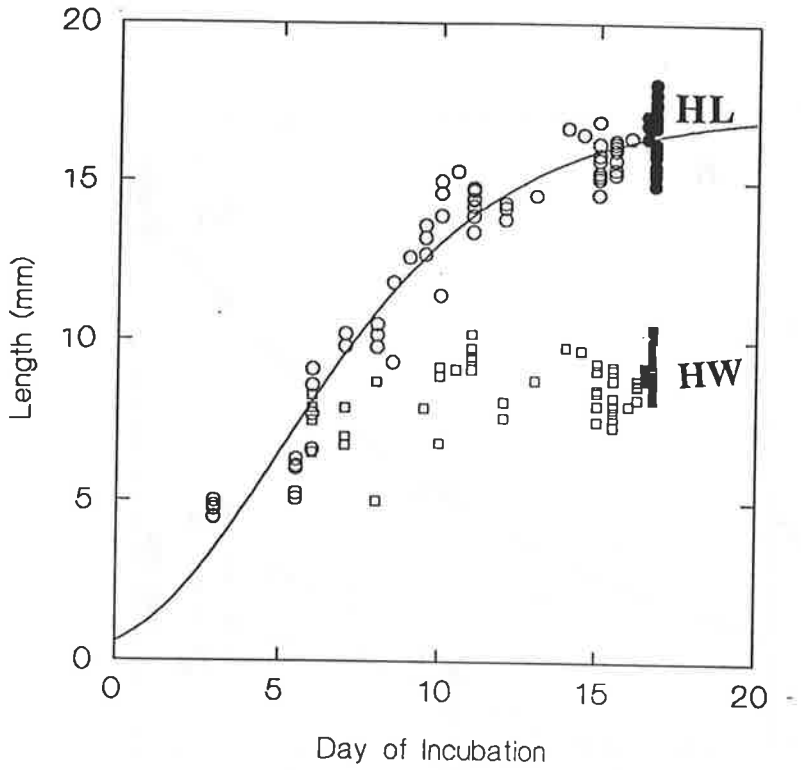

Fig. 5. Same as figures 3-4. Symbols refer to body parameters head width (HW) and head length (HL).

Table 2. Gompertz and exponential functions for the relationships between growth parameters and day of incubation for cockatiel embryos. Fitted equations are defined in text (eq. 1-2), and included hatchlings (n=11) except where noted. True embryo mass (g) is the yolk-free embryo mass (wet and dry), and total embryo mass (wet) includes yolk reserve. All body measurements are in mm, K_G is day^{-1} and w_i in days.

Gompertz curves	A	K_G	w_i	r^2	F	P
True Embryo (wet)	4.69	0.243	13.9	0.975	39.625	0.001
True Embryo (dry)	0.85	0.235	14.9	0.990	99.364	0.001
Total Embryo	6.95	0.176	16.0	0.966	28.840	0.001
hand	9.83	0.320	9.9	0.996	236.852	0.001
tarsus	11.58	0.118	13.2	0.993	138.743	0.001
middle-toe	7.10	0.359	10.1	0.994	159.812	0.001
Exponential Curves	**a**	**b**		**r^2**	**F**	**P**
head width	1.596	0.038		0.995	211.262	0.001
culmen	0.450	0.080		0.987	77.272	0.001
shoulder-tail	1.646	0.083		0.998	609.456	0.001

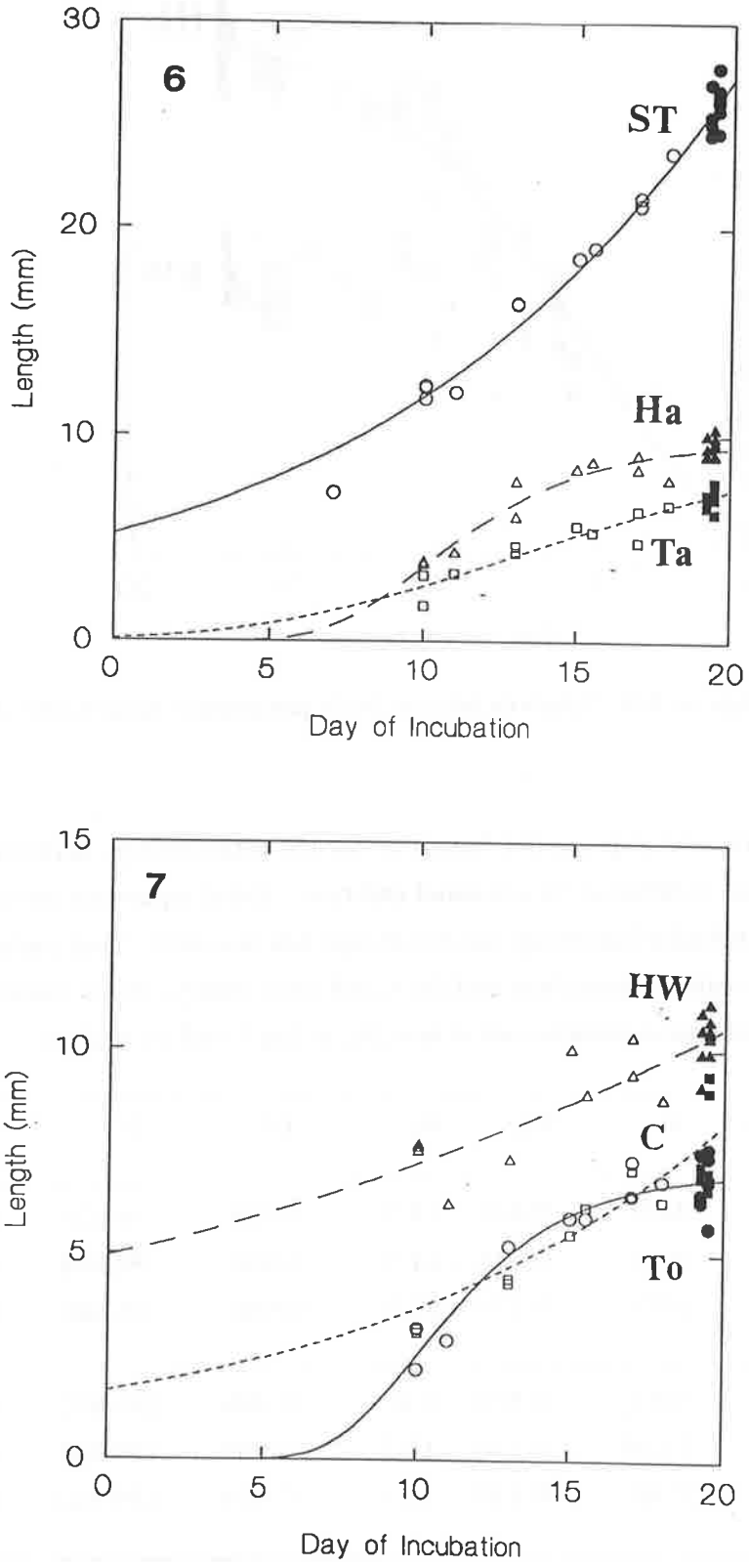

Fig. 6-7. Relationship between body parameters of cockatiel embryos (*open*, n=12) and hatchlings (*filled*, n=11) and day of incubation. Lines indicate significant relationships listed in Table 2. Symbols in figures refer to body parameters shoulder-tail (ST), hand (Ha), tarsus (Ta), middle-toe (To), culmen (C), head width (HW) and head length (HL).

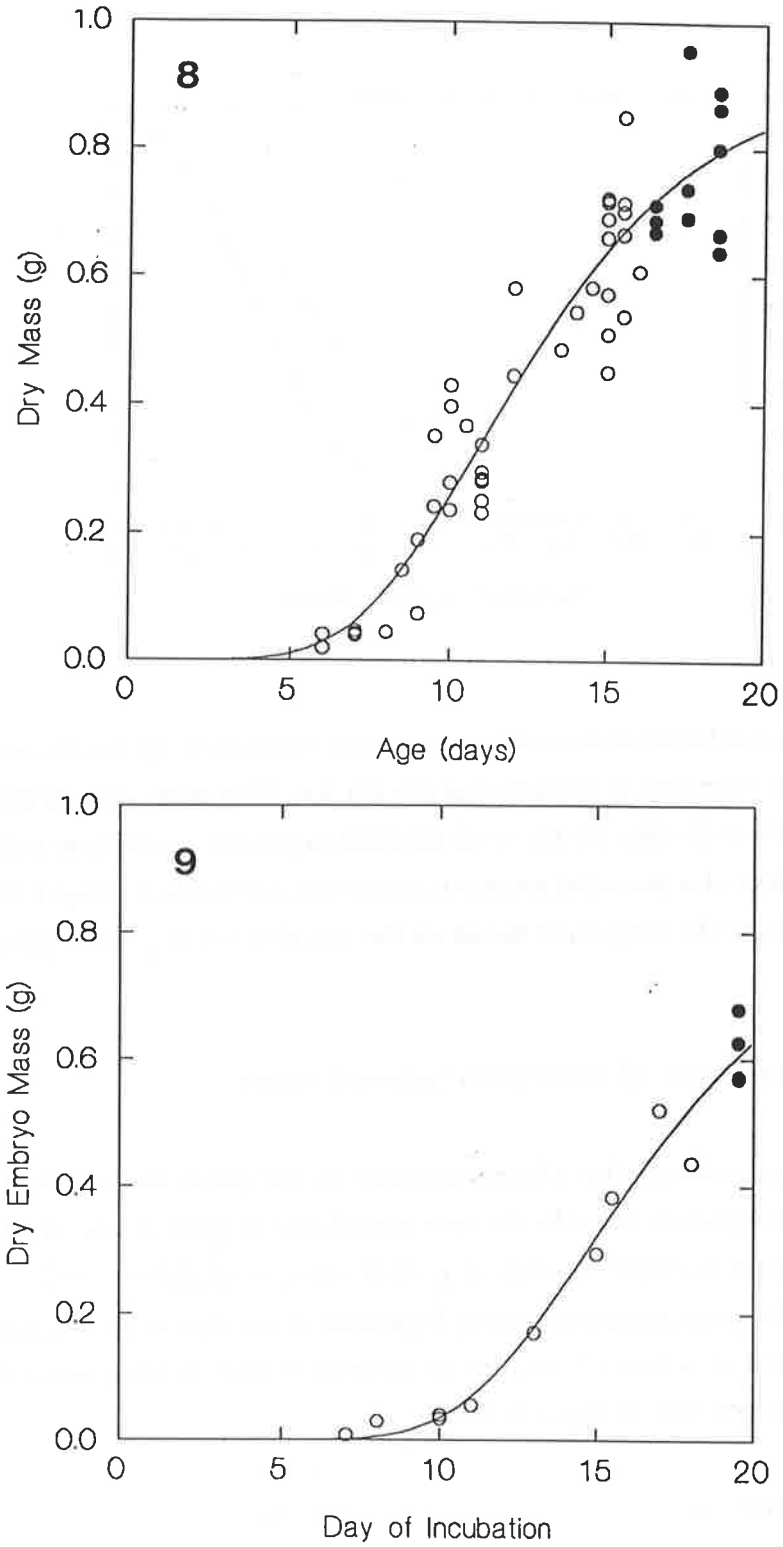

Fig. 8-9. Relationship between dry embryo mass and day of incubation in the king quail (fig. 8) and the cockatiel (fig. 9). Solid lines indicates a significant relationship in Table 1. *Open symbols*: embryos (quail n=61, cockatiel n=12), *filled symbols*: hatchlings (hatchlings for both species n=3) and chicks up to 2 days old (quail only n=8).

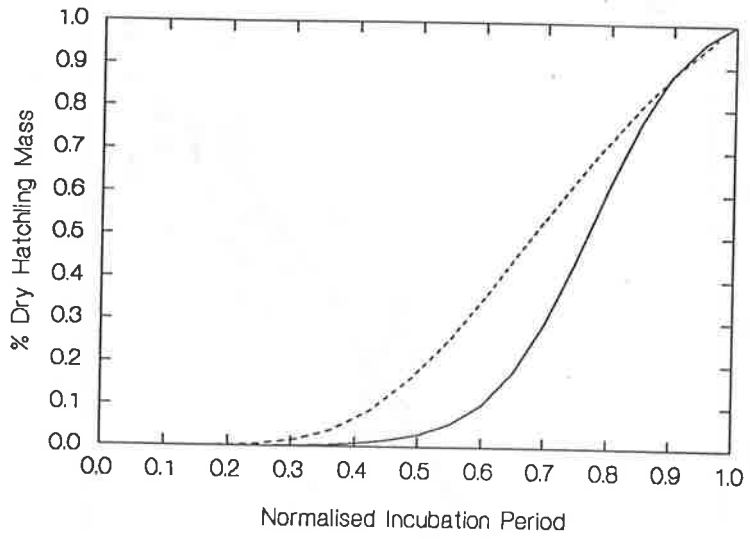

Fig. 10. Relationship between dry embryo mass and incubation age for the king quail. Dry embryo mass is expressed as a fraction of the dry hatchling mass, and incubation age is the day of incubation divided by the total incubation period. Solid line indicate the predicted growth curve of a precocial species respectively according to Hoyt (1987), and the dashed line indicate the king quail based on the equation for dry mass presented in Table 1, p.107.

Allometric comparisons of embryonic growth rates

Embryonic growth rates have been estimated by the parabolic equation (eq. 3). The constants of this equation describe the factorial change in growth rate at all ages, *a*, and describe the rate of decrease in relative growth rates, *b* (Ricklefs 1987). Growth rates were obtained by regressing the natural logarithm of embryo mass (M) against the natural logarithm of (t - *i*), where t is the day of incubation and *i* is a lag time before the onset of parabolic growth (eq. 4) (fig. 12-13):

$$\ln M = \log a^* + b^* \ln (t - i) \qquad \text{(eq. 4)}$$

The constants of the fitted relationship for king quail were ln a*= -5.592 and b*= 2.50 with i = 0.5 days (s_b= 0.068 r^2= 0.957 $F_{1,61}$= 1361.73 P<0.001), and for the cockatiel ln a* = -5.641 and b*= 2.514 with i = 3.0 days (s_b= 0.103 r^2= 0.916 $F_{1,21}$= 601.162 P<0.001). The parabolic constants were then obtained by transforming values of a* and b* with the equations $b = (1 - 1/b^*)$ and $a = b^*(a^*)^{1/b^*}$. Therefore the parabolic constants were a = 0.267 and b = 0.60 for the king quail, and a = 0.267 and b = 0.602

for the cockatiel. The constants for both species were less than the average values for the species in Ricklefs (1987), but not significantly so. Ricklefs (1987) predicted that values of a, b or both should decrease as egg mass decreases. The results obtained here for two species with small eggs supports that prediction.

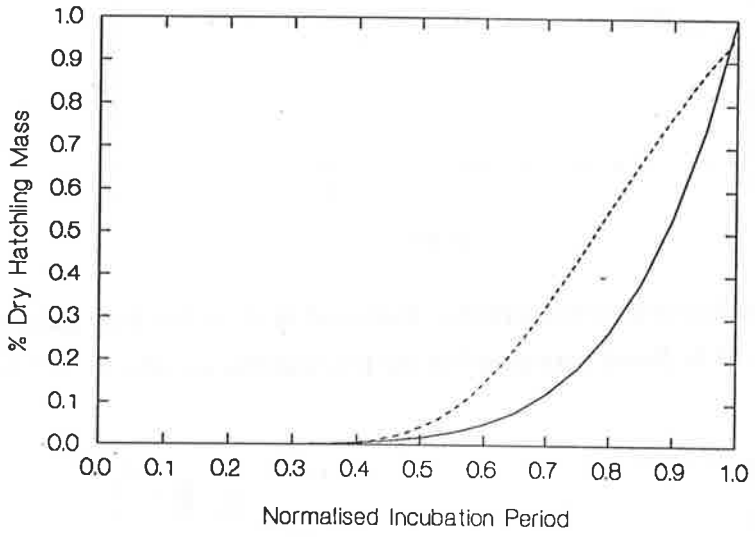

Fig. 11. Relationship between dry embryo mass and incubation age for the cockatiel. Dry embryo mass is expressed as a fraction of the dry hatchling mass, and incubation age is the day of incubation divided by the total incubation period. Solid lines indicate the predicted growth curve of an altricial species respectively according to Hoyt (1987), and the dashed lines indicates the cockatiel (fig. 11) based on the equation for dry mass presented in Tables 2, p.109.

Water content of embryos

The water content of yolk-free king quail embryos decreased exponentially from 92-95% at day 6-7 of incubation to 80% on average at day 10 of incubation and 75% at hatching (fig. 11). Coincident with the slow decrease in water content from day 10 on, was the decline in growth rate of embryos. Despite large variability in quail embryo water content, water content of embryonic tissues was significantly correlated with incubation age (fig. 11). From IP to hatching, water content was a stable mean of 76.2 ± 1.5% (n=24), and only subsequently declines to adult levels after hatching. At mid-incubation (day 10) the water content of cockatiel embryos was 88%, after which it decreased to 80% from day 13 to hatching (fig. 12).

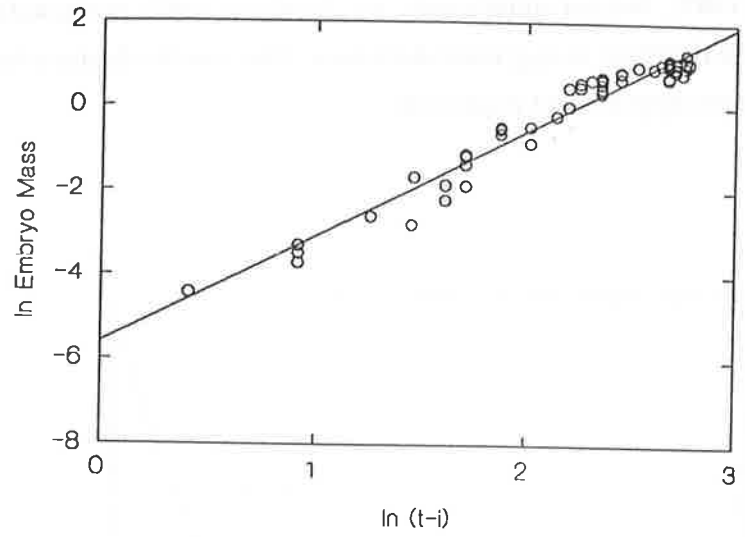

Fig. 12. The relationship between ln embryo mass and ln (t - *i*) for king quail embryos and hatchlings (n=64). The fitted constants for the relationship are a*= -5.592, b*= 2.50 and *i*= 0.5.

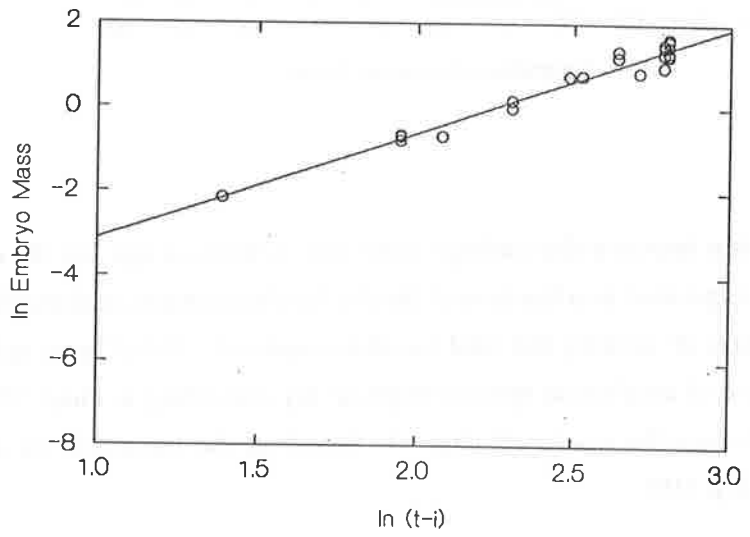

Fig. 13. The relationship between ln embryo mass and ln (t - *i*) for cockatiel embryos and hatchlings (n=23). The fitted constants for the relationship are a*= -5.641, b*= 2.514 and *i*= 3.0.

Ricklefs (1987) hypothesised that the acquisition of mature function in embryos is correlated with the accumulation of solids in embryonic tissues. His findings suggested that there was a direct relationship between the rate of increase in solids and the rate of decrease in growth rate of the embryo (using the parabolic model) with respect to increasing embryo mass. The regression of log dry mass (M) on log wet embryo mass was examined for the king quail and cockatiel and the allometric constants compared with values predicted by Ricklefs (1987) according to the parabolic constant *b* for embryonic growth rate. A significant relationship was obtained for the king quail (eq. 5) and

cockatiel (eq. 6). Allometric exponents higher than unity (b=1), indicate that there was an increase in the proportion of solids in embryos with respect to increasing embryo mass, and thus more differentiation of tissues.

ln dry M = -1.883 + 1.391 ln wet M (eq. 5)
(s_b= 0.058 r^2= 0.914 $F_{1,34}$= 575.338 P<0.001)

ln dry M = -2.176 + 1.335 ln wet M (eq. 6)
(s_b= 0.056 r^2= 0.979 $F_{1,12}$= 561.371 P<0.001)

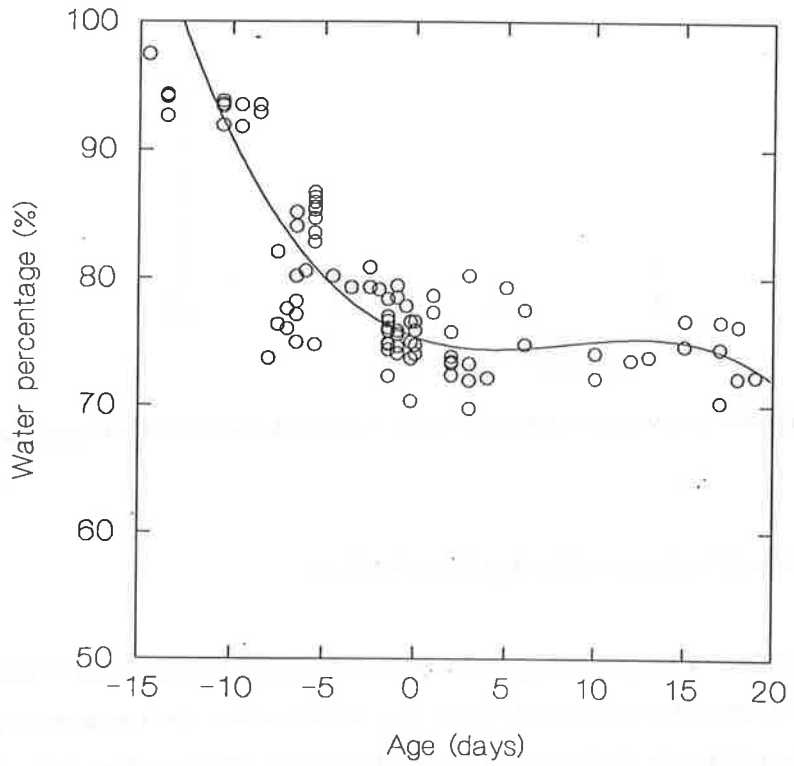

Fig. 14. Relationship between water content and age of king quail embryos and chicks. Age is expressed relative to the day of hatch. Solid line indicates a significant quadratic regression (% water content = 75.37 - 0.498 age + 0.076 age^2 - 0.003 age^3, r^2 = 0.998 $F_{1,83}$= 521.359 P<0.001).

The allometric constants of equations 5 and 6 were lower than predicted by Ricklefs (1987) on the basis of the parabolic constant *b* (predicted value b= 1.6). This suggests that less solids have accumulated in the embryo than predicted by the rate of decrease in relative growth rate and increasing tissue differentiation. Small egg mass limits the total solids that can be invested in eggs (Sotherland and Rahn 1987), and the average yolk-free hatchling energy density per gram dry mass was relatively low in both

the king quail and cockatiel (see Section 3.1, p.66). This suggests that relatively more of the solids in king quail eggs were utilised for cell proliferation in king quail and cockatiel embryos, and less was used for tissue differentiation.

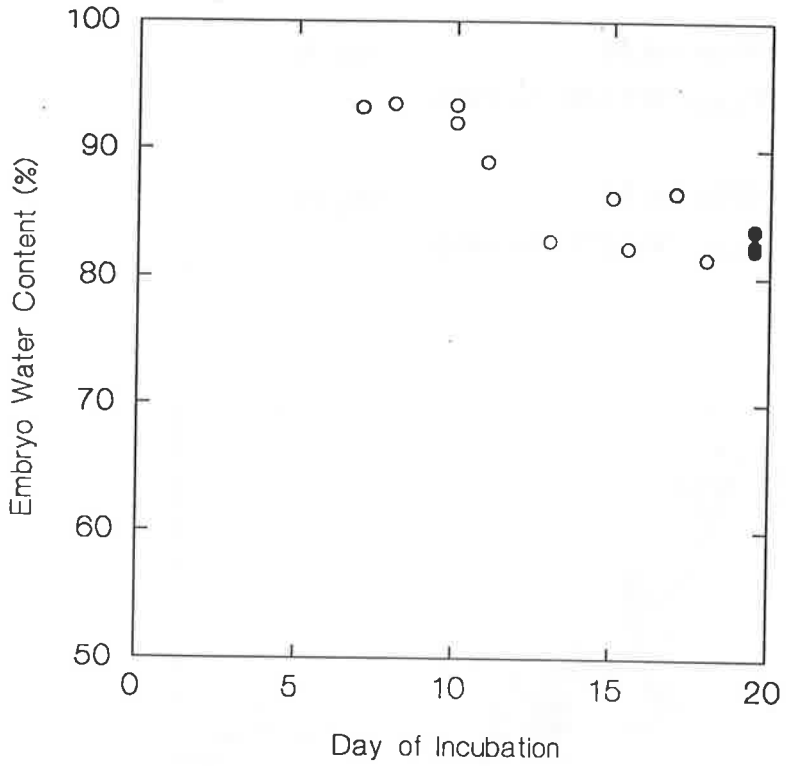

Fig. 15. Relationship between water content of yolk-free cockatiel embryos and day of incubation (n=15).

Changes in yolk content of eggs during incubation

The wet yolk content of king quail eggs decreased the most between day 5 and 10 of the incubation period, and at a slower rate until day 15-16 when the remaining yolk was withdrawn into the embryo's abdomen as an internal yolk reserve (fig. 16). The variance in wet yolk mass at all stages of incubation was attributed to the variability in egg mass. The changes in wet yolk content of king quail eggs was paralleled by decreases in water content during incubation (fig. 17). In the first half of the incubation period the water content of the external yolk was 60-70%, but in the second half it was between 30-60% water. The mean water content of yolk reserves in hatchlings and embryos was 49.4 ± 6.4% (n=9) in the king quail, and 58.7 ± 10.4% (n=6) in the cockatiel.

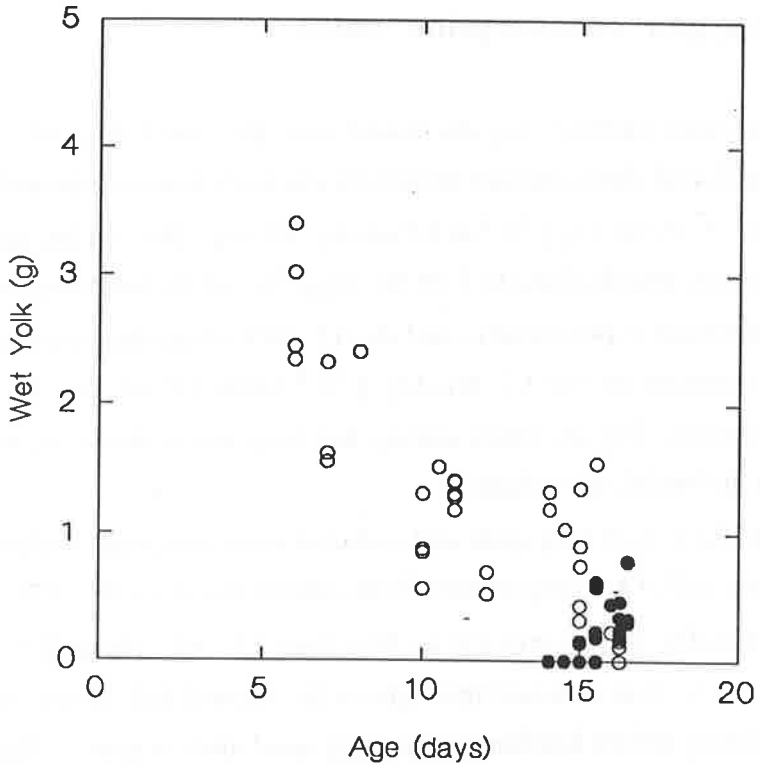

Fig. 16. Relationship between wet yolk content of king quail eggs and day of incubation (n=32). *Open symbols*: external yolk mass, *filled symbols*: internal yolk.

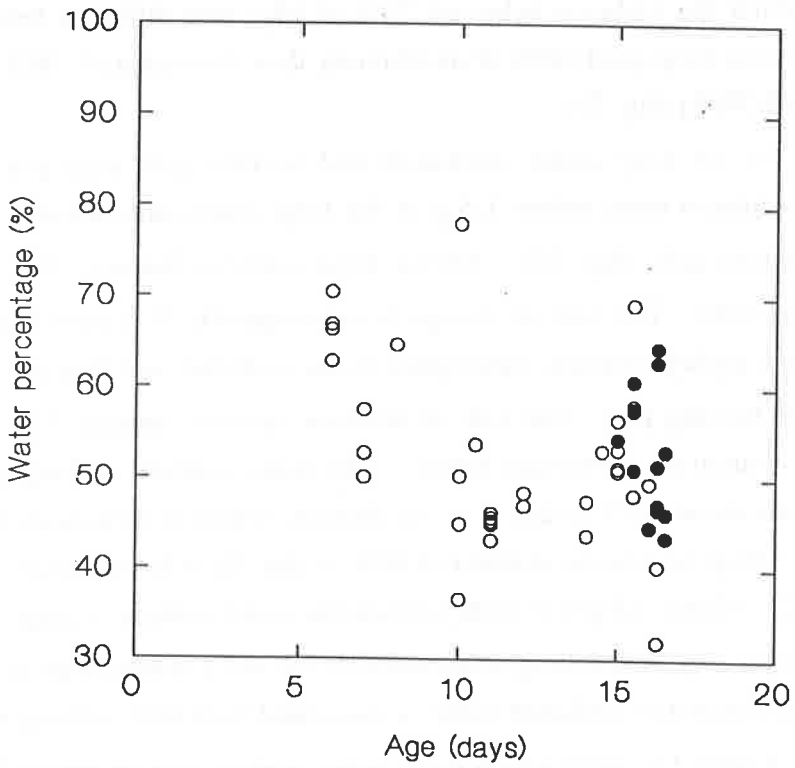

Fig. 17. Relationship between water content of yolk in king quail eggs and day of incubation (n=32). *Open symbols*: external yolk, *filled symbols*: internal yolk.

Mass-specific oxygen consumption rates

Mass specific (wet) embryo $\dot{V}O_2$ decreased over the first 9 days of incubation (50%) in the king quail, and then constant metabolic intensity was maintained until day 14 when it increased to 1.55 mL O_2 $g^{-1}h^{-1}$ at EP on day 16 (fig. 18). Subsequently $\dot{V}O_2$ increased during hatching, and declined to 3.08 mL O_2 $g^{-1}h^{-1}$ in the hatchling (<0.5 day). Mass-specific $\dot{V}O_2$ decreased exponentially until day 13 (68% of incubation period) in the cockatiel, and was constant at 1.0-1.2 mL O_2 $g^{-1}h^{-1}$ until EP on day 18 (fig.19). However, the mass-specific $\dot{V}O_2$ increases during hatching and remains higher at 2.0-2.10 mL O_2 $g^{-1}h^{-1}$ in the hatchling cockatiel.

The mass-specific $\dot{V}O_2$ of king quail and cockatiel were compared with that of the semi-precocial Herring gull, *Larus argentatus*, from data in Drent (p.82, 1970). In all three species mass-specific $\dot{V}O_2$ decreased to less than 2.0 mL O_2 $g^{-1}h^{-1}$ by mid-incubation (fig. 20). $\dot{V}O_2$ was constant throughout the second-half of the incubation period, except immediately before hatching in the king quail and cockatiel. The Herring gull embryo $\dot{V}O_2$ remained unchanged during hatching and in the hatchling. The metabolic intensity of the three species was lowest and constant shortly after the embryos were 20% of the yolk free hatchling mass (M_{yfh}) (fig. 20). However, the relative time during incubation at which the embryos achieved 20% of M_{yfh} was different between species, being earliest in the king quail (43% of incubation), then the cockatiel (58%) and latest in the Herring gull (70%) (fig. 21).

Mass-specific $\dot{V}O_2$ of king quail, cockatiel and herring gull embryos was significantly related to embryo mass below 1.5 g in the king quail and cockatiel, and below 20 g in the herring gull (fig. 22). Above these embryo masses, $\dot{V}O_2$ was independent of embryo mass. The rate of change in mass-specific $\dot{V}O_2$ with embryo mass, below these critical embryo masses, was highest in the cockatiel, and then the king quail and lowest in the herring gull. The rate of decrease in mass-specific $\dot{V}O_2$ was correlated with water content of embryonic tissues. The water content of king quail embryos decreased from about 93% at day 5 of incubation, which corresponds to an embryo mass of about 0.85 g, to a water content of 80% at day 10, when embryo mass was 1.5 g (fig. 14 & 22). Above 1.5 g wet embryo mass the water content of king quail embryos decreased more slowly to hatchling water content (74-76%), at which point $\dot{V}O_2$ was constant. The water content of cockatiel embryos decreased from 88% at 0.4 g mass (day 10) to 80% at 1.1 g (day 13), after which point water content was unchanged and $\dot{V}O_2$ was constant (fig. 15 & 22). Thus highest mass-specific $\dot{V}O_2$ in early embryonic development was correlated with higher water content of tissues, which reflects the higher metabolic intensity in wet tissues. The $\dot{V}O_2$ of king quail embryos decreased earlier in the incubation period as the relative growth rate and water content decreased

(fig. 22). In comparison relative embryonic growth rate of cockatiel decreased later in the incubation period, which was correlated with higher water contents of embryonic tissues and higher metabolic intensity than the king quail.

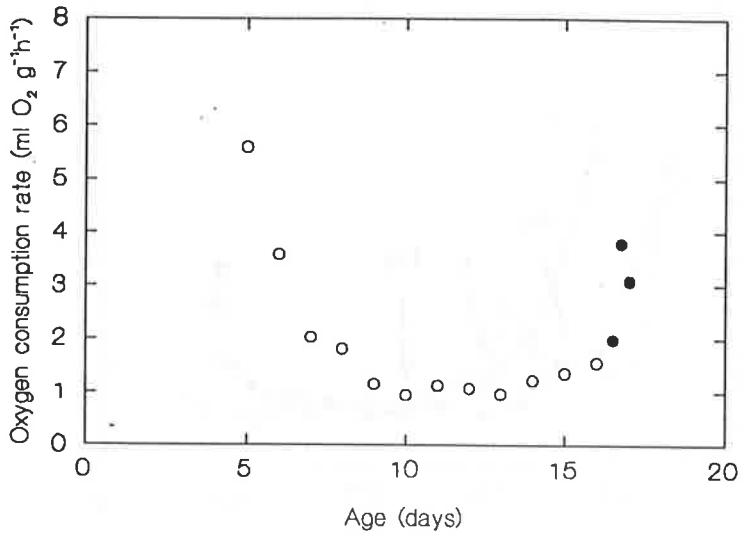

Fig. 18. Relationship between mass-specific $\dot{V}O_2$ and day of incubation in king quail embryos. *Open symbols*: embryos, *filled symbols*: hatching embryos and hatchlings. Points based on estimated embryo mass according to equation for yolk-free embryo mass (Table 1, p.107) and daily $\dot{V}O_2$ means (Section 3.2) for embryo $\dot{V}O_2$ per day.

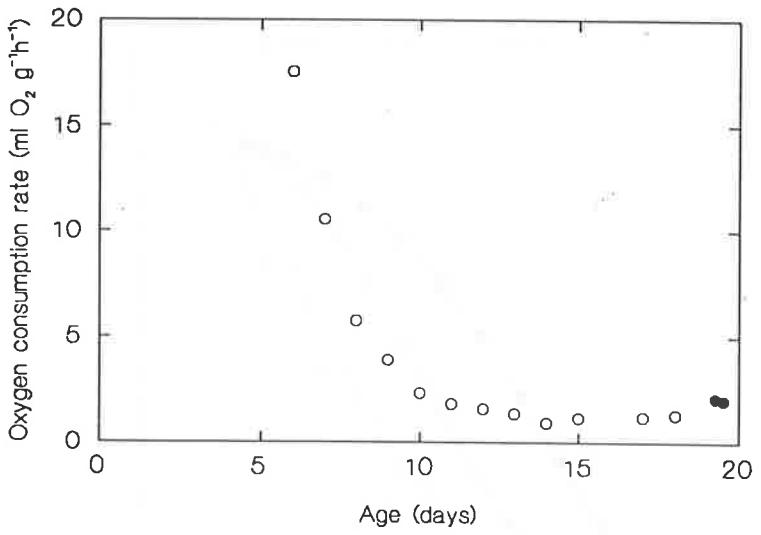

Fig. 19. Relationship between mass-specific $\dot{V}O_2$ and day of incubation in cockatiel embryos. *Open symbols*: embryos, *filled symbols*: hatching embryos and hatchlings. Points based on estimated embryo mass according to equation for yolk-free embryo mass (Table 2, p.109) and daily $\dot{V}O_2$ means (Section 3.2) for embryo $\dot{V}O_2$ per day.

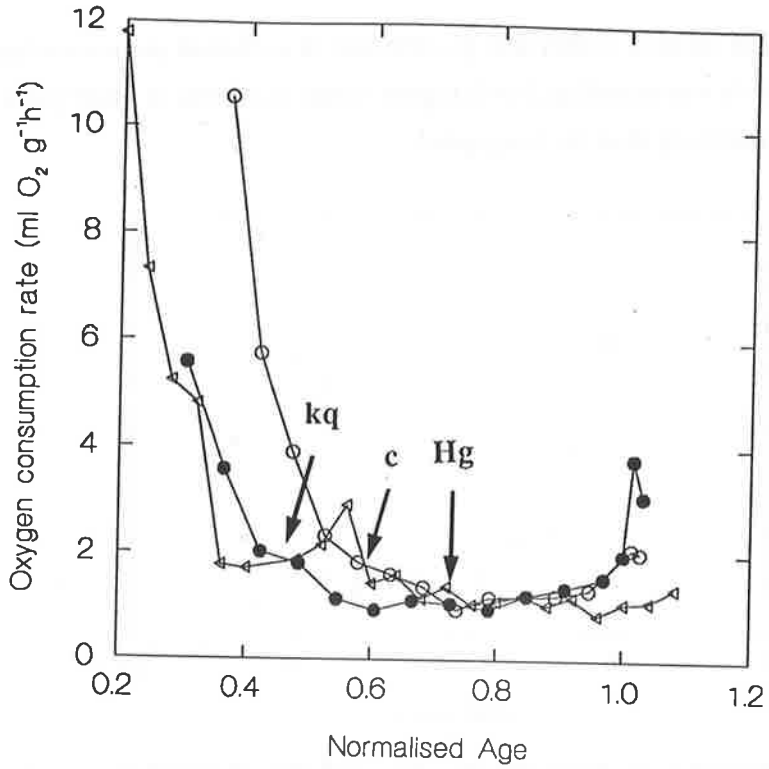

Fig. 20. Relationship between mass-specific $\dot{V}O_2$ and embryo age as a fraction of incubation period for king quail (*filled circles*), cockatiel (*open circles*) and the herring gull (*triangles*). Data for king quail obtained from figures 18 & 19, and that for the herring gull from Drent (p. 82, 1970). Arrows indicate age at which embryos reach 20% of the yolk-free hatchling mass.

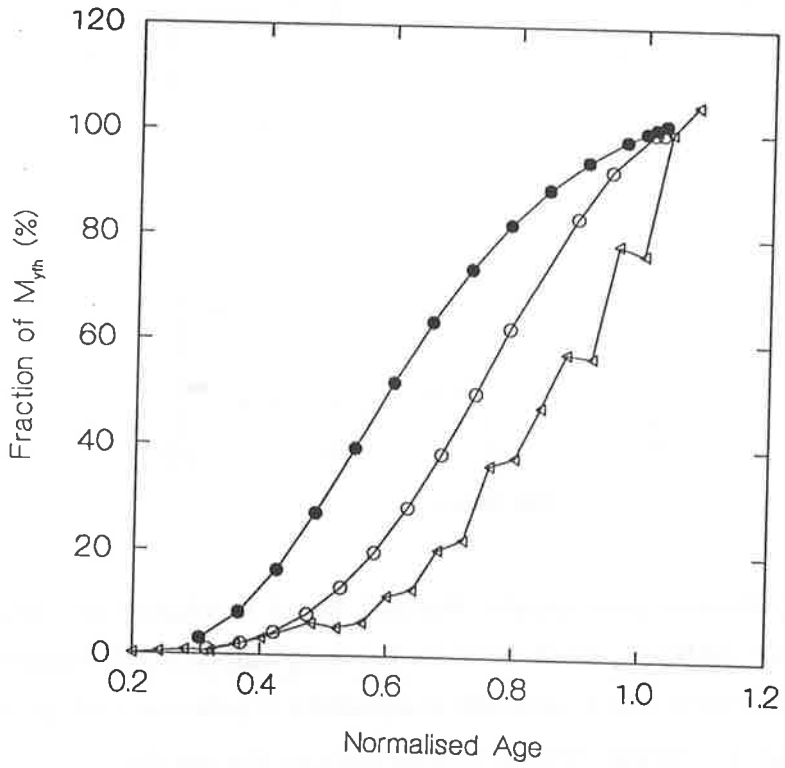

Fig. 21. Relationship between yolk-free hatchling mass and embryo age as a fraction of incubation period for the same species indicated in figure 20.

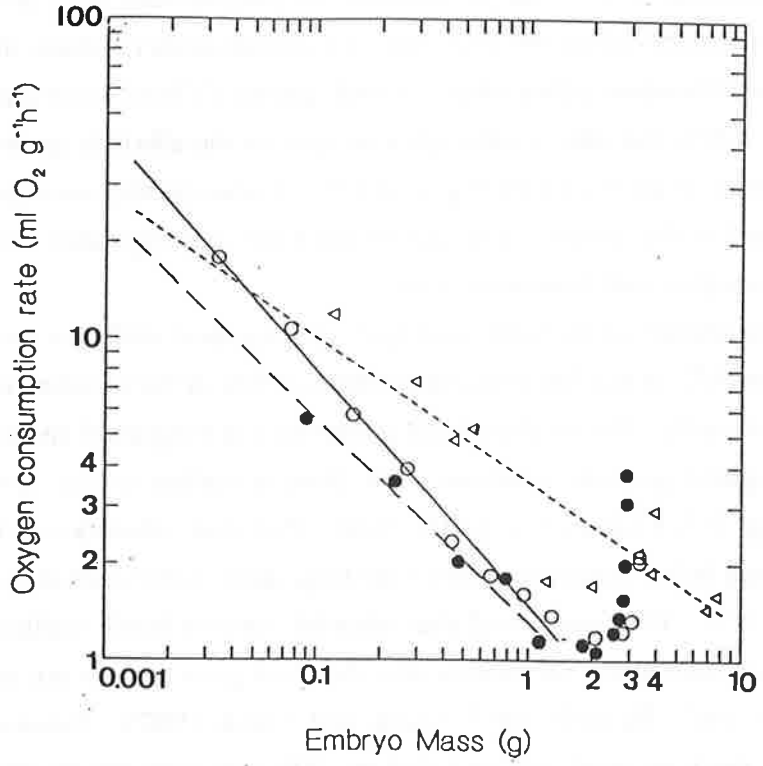

Fig. 22. Relationship between mass-specific $\dot{V}O_2$ and yolk-free embryo mass (M_{yf}) during incubation for the same species indicated in figure 20-21 (same symbols). Lines indicate significant relationships. *Solid line*: cockatiel <1.5 g ($\log \dot{V}O_2 = 0.168 - 0.735 \log M_{yf}$; $s_b = 0.028$ $r^2 = 0.991$ $F_{1,6} = 683.844$ $P<0.001$), *large dashed line*: king quail <1.5 g ($\log \dot{V}O_2 = 0.116 - 0.634 \log M_{yf}$; $s_b = 0.047$ $r^2 = 0.979$ $F_{1,4} = 183.168$ $P<0.001$), *fine dashed line*: herring gull <20 g ($\log \dot{V}O_2 = 0.554 - 0.447 \log M_{yf}$; $s_b = 0.055$ $r^2 = 0.859$ $F_{1,11} = 66.910$ $P<0.001$).

Discussion

Embryonic growth rates of king quail and cockatiel

King quail embryos hatch after a short incubation period before growth rate declines significantly, unlike larger precocial species. Yolk-free embryo mass increases exponentially throughout the first 70 % of the incubation period (fig. 1b, p.105), which is marginally longer than previous reports for larger precocial embryos, but is still typical of embryo growth in precocial species (Rahn, Paganelli and Rahn 1974; Hoyt, Vleck and Vleck 1978; Vleck, Hoyt and Vleck 1979; Hoyt and Rahn 1980). During the remaining 30% of the incubation period, growth rate actually decreases considerably in the largest embryos (Hoyt, Vleck and Vleck 1978). In contrast the absolute growth rates of king

quail embryos decreases significantly, but growth does not plateau until 95% of the way through the incubation period (after IP) (fig. 1b). Cockatiel embryo mass increases exponentially throughout incubation like other altricial species (Vleck, Hoyt and Vleck 1979; Hoyt and Rahn 1980), but unlike other altricial species the absolute growth rates decrease prior to hatching in the cockatiel (fig. 2, p.106). Consequently an exponential curve could not be fitted to the growth of cockatiel embryos, but increases in embryo mass are described by a significant Gompertz curve.

Most growth parameters of the limbs and body of king quail embryos are almost fully developed (at least 80% of hatchling measurements) at 60% of the incubation period (day 10) (fig. 3-5, p.108-109). The smallest body parameters of king quail and cockatiel embryos have the highest growth constants, and plateau earlier in the respective incubation periods (fig. 3-7) (Tables 1-2, p.107, 109). However, shoulder to tail and middle-toe do not plateau before hatching in either the king quail or the cockatiel embryo (fig. 4, 7 and Table 1-2). It is suggested that altricial species hatch earlier in the developmental sequence than precocial species, and therefore growth rates are still high before hatching (Hoyt 1987; Ricklefs 1987; Vleck and Vleck 1987). However, the patterns of growth for the king quail and cockatiel are different from the precocial and altricial extremes of development that have been described so far. Unlike larger precocial species, growth rates of king quail embryos are still high at hatching, which supports the prediction made in this study that as egg mass decreases, precocial species will have less time to complete growth and maturation before hatching. Although the morphological and physiological maturity of king quail at hatching indicates that they do not hatch as early in the developmental sequence as altricial species (see Section 3.2). The cockatiel pattern of growth differs from the previously described pattern of altricial growth (Vleck, Hoyt and Vleck 1979) in that growth at the end of the incubation period starts to decline and is no longer exponential. The decline in growth rates are attributed to the longer incubation periods of parrot species in general.

Ricklefs (1987) advocated the use of the parabolic equation (eq. 3) to estimate growth rates of embryos, in contrast to earlier studies (Pettit et al. 1981, 1982a, b) because he believes a major short-coming of the logistic or Gompertz equation method is the constraint of the asymptotic mass, since most embryos grow continuously throughout their incubation periods, even after the growth rates plateau or decline. Ricklefs (1987) believes that such a method invariably and unrealistically overestimates the asymptote for the embryo, often considerably higher than the hatchling mass, and therefore growth rates based on such equations are inaccurate. In this study, the Gompertz equation fitted an asymptotic mass of 3.71 g and 4.69 g respectively for king quail and cockatiel, which exceeded the yolk-free hatchling mass by 31% and 40% respectively (Table 1-2). Therefore Ricklefs (1987) conclusions appear to be supported for the king quail and cockatiel.

Ricklefs (1987) has concluded from his analyses using the parabolic function, that values of a or b, or both should increase with egg mass. The constant a is considered to be the absolute growth rate of an embryo of unit mass, and b the rate of decrease in relative growth rate throughout development. Parabolic constants for embryonic growth of king quail and cockatiel (fig. 12-13, p.114), are $a = 0.267$ and $b = 0.60$ for the king quail and $a = 0.267$ and $b = 0.602$ for the cockatiel. According to the parabolic model king quail and cockatiel embryos have low absolute growth rates, and rapidly declining relative growth rates which conforms with Ricklefs (1987) predictions for small eggs with short incubation periods. The parabolic constants are identical for the king quail and cockatiel which have similar hatchling masses but different egg masses and incubation periods. According to the Ricklefs (1987), differences in the incubation period and point of hatching along the developmental sequence may result in changes to a or b, or both. Using a hatchling mass of 3.8 g for both the king quail and cockatiel (see Section 3.1), and the values of a and b obtained here, the predicted incubation periods of both species are 16.5 and 19.0 days (eq. 9, Ricklefs 1987), which agree well with the incubation periods (16.5 and 19 days, respectively, for king quail and cockatiel) found here. The identical values of b suggests that the relative growth rate of the king quail embryo declines earlier in the incubation period than the cockatiel embryo on the basis of egg mass, and thus differentiation occurs earlier in the precocial quail embryo. Similarly on the basis of egg mass, a lower value of absolute growth rate is predicted for the king quail, but it is similar to that of the cockatiel, and therefore the king quail is expected to achieve hatchling mass earlier than the cockatiel.

Changes in embryonic water content during incubation

The increase in dry embryo mass during incubation of king quail and cockatiel is best described by sigmoidal curves (fig. 8-9), although the fitted asymptotes exceed the measured hatchling values (Table 1-2). The curve describing the increase in dry mass has a lower growth constant, and inflects later in the incubation period than wet mass curves, indicating the accumulation of solids in embryonic tissues. After taking into account differences in incubation period between species, dry embryonic mass of king quail and cockatiel both exceed the predicted dry masses of typical precocial and altricial species throughout most of the incubation periods (fig. 10-11, p.112-113) (Hoyt 1987). These deviations are attributed to deviations in the incubation periods of both species from predictions on the basis of egg mass. The king quail hatches earlier than predicted before growth plateaus and thus the growth curve appears to be shifted to the right. The cockatiel hatches after a longer incubation period and similarly appears to be shifted to the left after incubation period is taken into account.

Ricklefs (1987) suggests that the allometric exponent (b>1) of the logarithmic relationship between dry mass and wet mass of embryos throughout the incubation period, indicates the increasing proportion of solids in embryonic tissues, and decreasing water content of tissues. Thus this exponent is indicative of the level of tissue differentiation in embryos before hatching. The allometric exponents for the same relationships in king quail and cockatiel are similar (b= 1.391 and 1.335 respectively), but lower than predicted by the trend indicated in Ricklefs (1987) on the basis of the rate of decrease in relative growth rate (fig. 23, p.125). However, this relationship is based primarily on larger species. It is unlikely that both the king quail and cockatiel are anomalous for the following reasons. Hatchling water contents are generally similar to that of the initial egg water content (Ar and Rahn 1980; Rahn 1984; Vleck, Vleck and Seymour 1984). The initial water content of eggs decreases with increasing egg mass and precocity of the hatchling (Sotherland and Rahn 1987). It is suggested here that the low rate of accumulation of solids in embryonic tissues of king quail and cockatiel reflects the higher metabolic costs of maintaining a larger, more mature embryo mass (fig. 21) for a longer proportion of the incubation period (fig. 10-11). As a result both the king quail and cockatiel hatchlings have lower than predicted energy densities. Support for this hypothesis can be found in studies of semi-precocial American coots, *Fulica americana*, which have hatchlings with water indices intermediate between precocial and altricial species (Alisauskas 1986). The allocation of energy was found to decrease, along with yolk content and egg mass, in successive eggs within clutches of coots, and as a result the larger eggs hatched larger chicks with relatively more mature tissues as reflected in their tissue water indices. These first hatched chicks with the lower water indices also displayed greater mobility, which may reflect differences in the degree of precocity of *F. americana* hatchlings (Alisauskas 1986)

Mass-specific oxygen consumption rates

Mass-specific $\dot{V}O_2$ for wet king quail, cockatiel and the herring gull, *Larus argentatus*, embryos are presented in figure 20 after normalisation of incubation period. Similar patterns of embryonic $\dot{V}O_2$ are described for the precocial Japanese quail, *Coturnix coturnix*, and altricial species, including *Agapornis roseicollis*, *Peophila guttata*, *Pelecanus occidentalis* and *Pygoscelis adeliae* (Bucher and Bartholomew 1984; Bucher et al. 1986). All avian embryos have high mass-specific $\dot{V}O_2$ (>5.0 mL O_2 $g^{-1}h^{-1}$) at wet masses smaller than 0.3 g (Fig. 20-22). Mass-specific $\dot{V}O_2$ decreases in an exponential function as embryo mass increases, the slope of which varies between species of different egg mass (fig. 22). At small embryo masses hatchling maturity does not influence the relationship between mass-specific $\dot{V}O_2$ and embryo mass, because there is no significant difference in slope between the relationships for the king quail and cockatiel despite the differences in their level of physiological maturity at hatching

(ANCOVA F=3.670 N.S.). At a wet mass of 1.0 g, both the king quail and cockatiel are 30% of the yolk-free hatchling mass (M_{yfh}). As mass increases further $\dot{V}O_2$ is constant at 1.0-1.3 mL O_2 $g^{-1}h^{-1}$ until the king quail reaches 3.0 g and the cockatiel 2.5 g (fig. 21). Other species, including both altricial and precocial embryos also maintain relatively constant $\dot{V}O_2$ after the embryos reach 20% of the M_{yfh} (Fig. 2, Bucher and Bartholomew 1984). However, the level of metabolic intensity maintained by embryos after they reach 20% of M_{yfh} is influenced by the pattern of growth, incubation period, and embryo mass at that point of the developmental curve. In figure 21 king quail reach 20% of M_{yfh} at 45% of the incubation period, but cockatiel reach the same fraction at 55% of the incubation period, and the semi-precocial *Larus* at 70% of the incubation period. Embryos of *Coturnix coturnix*, king quail and cockatiel maintain higher mass-specific $\dot{V}O_2$ in the second half of the incubation period than two other altricial species, *A.roseicollis* and *P.occidentalis* (Bucher and Bartholomew 1984). The higher metabolic intensities of the precocial embryos are thought to reflect the higher maintenance costs of more metabolically mature tissues (Bucher and Bartholomew 1984; Hoyt 1987; Vleck and Vleck 1987). The higher metabolic intensity of the cockatiel embryo throughout incubation and the higher degree of hatchling metabolic maturity (see Chapter 4) suggest it is more precocial during embryonic development than other altricial species.

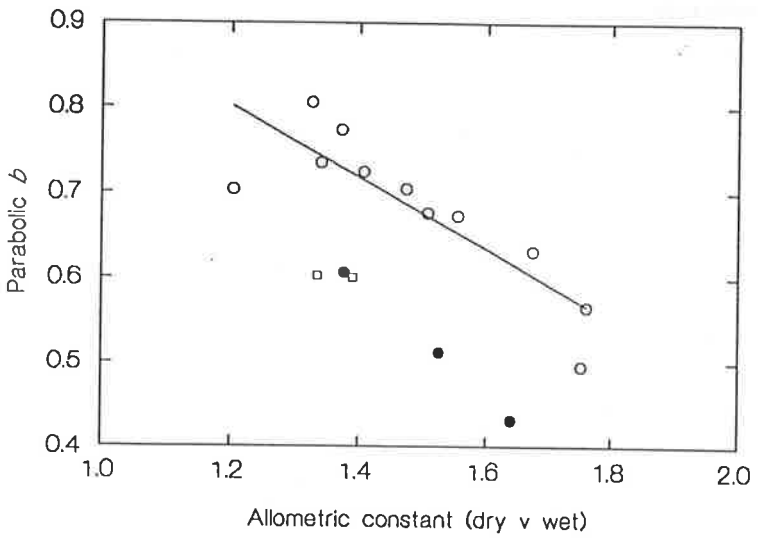

Fig. 23. Relationship between the parabolic constant (*b*) relating growth rate to embryo mass (eq. 4) and the allometric constant (b) relating the dry mass to the wet mass of the embryo. *Filled circles*: pelagic seabirds (Ricklefs 1987), *open circles*: species other than pelagic seabirds (Ricklefs 1987), *squares*: king quail and cockatiel.

Further evidence for increasing maintenance costs in more precocial embryos, including the cockatiel, are the significant increases in mass-specific $\dot{V}O_2$ during the last 10-20% of the incubation period (fig.22). The $\dot{V}O_2$ of the late term altricial cockatiel embryo in fact increases more than the semi-precocial gull *Larus* embryo (Drent 1970) (fig. 20).

Changes in the relative growth rates are paralleled by changes in water content of embryos and nestling birds (Ricklefs 1979, 1987). King quail and cockatiel hatch at a similar mass, but have different patterns of embryonic growth (fig. 1-2). The metabolic intensity of king quail and cockatiel embryos is similar throughout most of the second half of the incubation period and is independent of embryo mass even though king quail are larger than cockatiel during this period until shortly before hatching (fig. 22). Over the same interval of incubation, the Japanese quail, *Coturnix c. japonica*, has a comparable metabolic intensity (Buchēr and Bartholomew 1984). In the first half of the incubation period the relationship between metabolic intensity and cockatiel embryo mass is not significantly higher in slope than the relationship for king quail (ANCOVA F= 3.670, N.S.) (fig. 21). Bucher and Bartholomew (1984) suggest that the lower metabolic intensity of *C. japonica* embryos throughout the first half of the incubation period reflects a rapid decrease in relative growth rate early in the development of precocial species. This is supported by decreases in metabolic intensity earlier in the incubation period of king quail compared to the cockatiel (fig. 20), which is attributed to decreases in relative growth rate.

CHAPTER 4

Development of Thermoregulation and Posthatching Growth

Introduction

Prior to reaching homeothermy, chicks must be provided with a suitable thermal environment by their parents during development, or chicks must be capable of tolerating lower body temperatures when unbrooded. Megapode hatchlings that can fully thermoregulate are independent after hatching (Booth 1984, 1985). Anseriform hatchlings are also homeothermic and are frequently required to follow parents to suitable feeding grounds (Untergasser and Hayward 1972). Most other groups of birds have lower thermoregulatory abilities and thus require parental brooding to contribute to the cost of temperature regulation. For small precocial hatchlings which are self-feeding, parental brooding can be as high as 75% of the day (Visser and Ricklefs 1993), and thus foraging time may be limiting growth. Foraging time is determined by the degree of homeothermy of precocial chicks and their tolerance of low T_b (Myhre and Steen 1979; Pedersen and Steen 1979; Visser 1991). Thus this study examines the relationships between thermoregulatory abilities, T_a and foraging time in king quail chicks to determine how posthatching growth rates are affected by T_a.

The T_b of most hatchlings is normally below that of adult birds (Myhre and Steen 1979; Pedersen and Steen 1979). The difference between adult and chick T_b set-points are only 1-2 °C for some precocial species, such as Anseriform hatchlings, but as great as 5-10 °C for other hatchlings over the altricial-precocial continuum (Myhre and Steen 1979). Most small hatchlings are unable to prevent cooling of T_b because they can not raise their total metabolic rate high enough to balance heat loss. However the heat production of small precocial hatchlings enables them to slow the rate of cooling (Hissa et al. 1983). Tolerance of hypothermia varies between groups of birds and is an important consideration when examining posthatching development in birds. Species which are able to tolerate hypothermia should be able to forage longer during adverse weather conditions.

The timing of homeothermy is dependent on increases in thermogenic powers, body mass, and usually improvements in insulation. For small hatchlings the importance of each factor in attaining homeothermy varies between hatchling developmental types. Precocial chicks soon increase their thermogenic powers after hatching to levels equivalent of adult birds of similar body mass (Dawson, Bennett and Hudson 1976; Hissa et al. 1983). For altricial chicks the timing of acquisition of significant heat production capacities is later in the developmental period, after large increases in body mass have occurred, and is correlated with improvements in insulation (Dawson and Evans 1957, 1960; Hamas 1981; Hill and Beaver 1982; Olson 1992; Webb 1993). However, the parrot, *Agapornis roseicollis*, attains thermogenic responses earlier in their development than passerines of comparable mass (Bucher and Bartholomew 1986). The asymptotic mass and hatchling mass of cockatiel are both higher than *A. roseicollis*, and

so the achievement of homeothermy is predicted to be earlier in development. This study examines the thermogenic responses of king quail and cockatiel chicks to decreasing T_a during gradual cooling to detect transient and sustained metabolic responses, which will more accurately determine the development of homeothermy (Olson 1992).

Increases in the chick body mass over time is high early in the nestling period, and then the rate of increase slows down as chicks approach adult body mass. Curve-fitting techniques make it possible to compare relative growth rates between species of different adult body mass or asymptotic mass (Ricklefs 1967). The most commonly used growth equation that is fitted to growth data is the Gompertz equation (eq. 1), which may be calculated by non-linear least squares regression.

$$BM = A \cdot e^{(-e^{-K_G[t - w_i]})} \qquad \text{(eq. 1)}$$

where BM is body mass (g) at age t (days), A is the asymptotic body mass (g), K_G is the Gompertz growth constant (day^{-1}), and w_i is the age at inflection of the curve. Relative growth rates (RGR, day^{-1}) at any body mass can be calculated by:

$$RGR = -K_G \cdot \log_e (BM \div A) \qquad \text{(eq. 2)}$$

Absolute growth rates (AGR, g/day) at any body mass can be calculated by:

$$AGR = -K_G \cdot BM \log_e (BM \div A) \qquad \text{(eq. 3)}$$

AGR is highest at the inflection point. RGR and AGR follow the definitions of Ricklefs (1983).

Growth rates of avian species are significantly related to adult body mass, hatchling developmental type, nestling period and food availability (Ricklefs 1968, 1973). Growth rates are fastest and nestling periods shortest in smaller species, and at any given adult body mass, growth rate is highest in species with the lowest degree of hatchling maturity. Growth is thought to be limited by the amount of tissue which is capable of cell proliferation (Ricklefs 1969). Immature tissues are correlated with high water content, but, as tissues differentiate, the water content decreases to adult levels. Ricklefs (1973, 1979a) suggests that the early acquisition of mature function in birds is incompatible with rapid cell-proliferation or high growth rates. Lower growth rates in precocial species are thought to reflect the allocation of more energy to maturation of functions, in particular the development of temperature regulation, and muscular activity (Ricklefs 1968, 1973, 1979a). Precocial species achieve independence at the earliest possible age which allows chicks to forage and escape predators. Consequently precocial birds hatch with well developed legs, and develop the powers of flight and homeothermy earlier. The altricial strategy optimises the energy allocated to biosynthesis

and delays the onset of thermoregulation and activity costs (Dawson and Evans 1957, 1960; Williams and Prints 1986; Olson 1992).

Ricklefs (1973) did not consider the orders of parrots (Psittaciformes) and woodpeckers (Piciformes) in the relationship between relative growth rates and asymptotic mass of altricial land birds. These two orders exhibit neither rapid growth rates nor early maturity during development (Bucher 1983; Weathers et al. 1990). Lack (1968) attributes the low growth rates of such cavity nesting birds to the absence of selective pressure of predation for rapid growth. Allometric comparisons of Piciform species with other altricial birds suggests that the longer nestling periods of Piciformes compensate for the shorter than expected incubation periods (Yom-Tov and Ar 1993). However, an alternate explanation is suggested here for Psittaciformes. The parrot, *Agapornis roseicollis*, attains high metabolic capacities early in development (Bucher 1983, Bucher and Bartholomew 1986). In passerines and other altricial birds, the delayed acquisition of endothermy is correlated with the highest recorded relative growth rates (Dawson and Evans 1957, 1960; Olson 1992). Thus it is plausible that parrots may exhibit early maturation of function, which precludes them from achieving growth rates similar to other altricial orders. In this study the growth rates of cockatiel nestlings is examined in relation to the development of temperature regulation.

In precocial land birds (Galliformes and Gruiformes) the slope of the allometric relationship between growth rate constants and asymptotic body mass is -0.36 (Ricklefs 1973). The same relationship in altricial land birds is not significantly different in slope, but is significantly higher in intercept. However, the relationship for precocial land birds is based on species of an asymptotic mass greater than 100 g. It is recognised that the hatchlings of many precocial birds which are smaller than 100 g are not homeothermic at hatching (Visser 1991; Whittow and Tazawa 1991; Visser and Ricklefs 1993). One consequence of small body mass is that precocial chicks require greater increases in heat production to maintain high body temperatures above T_a during foraging periods. However, heat loss exceeds heat production in many small precocial chicks away from the nest, so they must return to the parents for brooding before T_b cools below incapacitating limits. The time precocial chicks spend being brooded is not available for feeding. The degree of homeothermy at hatching and the time for chick T_b to cool to T_a decreases with hatchling mass (Visser 1991; Visser and Ricklefs 1993). In the smallest precocial hatchlings, foraging time may depend on their thermoregulatory abilities. Consequently posthatching growth rate may decrease from allometric predictions for precocial land birds as asymptotic mass decreases.

Weather affects the growth of chicks of all developmental types (Bientema and Visser 1989; Konarzewski and Taylor 1989; Olson 1991, 1992). However, the effect in altricial chicks is much less than in precocial chicks due to the insulation of the nest (Olson 1991). The allometric exponent for the relationship between relative growth rate and asymptotic mass may be lower for precocial birds than altricial birds due to the

greater dependence of small precocial chicks on parental brooding at low T_a. Thus at small body masses the difference in relative growth rates between altricial and precocial birds may increase. The effect of low T_a on relative growth rates in altricial chicks is expected to be less than in precocial species because thermoregulatory costs are delayed in development.

This study also examines the age at which king quail and cockatiel chicks achieve homeothermy, and the effect of T_a on the development of homeothermy. Bernstein (1973) concludes that king quail achieved homeothermy at 25-28 days. However, his quail chicks were raised at a constant T_a of 35 °C, and thus their thermoregulatory abilities and posthatching growth rates may not be the same as chicks exposed to lower T_a. Webb (1993) hypothesised that there is coordination of physiological and morphological development in altricial birds, such that the development of metabolic capacities is coordinated with the acquisition of significant insulation. This study examines if parrots acquire elements of homeothermy before their insulation is improved.

Materials and Methods

Growth of king quail and cockatiel

Chicks were temporarily removed from the aviaries for measurements of body parameters (Chapter 2) from the day of hatch through to fledging. Fledging in king quail was defined as the age at which chicks were first capable of flight to escape, and in the cockatiel, fledging was defined as the age when they first left the nestbox. Most altricial species are capable of true flight at the time they first leave the nest, but defining the age of fledging in precocial species is more problematic, because many precocial land birds are capable of weak flight before they are capable of true flight (Lack 1968; Ricklefs 1979b). Precocial chicks fledge earlier in their development than altricial species at subadult body mass. However, king quail body parameters were measured until adult mass was achieved and thermoregulatory abilities were measured until 50 days of age. Chicks were removed from the aviaries during the day only and placed in cotton bags and weighed to 0.01 g on a Sartorius 1265MP balance. Length of body parameters was determined to 0.1 mm with plastic vernier calipers. Developmental changes in plumage were noted when chicks were measured.

Gompertz growth functions were fitted to body mass and body parameters by non-linear least-squares regression according to equation 1 (Ricklefs 1967) using NONLIN module of SYSTAT (Wilkinson 1990). In this study cockatiel laid eggs and successfully raised chicks throughout the year. The growth rates of cockatiel chicks was separated into two groups, those that hatched in spring and summer were defined as

the'warm' group and those that hatched in winter as the 'cold' group. King quail were similarly separated into warm and cold groups on the basis of growth rate. The cold king quail group hatched in spring (September to November) and the warm group in summer (December to February).

Development of temperature regulation

Oxygen consumption rate ($\dot{V}O_2$) was measured as described in Chapter 2, with the following changes to the general method. Chicks on the day of hatch were measured in 0.3 L metabolism chambers with dry air entering the chamber at flow rate of 300 mL min^{-1}. Subsequent measurements with older chicks were made in chambers of 1.0 or 2.0L, dependent on the body mass of the chick (cockatiel chicks older than 12-15 days were placed in 2.0 L chambers) with dry air entering the chambers at flow rates appropriate for the mass of the chick (300-1000 mL min^{-1}). Cockatiel chicks were measured in a fed state to minimise the chance of starvation or abnormal development and for comparison with other studies of altricial birds. King quail chicks were measured in a postabsorptive state; because quail chicks feed independently, they were able to obtain sufficient food after experiments. Postabsorptive periods were 1 h for the youngest quail and increased to 4 h for subadult quail. However, hatchling quail were not strictly postabsorptive because they contained residual yolk reserves. $\dot{V}O_2$ measurements of quail and cockatiel chicks were made between 10:00 and 13:00 on each occasion. Thus all chicks were able to feed in the rest of the daylight hours. The periods in the metabolism chambers were considered to have minimal impact on growth of chicks because $\dot{V}O_2$ measurements were less than 2-3 hours and measurements were performed at most once every three days.

$\dot{V}O_2$ measurements were made at thermoneutrality initially, and then T_a was reduced gradually during the experiment (see Chapter 2). Chick body mass was measured before and after each $\dot{V}O_2$ measurement. T_b was measured at different T_a throughout experiments by insertion of a copper-constantan thermocouple into the chick's cloaca to a depth between 5 and 10 mm dependent on age (see Chapter 2). In addition T_b was measured in brooded quail and cockatiel chicks within 30 s of being removed from beneath brooding adults. The T_b, T_a (in nestbox) and body mass of huddled cockatiel broods were measured during parental absences to determine the effect of huddling behaviour to temperature regulation.

Results

Allometric relations of hatchling metabolism

The mean hatchling resting metabolism (RMR_h) of king quail and cockatiel were significantly higher than the predicted RMR_h for hatchlings of all developmental types on the basis of hatchling mass (eq. 1, Klaassen and Drent 1991). King quail RMR_h were 215 mL O_2 day^{-1} or 36% higher for a mean hatchling mass of 3.87g. Cockatiel RMR_h were 172 mL O_2 day^{-1} or 47% higher for a mean hatchling mass of 3.91 g.

Allometric relations between RMR_h (mL O_2 day^{-1}) and hatchling body mass (M_h) were recalculated from Klaassen and Drent (1991) for both Galliformes and Psittaciformes (fig. 1). RMR_h found in this study were included with published data from Klaassen and Drent (1991), to obtain new allometric relations (eq. 1 & 2). The RMR_h of cockatiel hatchlings was greater than the 95% confidence limits of the regression mean for Psittaciformes. The RMR_h of king quail in this study and Bernstein's (1973) study were within the confidence limits of the regression mean, but the value in this study was considerably higher than that of Bernstein (1973).

Galliformes:

$\log (RMR_h) = 1.608 + 0.896 \log (M_h)$ (eq. 1)

($r^2 = 0.929$, $s_b = 0.083$; $n=10$ $P < 0.001$)

Psittaciformes:

$\log (RMR_h) = 1.601 + 0.789 \log (M_h)$ (eq. 2)

($r^2 = 0.790$, $s_b = 0.180$; $n=7$ $P < 0.001$)

Hatchling MIM rates were calculated from hatchling metabolic rates using the yolk-free hatchling masses of 3.5 g for quail and 3.6 g for cockatiel (Bucher 1986, 1987). MIM values were 3.87 and 3.04 mL O_2 $h^{-1}g^{-0.67}$ for king quail and cockatiel, respectively, in this study. The ratio of hatchling MIM to adult MIM indicates the metabolic precocity of any hatchling relative to its parent (Bucher 1986). Using the SMR of adult birds in the α phase, ratios obtained were 0.49 for quail and 0.40 for cockatiel hatchlings, respectively.

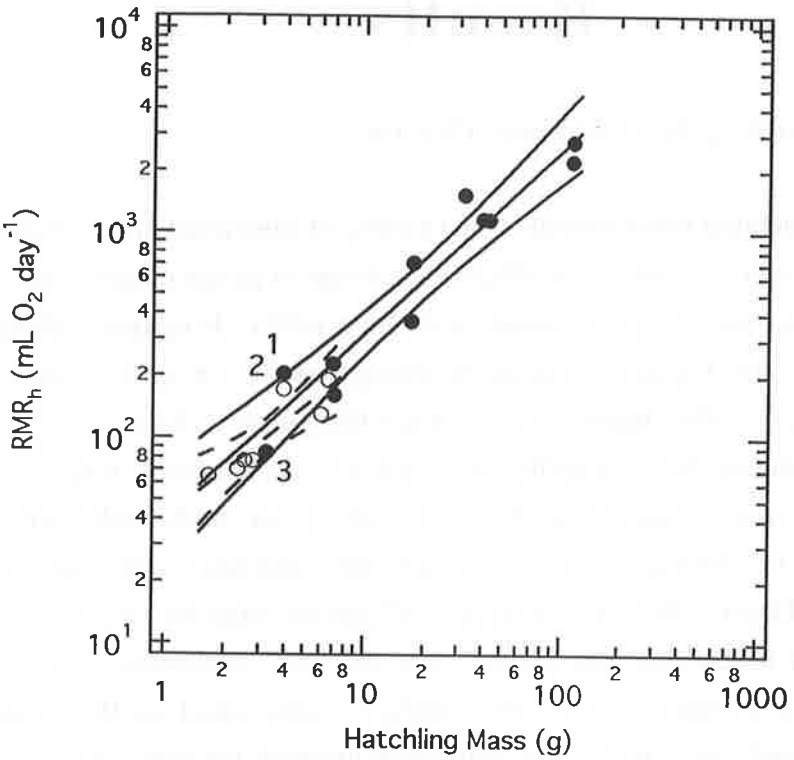

Fig. 1. RMR_h (mL O_2 day^{-1}) as a function of hatchling mass (g) for Galliformes (*Filled circles and solid lines*) and Psittaciformes (*Open circles and dashed lines*). Lines indicate significant regressions (eq. 1 & 2) ± 95% CI of regression means. Numeral 1 indicates king quail in this study; 2 is king quail in Bernstein (1973); and 3 is cockatiel in this study.

Development of metabolism and temperature regulation in quail

$\dot{V}O_2$ *of chicks less than 5 days old*

The mean $\dot{V}O_2$ of hatchlings at 35-40 °C (TNZ) was 2.87 ± 0.52 mL O_2 $g^{-1}h^{-1}$ (n=6) (fig. 2). $\dot{V}O_2$ of hatchlings below T_a 35 °C was between 2.4-5.5 mL O_2 $g^{-1}h^{-1}$. Some chicks at 0-1 days of age did not increase $\dot{V}O_2$ as T_a decreased, but maintained constant $\dot{V}O_2$ between T_a 20-40 °C. At 2-4 days of age the $\dot{V}O_2$ of chicks was 4.0-6.7 mL O_2 $g^{-1}h^{-1}$ at T_a <35 °C (fig. 2). The $\dot{V}O_2$ chicks 2-4 days old was significantly higher than the $\dot{V}O_2$ of chicks 0-1 days old (ANOVA $F_{1,66}$= 22.101 P< 0.001). All chicks when unbrooded became uncoordinated when exposed to T_a lower than 25 °C for any longer than 10 min.

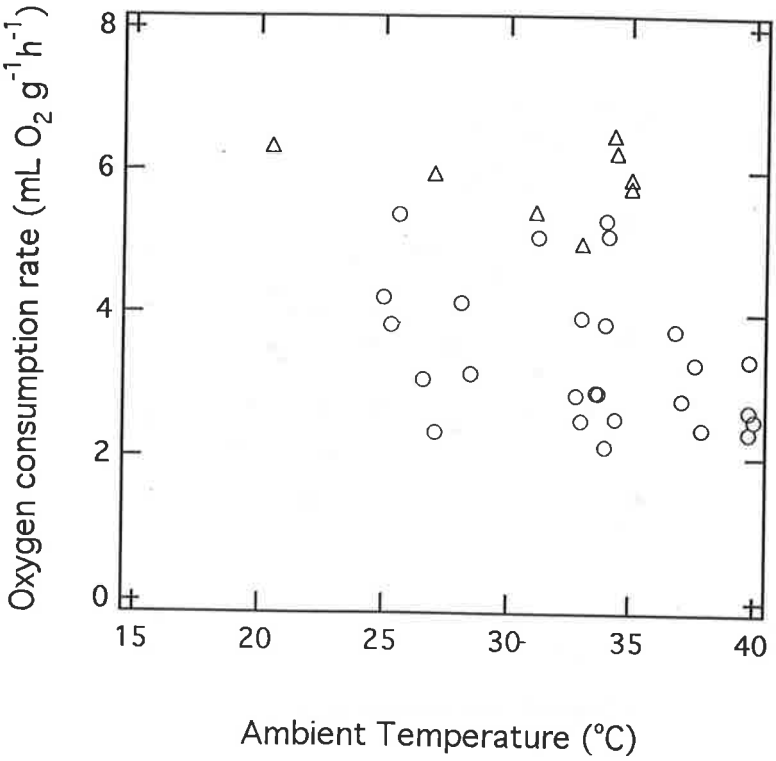

Fig. 2. The relationship between $\dot{V}O_2$ and T_a for quail chicks less than 5 days old. *Circles*: chicks 0-1 days old (n=6, N=26); *triangles*: chicks 2-4 days old (n=3, N=8).

$\dot{V}O_2$ *of chicks 6-17 days old*

Chicks 6 days old failed to increase $\dot{V}O_2$ at low T_a (15-25 °C) and maintained $\dot{V}O_2$ at a mean of 5.54 ± 0.48 mL O_2 $g^{-1}h^{-1}$ (mean mass 4.46 g n=3) over a T_a range of 17-32 °C, similar to the $\dot{V}O_2$ of chicks 4 days old between T_a 25-35 °C (fig. 3). The $\dot{V}O_2$ of all chicks between 6 and 17 days were significantly different in slopes and intercepts when body mass was used as a covariate (ANCOVA $F_{1,60}$= 22.693 P<0.001). $\dot{V}O_2$ of chicks at 10 days was variable at T_a below 35 °C, but some individuals showed an increase in $\dot{V}O_2$ at T_a 15-25 °C (mean 6.53 ± 1.30 mL O_2 $g^{-1}h^{-1}$ mean mass 5.99 ± 0.75 g n=5, N=15). Chicks older than 10 days old were less variable and increased $\dot{V}O_2$ significantly from 5.8 mL O_2 $g^{-1}h^{-1}$ at T_a 35 °C, up to 11.0 mL O_2 $g^{-1}h^{-1}$ at T_a 18-22 °C (r^2 = 0.811) (fig. 3). Variability in $\dot{V}O_2$ of chicks between the ages of 6 and 17 days was analysed by a stepwise multiple regression model, which included categories of age and chick body mass. Three classes of chick body mass were arbitrarily defined as covariate categories for chicks 6-17 days of age due to the variability in body mass at all ages; body mass <5.5 g, 5.5 to 7.5 g, and >7.5 g. The final model explained 74.1% of the variation in $\dot{V}O_2$ of quail chicks. Chick body mass was highly significant (F= 16.410 P<0.001), explaining 36.9% of the total variation in $\dot{V}O_2$. The effect of changes in body mass on $\dot{V}O_2$ across the T_a range, was also highly significant (F= 23.332 P<0.001), explaining a further 22.3% of variation in $\dot{V}O_2$. Larger quail chicks responded to decreases in T_a with

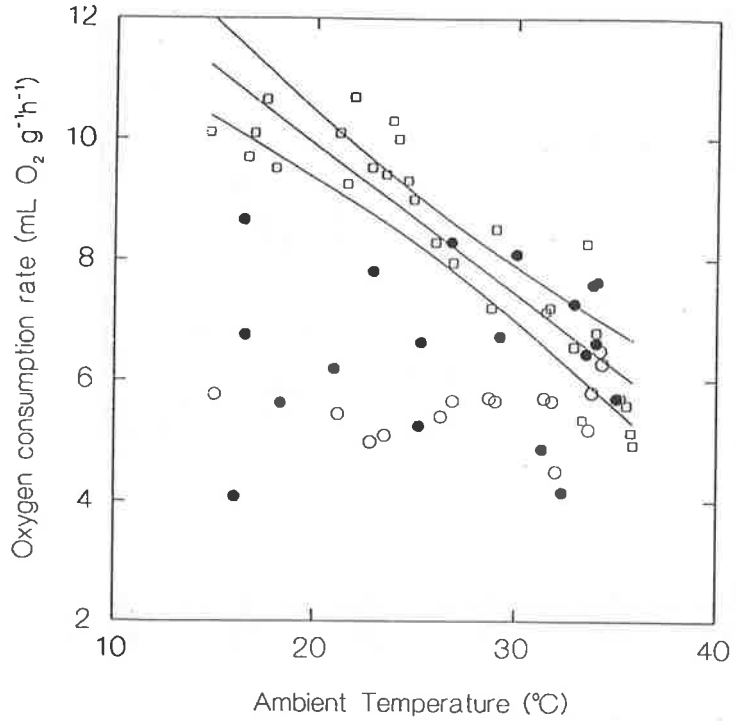

Fig. 3. Relationship between $\dot{V}O_2$ and T_a for quail chicks 6-17 days old. *Open circles* : chicks 6 days old (n=3, N=15); *filled triangles* : chicks 10 days old (5, 19); *open squares and solid line* : chicks 11-17 days old (4, 28). Solid line indicates a significant regression (± 95% CI) ($\dot{V}O_2 = 14.87 - 0.25\ T_a$). See Table 1 for regression statistics.

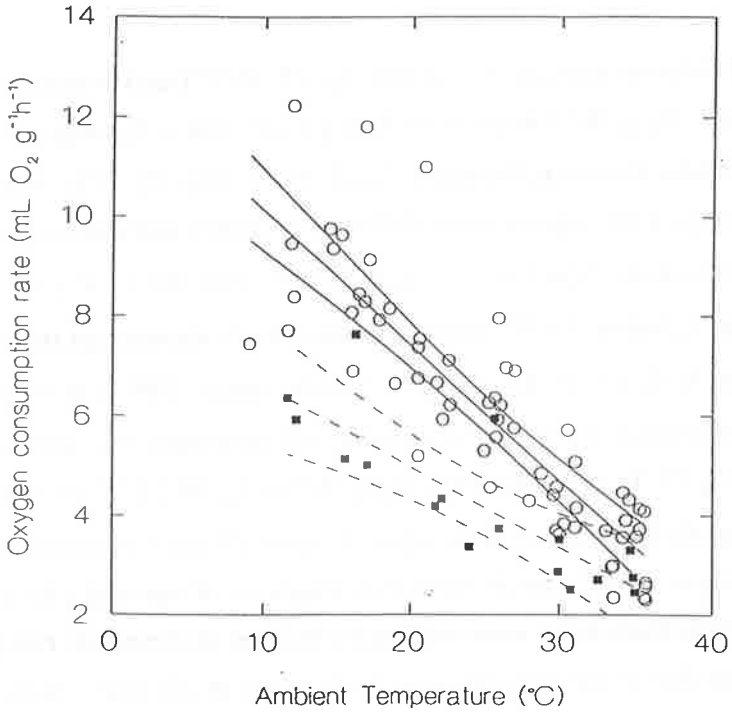

Fig. 4. The relationship between $\dot{V}O_2$ and T_a for quail chicks older than 26 days of age (± 95% CI). *Circles and solid lines*: chicks 26-35 days old ($\dot{V}O_2 = 12.81 - 0.27T_a$); *squares and dashed lines*: chicks 40-48 days old ($\dot{V}O_2 = 8.23 - 0.16T_a$). See Table 1 for regression statistics. The relationships were significantly different in slopes and intercepts (ANCOVA $F= 3.867$ $P<0.025$).

greater increases in $\dot{V}O_2$ in comparison to smaller chicks. Age was not significant in explaining variation in the model alone, but explained 1.1% of the variation when included in the final model (F= 2.406 N.S.). The variability in $\dot{V}O_2$ below T_a 35 °C between these age groups reflects the large variation in body mass during their development, which was between 5.5 and 11.0 g by day 17.

$\dot{V}O_2$ *of chicks older than 26 days of age*

The $\dot{V}O_2$ of all chicks older than 26 days of age was significantly related to T_a at T_a 10-35 °C, but was less than the $\dot{V}O_2$ of chicks at 11-17 days of age (Table 1, figs. 4-5). Between 11 and 48 days of age, $\dot{V}O_2$ at T_a 30-35 °C decreased with increasing age and body mass (figs. 4-5). Variability in $\dot{V}O_2$ of chicks older than 26 days of age was analysed by a stepwise multiple regression model, which included categories of age and chick body mass (<10 g, 10-15, 15-20, 20-30 and 30-40 g). The final model explained 88.1% of the variation in $\dot{V}O_2$ of quail chicks ($F_{1,88}$= 217.256 P<0.001). T_a explained 81.1% of the variation in $\dot{V}O_2$ (r^2= 0.657 F=127.919 P<0.001), but body mass (F= 67.799 P<0.001) and the interaction term between mass and T_a (F= 24.818 P<0.001) explained further variation (11.0% and 1.8% respectively). The interaction suggests that with increasing body mass the slope of the relationship between $\dot{V}O_2$ and T_a decreased significantly. However, age was not a significant factor in explaining the $\dot{V}O_2$ of quail chicks >26 days old.

Table 1. Relationship between $\dot{V}O_2$ and T_a below thermoneutrality for quail chicks older than 11 days of age. Linear regressions were fitted by least squares for each age group. Standard error of the regression coefficient (s_b) is presented for each regression.

Age (n, N)	Mean Mass (g) (range)	Regression (r^2; ± s_b)	F value	Probability
11-17 (4, 28)	9.54 ± 1.67 (7.04 - 11.50)	$\dot{V}O_2$ = 14.87 - 0.25 T_a (0.811; ± 0.023)	111.848	P<0.001
26-35 (11, 65)	17.21± 5.94 (8.99 - 28.45)	$\dot{V}O_2$ = 12.81 - 0.27 T_a (0.762; ± 0.019)	201.850	P<0.001
40-48 (3, 17)	29.12 (12.02 - 39.90)	$\dot{V}O_2$ = 8.232 - 0.163 T_a (0.710; ± 0.027)	36.181	P<0.001

Resting metabolic rates of chicks

The RMR of chicks increased with body mass initially, reaching a peak of 7.5 $mLO_2\ g^{-1}h^{-1}$ at 6-7 g, and then declined to adult levels at 25-40 g (fig. 5). RMR of chicks increased after 2 days of age with little change in body mass, but the mass of the yolk reserve was replaced by day 3. The $\dot{V}O_2$ of yolk-free hatchlings was 3.14 mL $O_2\ g^{-1}h^{-1}$. Therefore RMR increased by a factor of 1.6-2.4 after hatching (5.0-7.5 mL $O_2\ g^{-1}h^{-1}$), and then declined exponentially with further increases in body mass to 2.0 mL $O_2\ g^{-1}h^{-1}$ at body mass >25 g (fig. 5). Hatchling RMR was 81% of the predicted $\dot{V}O_2$ of non-passerines adult birds at 3.5 g (Aschoff and Pohl 1970) (fig. 6). Chick RMR exceeded the predicted adult value at 4-5 g, and continued to increase until 5-7 g, and then declined to the level of adults in this study, similar to the allometric relation of Ashoff and Pohl (1970) at 20 g. A significant negative relationship between log SMR and log Mass was found for quail >6 g (fig. 5). In comparison to the chicks in Bernstein's (1973) study, quail in this study had higher RMR at the same body mass, but the pattern of development was identical (fig. 6). In both studies the RMR was maximal at 6-10 g, but RMR of quail in Bernstein's study decreased with increasing body mass, below the allometric prediction. The regression coefficient for the chick RMR and body mass relationship decreased at a significantly steeper rate than the same relationship for adult birds (b= -0.50 and -0.28, respectively; fig. 5-6). The higher than expected RMR of the quail chicks <10 g, may reflect the higher thermal conductance of the thin skin and downy plumage of chicks, in comparison to adults, and thus small chicks require higher heat production to balance heat loss (Bernstein 1971).

Peak metabolic rates of chicks

In contrast to RMR, the PMR of chicks exposed to cold increased marginally in some chicks <9 g (1.0-1.7 × RMR) (fig. 5). PMR reached a maximal value mean of 8-15 mL $O_2\ g^{-1}h^{-1}$ at body mass between 9-10 g, which was at larger mass than the maximum in RMR. PMR declined significantly with further increases in body mass (fig. 5). The slope of decrease in PMR with body mass was not significantly different from that of relationship for RMR at the same body mass (ANCOVA F= 0.445 N.S.). The metabolic scope (PMR / RMR) of chicks >9 g was between 1.8-3.3 × RMR.

Residual analysis of metabolic rate and growth rate

The RMR and PMR of chicks were analysed to test if deviations in RMR were correlated intraspecifically with deviations from expected body mass at a given age. The residuals of the linear regression between RMR, PMR (RMR_{res} and PMR_{res}) and body mass were plotted against the residual body mass (M_{res}) for chicks >9 g (fig. 7). Neither

deviations in RMR nor deviations in PMR were correlated with M_{res} (RMR_{res} $F_{1,25}$= 3.860 N.S.; PMR_{res} $F_{1,19}$= 3.606 N.S.). Chicks with positive M_{res} did not have a significantly higher mean RMR_{res} or PMR_{res} than chicks with negative M_{res} (ANOVA RMR_{res} F= 3.399 N.S.; PMR_{res} F= 0.757 N.S.). The variability in RMR_{res} and PMR_{res} decreased with age in all chicks.

Thermogenic scope

The thermogenic scope (PMR - RMR) is defined as the maximum mass-specific heat production above thermoneutral levels that can be generated by a chick (Visser and Ricklefs 1993). Thermogenic scope was negligible in many hatchlings, but increased to a maximum of 20-60 mW g^{-1} at 10 g body mass (fig. 8). At body masses >20 g the thermogenic power decreased to a mean of 23.13 ± 7.27 mW g^{-1} (n=8). The T_a at which PMR is elicited during gradual cooling decreased from 35-40 °C at hatching to 20 °C at 5-7 g (fig. 9). At body masses >7 g the T_a at PMR decreased gradually despite large increases in mass.

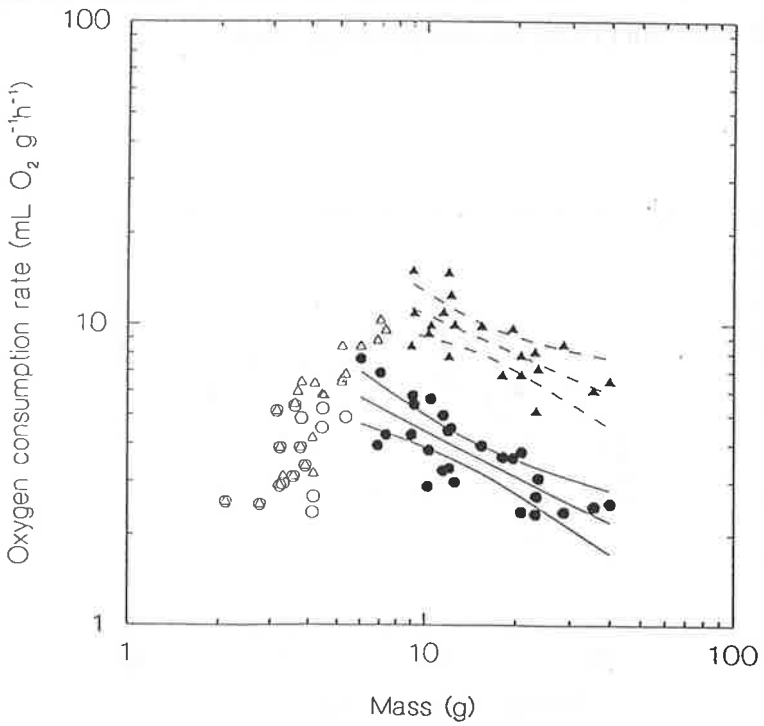

Fig. 5. Relationship between RMR (*circles*), PMR (*triangles*) and body mass for quail chicks. Filled symbols and lines indicate significant relationships (± 95% CI). *Solid line*: log RMR= 1.14 - 0.50 log M (body mass >6 g; s_b= 0.079 r^2= 0.617 $F_{1,25}$= 40.285 P<0.001); *dashed line*: log PMR= 1.46 - 0.44 log M (body mass >8 g; s_b= 0.099 r^2= 0.504 $F_{1,19}$= 19.316 P<0.001).

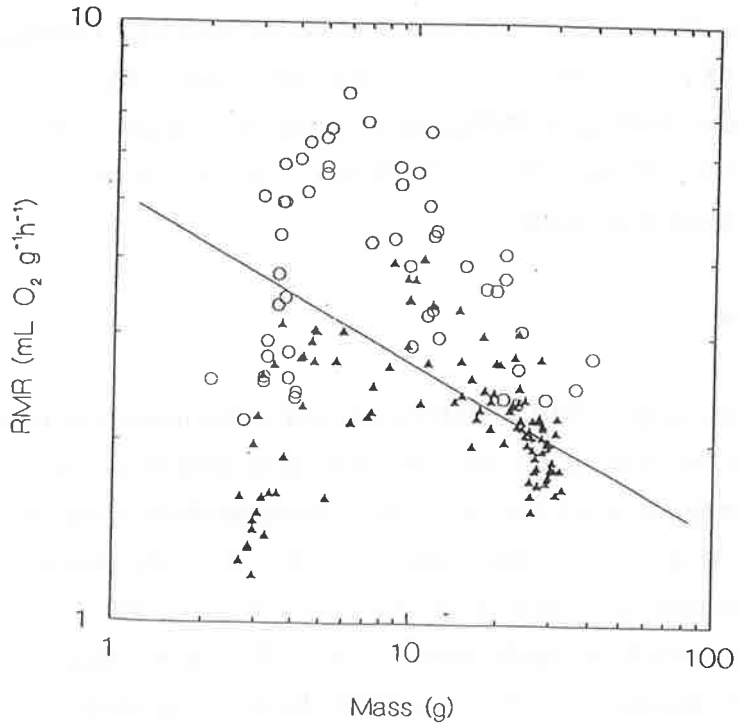

Fig. 6. The relationship between RMR and body mass for quail in this study (*circles*) and Bernstein (1973) (*triangles*). Solid line indicates the RMR predicted by allometric relationship of Aschoff and Pohl (1970) for non-passerine birds.

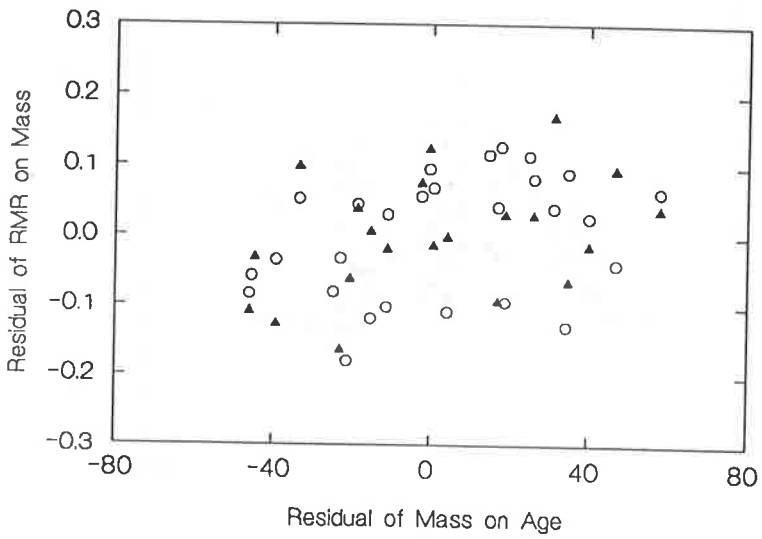

Fig. 7a. The relationship between deviations in RMR (*circles*), PMR (*triangles*) and deviations in body mass for quail >9 g. Residuals of metabolic rates based on linear regressions presented in figure 5.

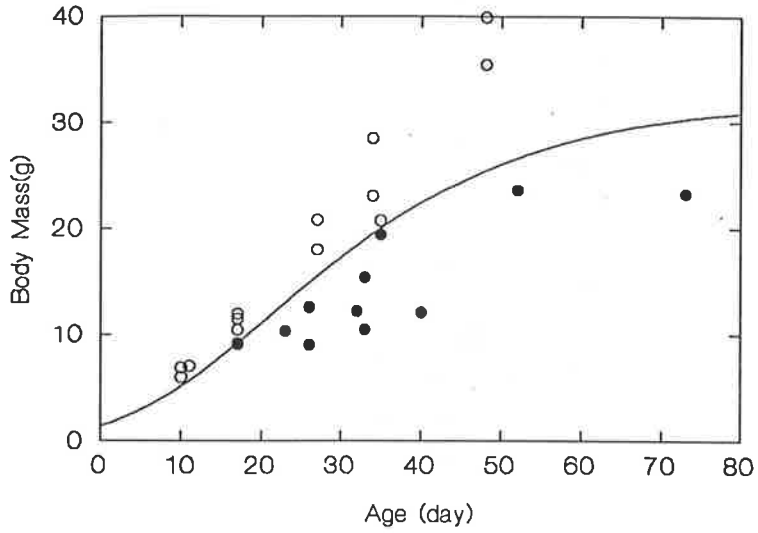

Fig.7b. (Continued from previous page) Growth of quail used in metabolism measurements (7a). Solid line indicates a significant relationship (A= 32.2 g, K_G= 0.054 day^{-1}, w_i= 21.2 d). *Filled symbols*: negative mass residuals, *open*: positive mass residuals.

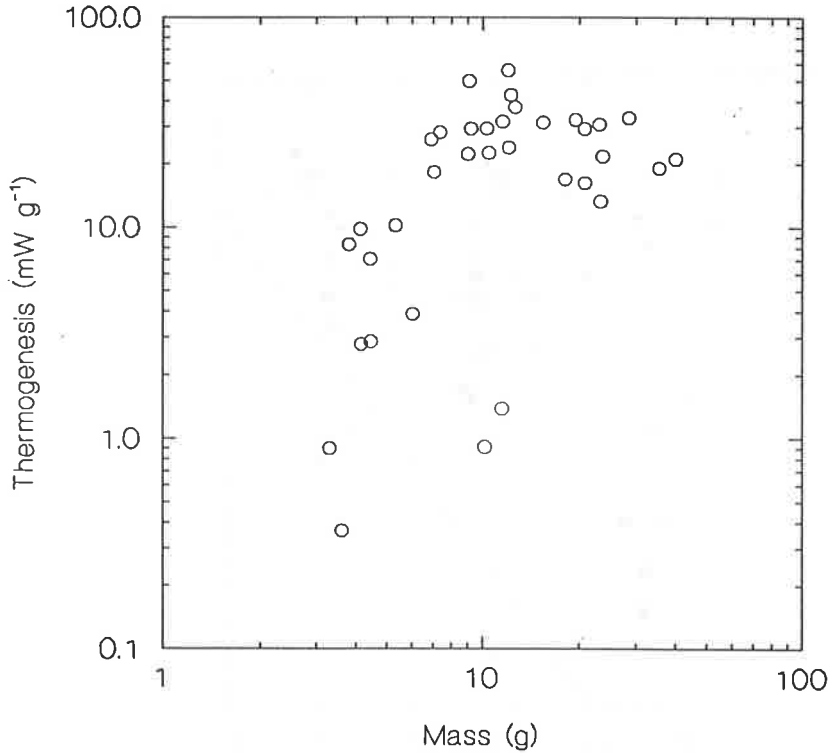

Fig. 8. The relationship between maximal thermogenic scope (mW g^{-1}) and body mass of quail during development.

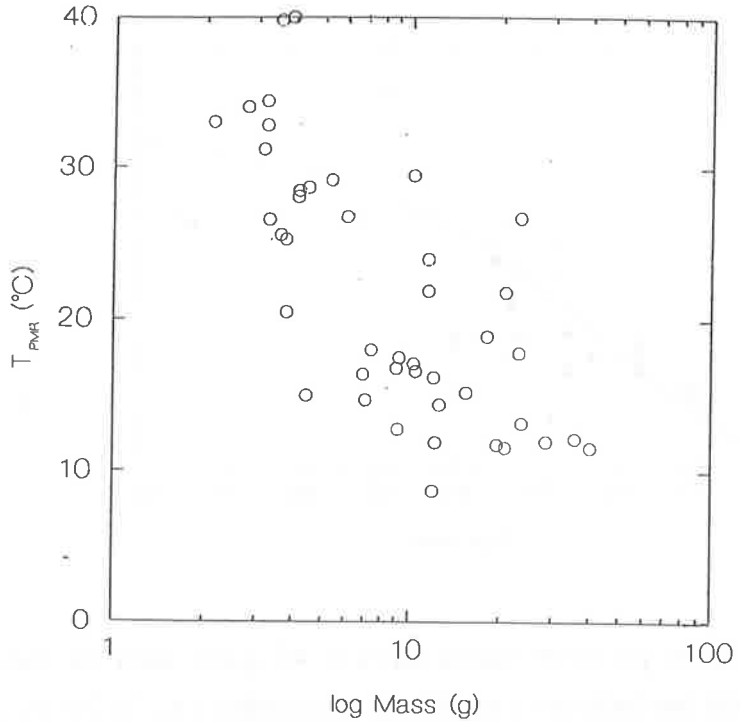

Fig. 9. The relationship between the T_a at which PMR (mL O_2 $g^{-1}h^{-1}$) was elicited during gradual cooling and body mass of quail.

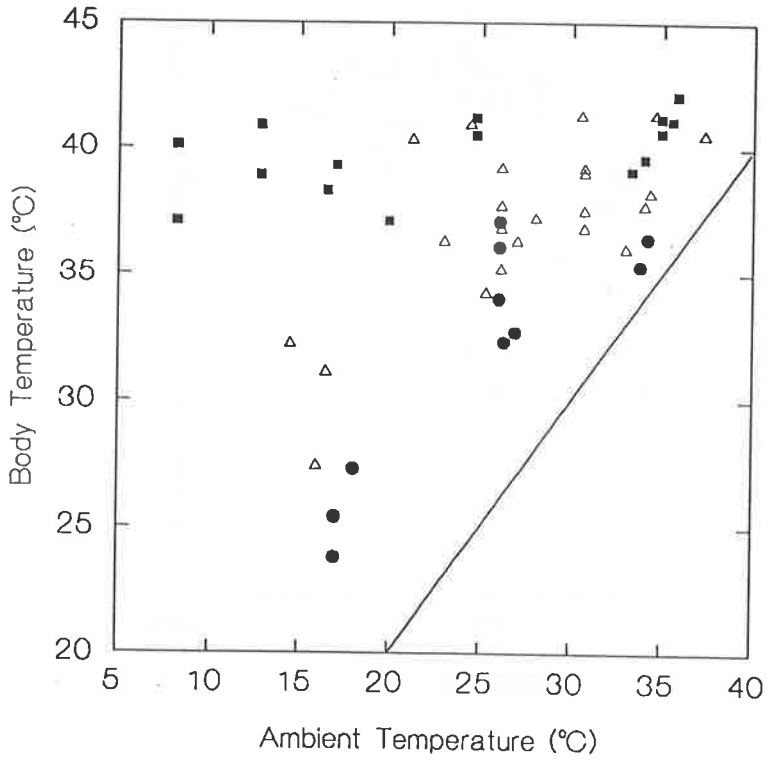

Fig. 10. Relationship between T_b and T_a in unbrooded quail between 6-18 days of age. *Circles*: chicks 6 days old (n=5, N=10); *triangles*: chicks 10-12 days old (10, 23); *squares*: 17-18 days old (6, 15). Solid line indicates T_b=T_a.

Body temperature of quail chicks

During short term cold exposure (T_a 15-30 °C), the T_b of unbrooded chicks declined in a poikilothermic manner in chicks less than 12 days of age (fig. 10). However, chicks 6-10 days of age were able to maintain considerable gradients between T_b and T_a. Chicks older than 12 days of age were able to maintain near constant levels of T_b at all T_a between 8-36 °C, but the set-point of T_b was variable, with the highest T_b being positively correlated with body mass. Chicks older than 26 days of age were fledglings and maintained constant T_b over the T_a range 10-35 °C when body mass was higher than 30 g (fig. 11). Chicks of the same age with lower body masses maintained T_b several degrees lower over the T_a range.

Development of metabolism and temperature regulation in cockatiel

$\dot{V}O_2$ *of chicks less than 13 days old*

$\dot{V}O_2$ was maintained at constant levels in most hatchlings during gradual cooling over T_a 23-37 °C, but was variable between chicks (fig. 12). $\dot{V}O_2$ increased with hatchling mass (3.90 ± 0.28 g n=9). Only a few chicks increased $\dot{V}O_2$ when T_a declined below the thermoneutral point (37.5 °C), but $\dot{V}O_2$ did not decline with T_a during gradual cooling in the rest of the hatchlings. The mean $\dot{V}O_2$ of hatchlings over the T_a range of 23-38 °C was 1.83 ± 0.32 mL O_2 $g^{-1}h^{-1}$ (n=9, N=20). The $\dot{V}O_2$ of two chicks at 3 and 4 days of age (mass 6.13 and 8.27 g) was higher than in hatchlings at thermoneutrality (2.5-4.5 mL O_2 $g^{-1}h^{-1}$) but declined below T_a 27 °C (fig. 13). The $\dot{V}O_2$ of chicks at thermoneutrality (33-37 °C) increased to a maximum at 5-6 days of age (mass 11.54 ± 0.66 g; 3.0-5.50 mL O_2 $g^{-1}h^{-1}$). After 5 days of age, chicks were all capable of increasing $\dot{V}O_2$ as T_a decreased, but 5-6 day old chicks were generally unable to increase $\dot{V}O_2$ below T_a 25 °C. The $\dot{V}O_2$ of chicks 8-13 days of age was significantly related to T_a between 20-37 °C (r^2= 0.530). Below T_a 20 °C, chicks less than 5 days of age were not capable of maintaining constant $\dot{V}O_2$, but the $\dot{V}O_2$ of chicks between 6-12 days of age was variable (4.5-9.0 mL O_2 $g^{-1}h^{-1}$) between T_a 12-20 °C (fig. 13).

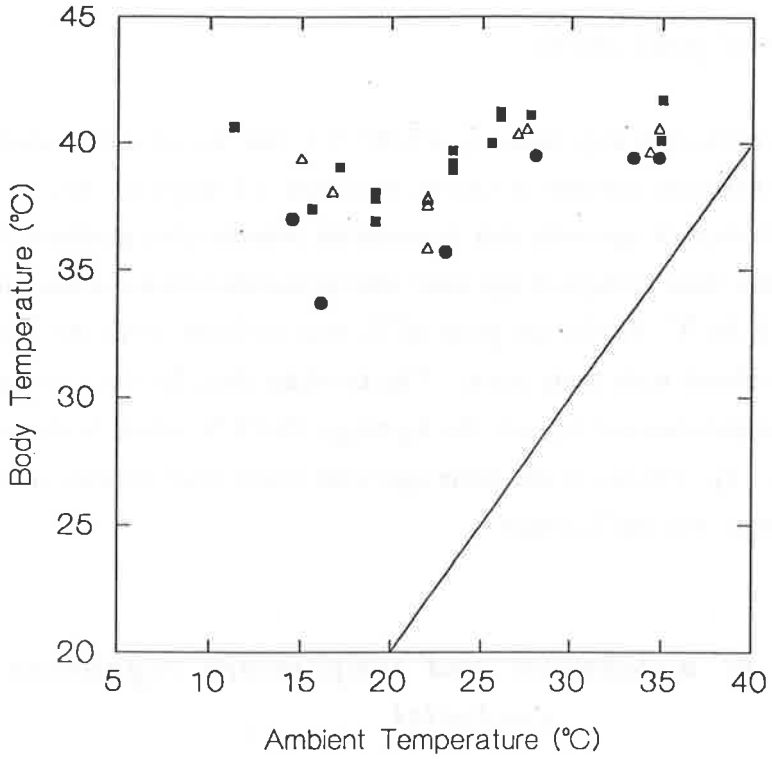

Fig. 11. The relationship between T_b and T_a in quail older than 26 days of age. *Circles*: chicks 26-27 days old (n=4, N=6); *triangles*: chicks 32-35 days old (7, 10); *squares*: chicks 40-48 days old (3, 15). Body mass of chicks is included in Table 2. Solid line indicates T_b=T_a.

$\dot{V}O_2$ *of chicks greater than 13 days old*

The $\dot{V}O_2$ of chicks at 14-17 days old was linearly related to T_a between 15-37 °C (Table 2, fig. 14). The $\dot{V}O_2$ of chicks between 20-37 °C was not significantly different between chicks 8-13 days old and 14-17 days old (ANCOVA slope F=2.060 N.S., intercept t= -0.923 N.S.). Below T_a 20 °C chicks 14-17 days old were able to increase $\dot{V}O_2$, but the $\dot{V}O_2$ of chicks 8-13 days old was either maintained at a constant level or decreased (figs. 13-14). Between T_a 10-15 °C the $\dot{V}O_2$ of chicks 14-17 days old was constant between 6.0-8.0 mL O_2 $g^{-1}h^{-1}$. The relationship between $\dot{V}O_2$ and T_a below the TNZ was not significantly different in chicks 18-27 days old from chicks 14-17 days old (ANCOVA F= 0.007 N.S.) (fig. 15). However, a TNZ in the older group was evident between T_a 30-36 °C. The $\dot{V}O_2$ of chicks 18-27 days old was lower in the heavier chicks at all T_a (fig. 15).

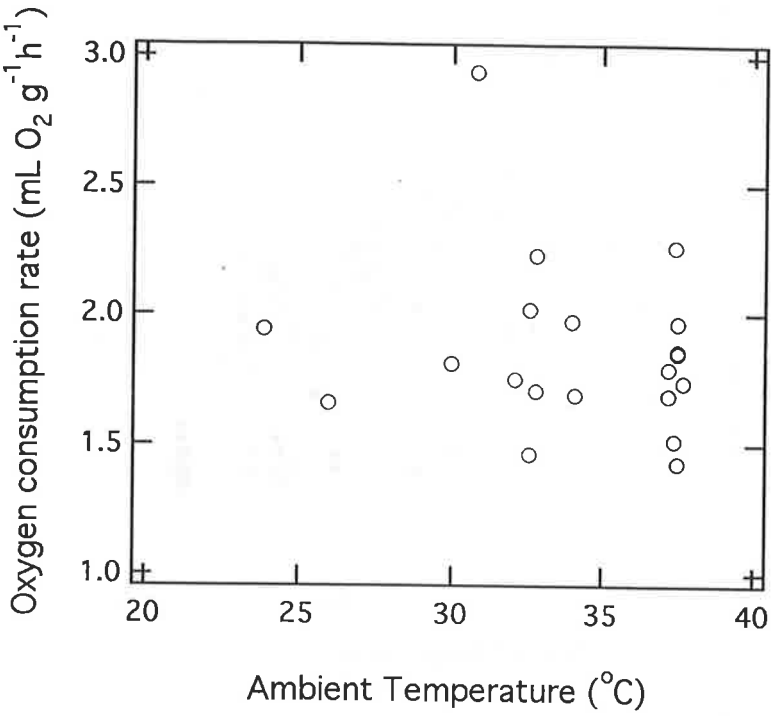

Fig. 12. The relationship between $\dot{V}O_2$ and T_a during gradual cooling in cockatiel hatchlings over the T_a 20-38 °C (n=9, N=18).

Table 2. Relationship between $\dot{V}O_2$ and T_a below thermoneutrality for cockatiel chicks older than 8 days of age. Linear regressions were fitted by least squares for each age group. Only significant relationships (P<0.001) are presented over the specified T_a range. ($\dot{V}O_2$ in mL O_2 $g^{-1}h^{-1}$).

Age (n, N)	Mean Mass (g) (range)	Regression (r^2; ± s_b)	T_a range (°C)	F value
8-13 (9, 26)	24.00 ± 10.90 (9.74 - 41.20)	$\dot{V}O_2 = 9.76 - 0.16\ T_a$ (0.530; 0.029)	20-37	29.266
14-17 (10, 49)	27.97± 15.31 (19.96 - 60.57)	$\dot{V}O_2 = 11.28 - 0.22\ T_a$ (0.664; 0.023)	15-37	92.960
18-27 (9, 37)	67.39 ± 14.73 (40.19 - 86.29)	$\dot{V}O_2 = 10.34 - 0.22\ T_a$ (0.775; 0.020)	12-33	120.581

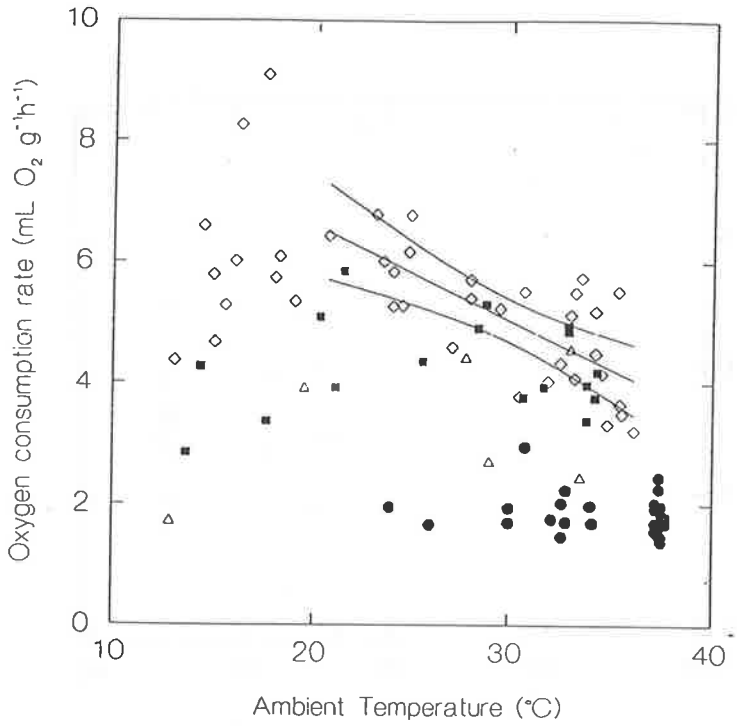

Fig. 13. The relationship between $\dot{V}O_2$ and T_a in unbrooded cockatiel chicks less than 13 days of age during gradual cooling at T_a 10-38 °C. *Circles*: hatchlings (same as fig. 12); *triangles*: 3 and 4 day old chick (n=2, N=6); *squares*: chicks 5-6 days old (4, 17); *diamonds and solid lines*: chicks 8-13 days old (9, 37). Solid line indicates significant regression (± 95% CI) for chicks 8-13 days old at T_a >20 °C ($\dot{V}O_2 = 9.75 - 0.16T_a$). See Table 2 for regression statistics.

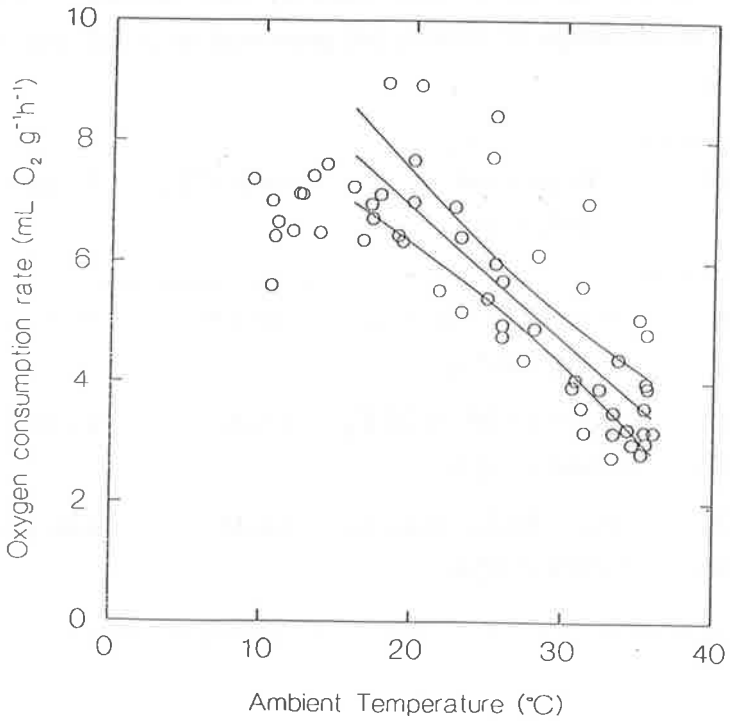

Fig. 14. The relationship between $\dot{V}O_2$ and T_a in unbrooded chicks at 14-17 days of age (n=10, N=59). Solid lines indicates a significant regression (± 95% CI) ($\dot{V}O_2 = 11.28 - 0.22T_a$). See Table 2 for regression statistics.

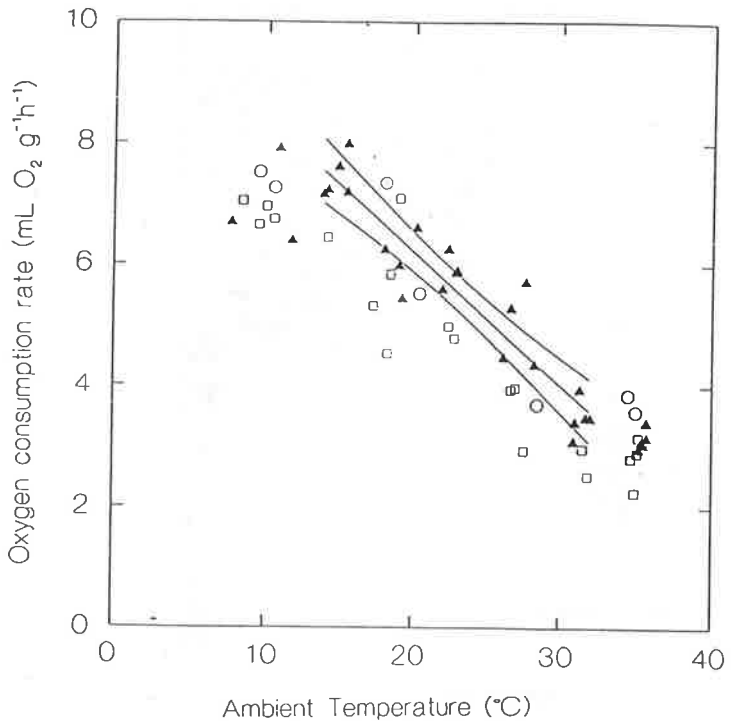

Fig. 15. The relationship between $\dot{V}O_2$ and T_a in unbrooded chicks at 18-27 days of age (n=9, N=56). Solid lines indicates a significant regression (± 95% CI) ($\dot{V}O_2$ = 10.34 - 0.22T_a). See Table 2 for regression statistics. *Circles*: chicks <50 g; *triangles*: chicks 50-80 g; *squares*: chicks >80 g.

Resting metabolic rates of chicks

RMR increased within three days of hatching to 4.0-6.0 mL O_2 $g^{-1}h^{-1}$ at 9-10 g (fig. 16). Unlike the quail, cockatiel chicks doubled their body mass in 3-4 days, including the utilisation of the yolk reserve in that period. The gap in the points of figure 16 between 6-10 g indicates this early period of rapid growth in cockatiel, during which $\dot{V}O_2$ was unfortunately not determined. The yolk-free RMR of cockatiel hatchlings was 1.99 mL O_2 $g^{-1}h^{-1}$ and therefore the RMR of chicks at 9-10 g increased 2-3 × hatching RMR, which was maximal in cockatiel (fig. 16). The RMR of cockatiel chicks was compared with the predicted RMR of adult parrots of the same mass (fig. 17). The allometric relationship between RMR (or BMR) in adult parrots and body mass was recalculated from Table 2 (eq. 6) of Williams et al. (1991) to obtain mass-specific RMR. Cockatiel chicks have RMR equivalent to adult RMR between 6-9 g, and exceed the adult RMR at body masses above 9 g throughout development by 30-200% (fig. 17). As body mass increased above 9 g, RMR decreased linearly to 3.0 mL O_2 $g^{-1}h^{-1}$ on average at 80-90g. The relationship between RMR and body mass was significant in chicks >9 g, and was identical in slope to the allometric relationship between predicted adult RMR and body mass (r^2= 0.634 $P< 0.001$).

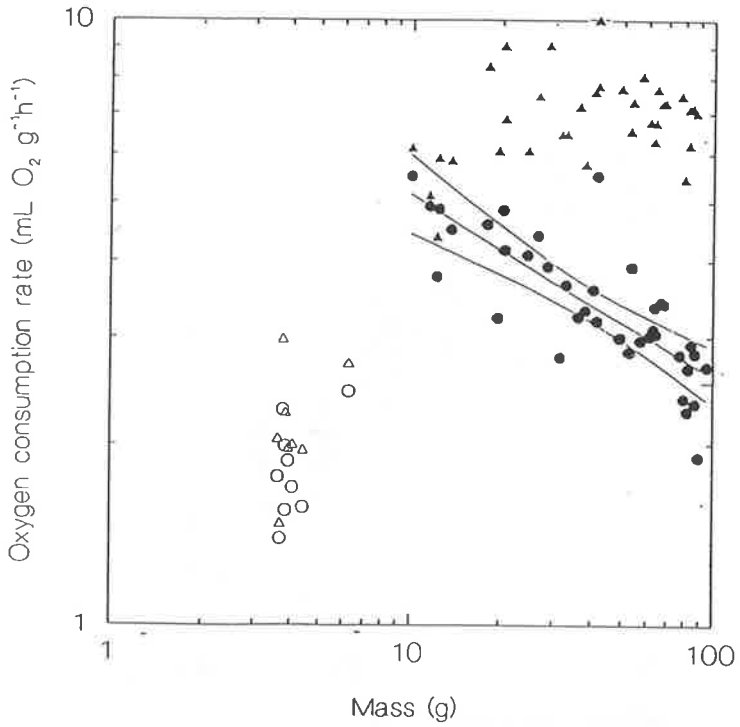

Fig. 16. Relationship between RMR (*circles*), PMR (*triangles*) and body mass for cockatiel chicks. Filled symbols and lines indicate significant relationships (± 95% CI). *Solid line*: log RMR= 1.00 - 0.30log M (body mass >9 g; s_b= 0.037 r^2= 0.634 $F_{1,36}$= 62.353 P<0.001); relationship between PMR and Mass not significant (log PMR= 0.78 - 0.08 log M body mass >9 g; s_b= 0.041 r^2= 0.102 $F_{1,33}$= 3.752 P<0.06).

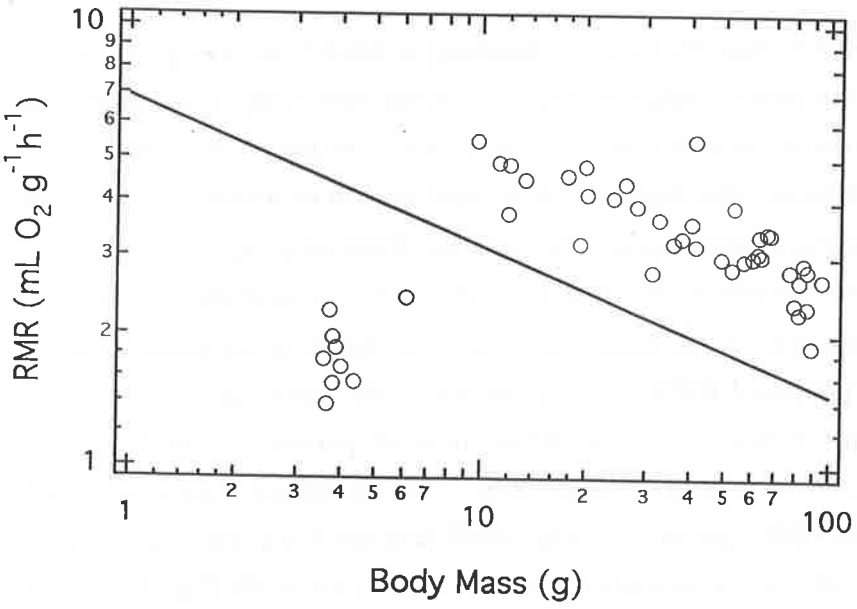

Fig. 17. Relationship between RMR and body mass of cockatiel chicks. Solid line indicates the predicted RMR of adult parrots of the same mass (Williams et al. 1991; log RMR= 0.838 - 0.336 log M).

Peak metabolic rates in chicks

The PMR of chicks <15 g increased with body mass, but was little higher (10-30%) than RMR (fig. 16). Above 10 g the RMR decreased with body mass, but PMR were maintained at constant but variable levels (mean 6.81 ± 1.18 mL O_2 $g^{-1}h^{-1}$). The relationship between PMR and body mass >10 g was not significant (r^2= 0.102 $F_{1,33}$= 3.752 P<0.06). The metabolic scope of cockatiel increased linearly with body mass from 1.0-1.5 × RMR at hatching to 2.5 × RMR at asymptotic mass (PMR÷RMR= 1.20 + 0.02 Mass, r^2= 0.734 $F_{1,43}$= 115.615 P<0.001).

Residual analysis of metabolic rate and growth rate of cockatiel

The residuals of the linear regression between RMR, PMR (RMR_{res} and PMR_{res}) and body mass were plotted against residual body mass (M_{res}), which is the deviation from the expected body mass for that age, for chicks >9 g (fig. 18). Deviations in RMR were not correlated with M_{res} (r^2= 0.039 $F_{1,37}$= 1.484 N.S.), but deviations in PMR were significantly correlated with M_{res} (r^2= 0.325 $F_{1,34}$= 16.341 P<0.001). The slope of this intraspecific relationship was low, but was significantly different from zero (PMR_{res} = 0.008 - 0.001M_{res}, slope t= -4.042 P<0.001). The variability in RMR_{res} and PMR_{res} decreased with age in all chicks.

Thermogenic scope

The thermogenic scope (PMR-RMR) was less than 2 mW g^{-1} at hatching, but increased to 15-20 mW g^{-1} at 20 g (fig. 19). The thermogenic power of chicks between 25-90 g was constant at a mean of 21.40 ± 3.94 mWg^{-1} (N=25 range 13.33-27.91 mW g^{-1}). The T_a at which PMR was elicited by some hatchlings during gradual cooling was only 2-5 °C below the thermoneutral point (37 °C) (fig. 20). As body mass increased the T_a at PMR decreased approximately linearly throughout development, but was variable.

Body temperature of chicks

Unbrooded chicks without sibling contact were first able to maintain high T_b (33-40 °C) at 10-13 days of age at T_a >15 °C (fig. 21). Below T_a 15 °C, chick T_b declined steeply with decreasing T_a in chicks at 10-13 days of age. Chick T_b at 14-17 days of age was generally maintained at higher levels than younger chicks, with most chicks maintaining constant levels of T_b >30 °C at T_a 10 °C. The mean T_b of unbrooded chicks between 18 days of age and prior to fledging at 35 days was 38.7 ± 2.8 °C (n=13, N=30) (fig. 21). However, chicks older than 18 days of age with low body mass for their age, had subadult T_b. Individual chicks 18 days old or greater than 50 g body mass were

effectively homeothermic. The T_b of huddled broods during parental absences during the day at T_a 10-25 °C was dependent on age and the body mass of each sibling in the brood (fig. 22). The T_b of broods with young chicks of small body mass (<10 g each) were only 2-3 °C above T_a, but the T_b of chicks was maintained at higher levels when each sibling was 20 g or more.

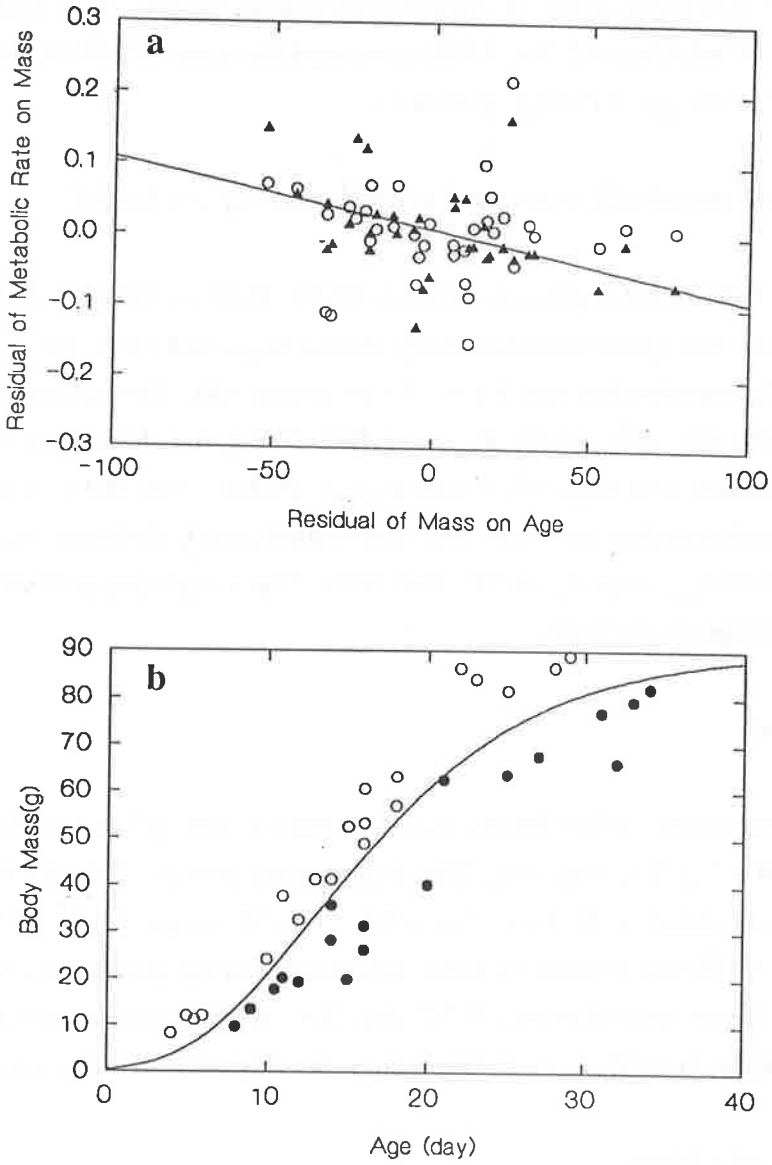

Fig. 18a. The relationship between deviations in RMR (*circles*), PMR (*triangles*) and deviations in body mass for cockatiel >9 g. Residuals of metabolic rates based on linear regressions presented in figure 16. Solid line indicates significant relationship (PMR_{res}= 0.008 - 0.001 M_{res}, r^2= 0.325 $F_{1,34}$= 16.341 P<0.001). **b.** Growth of cockatiel used in metabolism measurements (18a). Solid line indicates a significant relationship (A= 90.5 g, K_G= 0.130 day^{-1}, w_i= 13.0 d). *Filled symbols*: negative mass residuals, *open*: positive mass residuals.

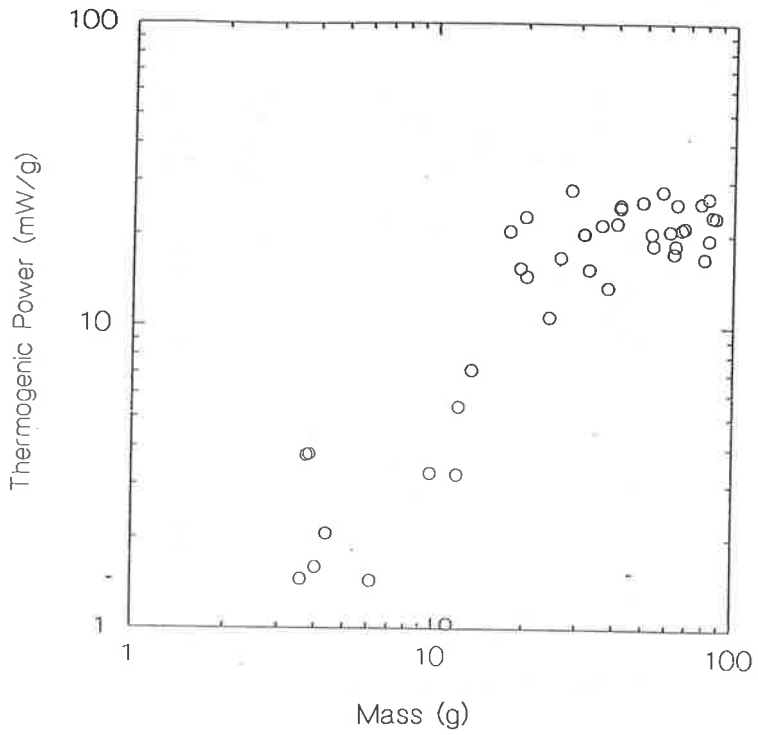

Fig. 19. The relationship between maximal thermogenic scope (mW g^{-1}) and body mass of cockatiel during development.

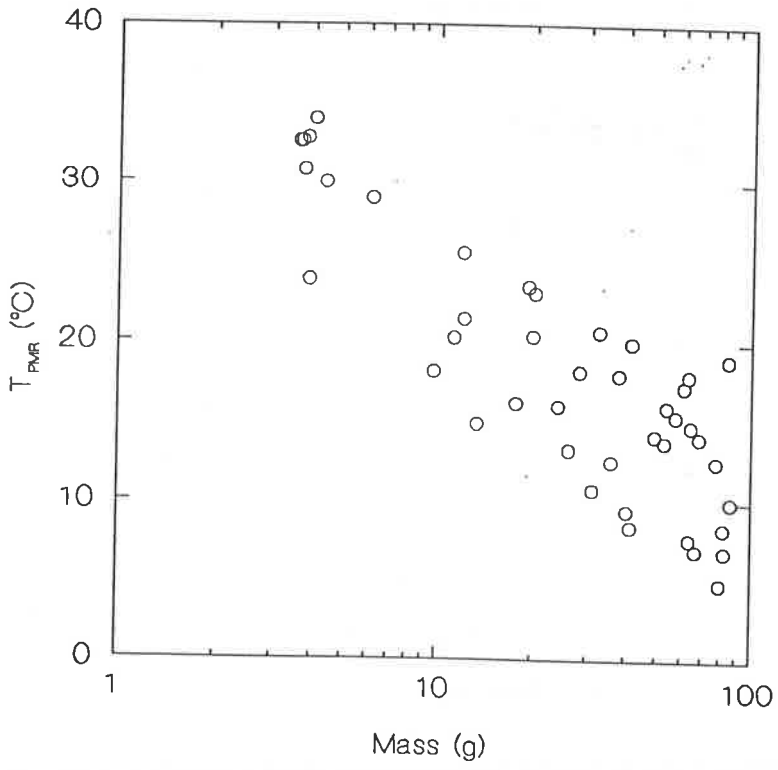

Fig. 20. The relationship between the T_a at which PMR (mL O_2 $g^{-1}h^{-1}$) was elicited during gradual cooling and body mass of cockatiel.

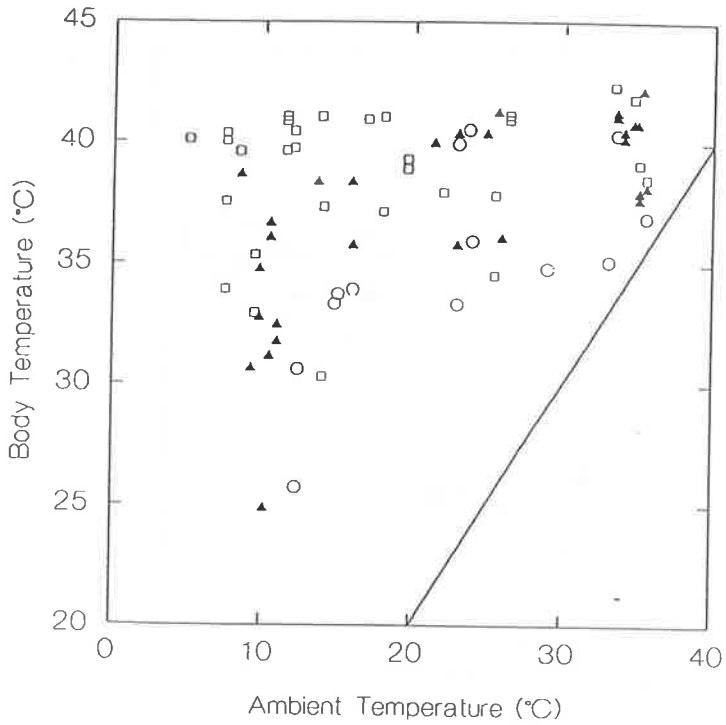

Fig. 21. Relationship between T_b and T_a for unbrooded cockatiel chicks between T_a 10-40 °C. *Circles*: chicks 10-13 days old (n=6, N=13); *triangles*: chicks 14-17 days old (12, 29); *squares*: chicks 18-35 days old (13, 30). Solid line indicates $T_b=T_a$.

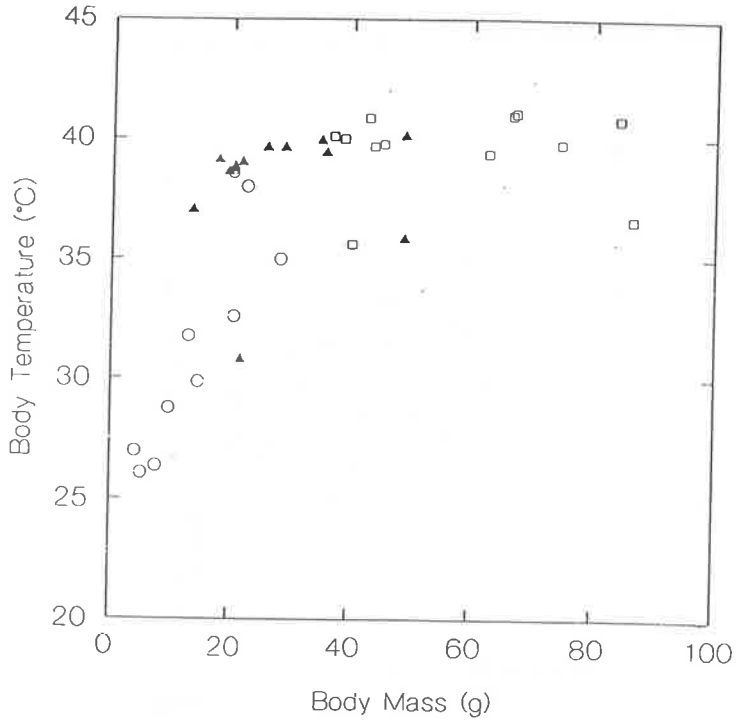

Fig. 22. Relationship between chick T_b and body mass for chicks huddled in broods of 2-4 chicks in the absence of parental brooding (T_a 10-25 °C). *Circles*: total brood mass <50 g (N=10); *triangles*: total brood mass 50-90 g (12); *squares*: total brood mass >90 g (13).

Achieving physiological homeothermy

The proportion of the adult thermal gradient maintained by individual king quail and cockatiel chicks during cold exposure (T_a 20-25 °C) was calculated as the thermoregulatory index (TI) of Dunn (1975). Physiological homeothermy (TI=100%) was achieved at 10 g in this study for king quail, 20 g for king quail in Bernstein's (1973) study, and 20-40 g in cockatiel (fig. 23). Effective homeothermy, as defined by Dunn (1975) as 75% of the adult thermoregulatory ability, was achieved at 5-7 g in this study and 7-10 g in Bernstein's study for king quail, and 20 g in the cockatiel. Cockatiel TI values were more variable than quail at all body masses. The age at which physiological homeothermy was achieved was dependent on growth rate. In Bernstein's study quail reached 20 g body mass at 20-25 days of age, but in this study the age at physiological homeothermy was between 12 days (warm group) and 30 days (cold group). Physiological homeothermy was reached between 12-13 days (warm group) and 15-20 days (cold group) in cockatiel.

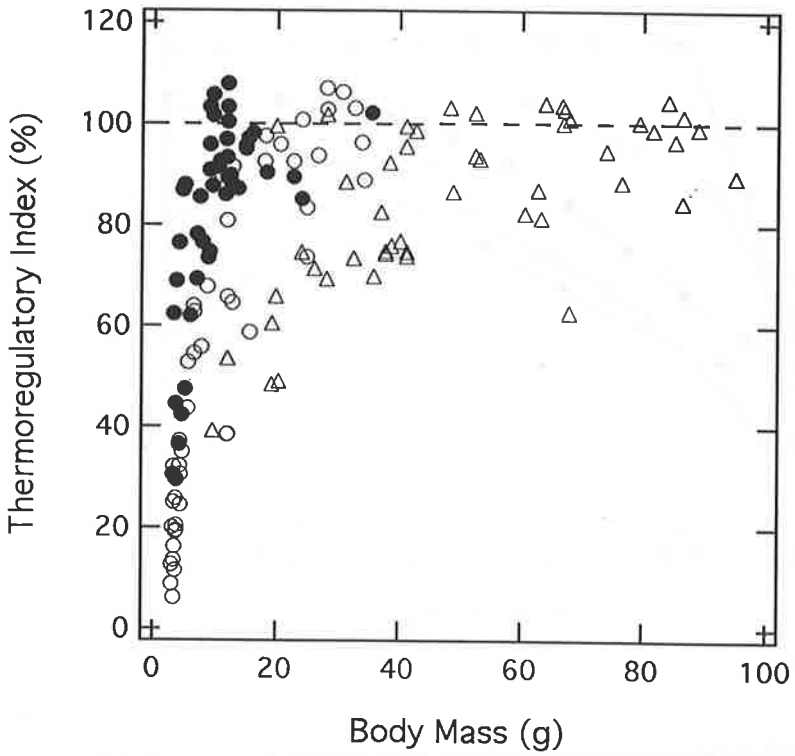

Fig. 23. Relationship between the fraction of the adult thermal gradient maintained between a chick and its environment and body mass of the chick. Thermoregulatory index defined by Dunn (1975) at T_a 20-25 °C. Dashed line indicates 75% of adult thermoregulatory ability. *Filled circles*: king quail this study; *open circles*: king quail (Bernstein 1973); *triangles*: cockatiel.

Physiological maturity during development

Mass-independent metabolic rates (MIM) were calculated from hatching to fledging for the precocial king quail (Galliformes) and altricial species including the cockatiel and lovebird (*Agapornis roseicollis*) from Psittaciformes, and the red-winged blackbird (*Agelaius phoeniceus*) and savannah sparrow (*Passerculus sandwichensis*) from Passeriformes. The relationship between MIM of chicks was compared between species after normalising the age during development (age÷fledging period) (fig. 24). MIM values were less than 5 mL O_2 $h^{-1}g^{-0.67}$ in all hatchlings. MIM was highest at hatching in the precocial king quail, and next highest in the passerine hatchlings, and lowest in the psittaciform hatchlings. But later cockatiel MIM increased to levels higher than even the precocial quail, and much higher than the passerines (fig. 24).

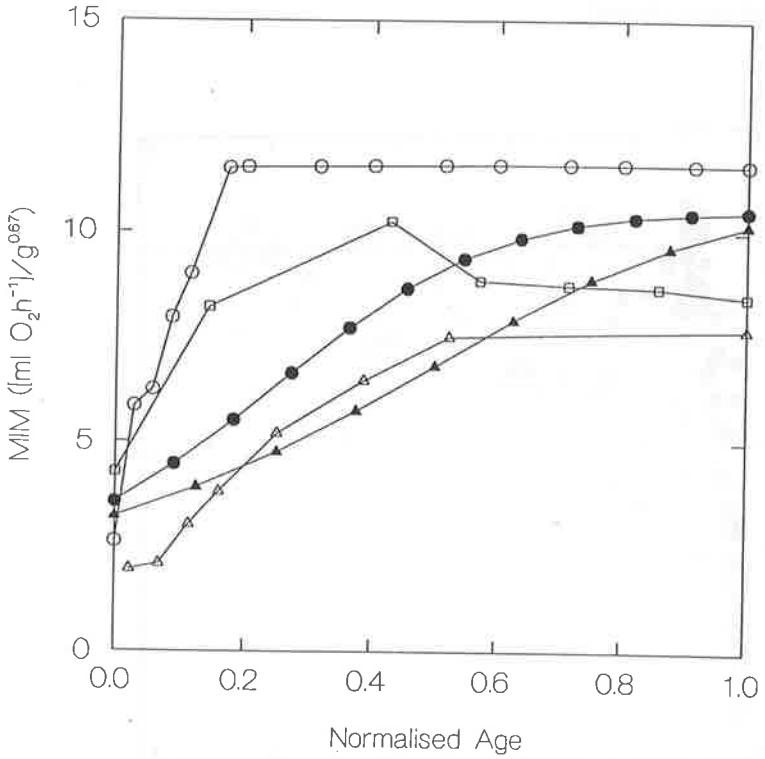

Fig. 24. The relationship between mass-independent metabolic rates (MIM) of chicks and age for four altricial species and a precocial species. Chick age from hatching to fledging was normalised for comparison (age÷fledging period). *Squares*: king quail (this study); *open circles*: cockatiel (this study); *closed circles*: red-winged blackbird (Olson 1992); *closed triangles*: savannah sparrow (Williams and Prints 1986); *open triangles*: lovebird (Bucher and Bartholomew 1986).

The degree of precocity at hatching and throughout development was assessed by dividing chick MIM (MIM_c) by the MIM of the fledging bird (MIM_{fl}) (Bucher 1986). The relationship between MIM_c:MIM_{fl} and age up until fledging was compared between species (fig. 25). The MIM ratios were higher in the cockatiel than in the Psittaciform species or the passerines, but all were lower than the king quail. MIM values for all hatchlings were underestimated because of the presence of metabolically inactive yolk reserve (Klaassen et al. 1987). King quail and cockatiel were underestimated by 16 and 45% respectively on the day of hatch in figure 25 (recalculated with yolk-free hatchling mass). MIM ratios presented in Bucher (1986), which were also calculated on the basis of yolk-free hatchling mass, were 17% higher for *Agapornis roseicollis* and 78% lower in *Agelaius phoeniceus*. This suggests that the ranking amongst altricial species at hatching in figure 26 are not accurate. However, correcting for yolk reserve was not possible because the yolk reserves were not reported for *Passerculus sandwichensis* (Olson 1992). Quail and cockatiel MIM ratios increased to fledging MIM at about 20% of the fledging period for both species. The lovebird increased in metabolic maturity more slowly to a maximum at 55% of the fledging period. The passerine MIM ratios increased isometrically with age and did not reach fledging values until 70 and 100%. This pattern of development suggests that parrots have a higher degree of physiological maturity compared to passerines, but to a varying extent between species, which develops within days after hatching.

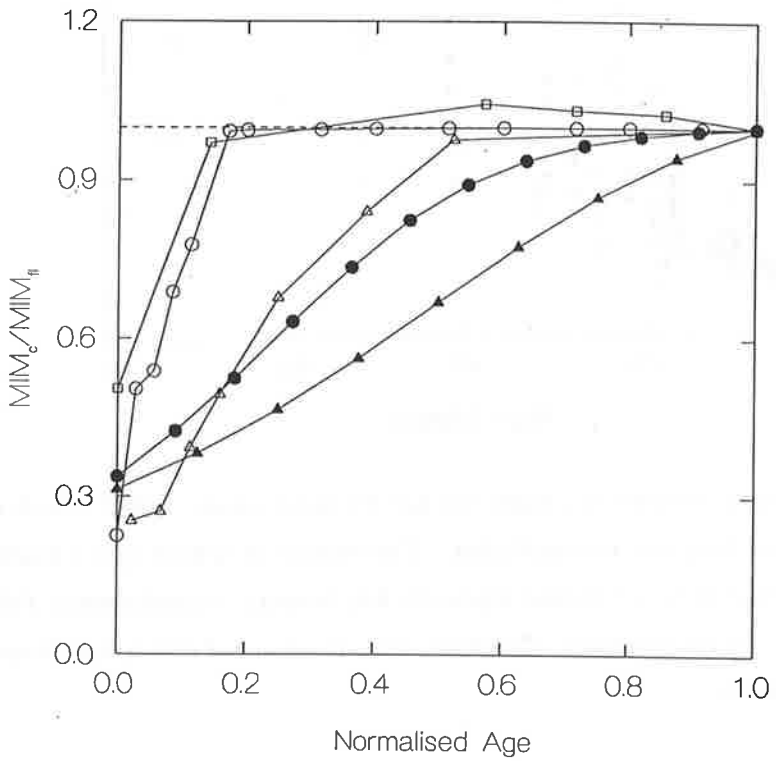

Fig. 25. The relationship between the ratio of chick MIM to fledging MIM and normalised age in the same species presented in figure 24.

Posthatching growth of king quail

Chick mortality was greatest in the first two weeks after hatching and few quail survived to maturity. Most deaths were attributed to fatal cold exposure during periods of cold and wet conditions early in the breeding season (September - October). A few chicks were killed by adult birds and rodents. The body mass of king quail chicks during development was variable between months in which they hatched (fig. 26). The growth rates of some quail which hatched in summer (December-February) were higher than for the same species in the study of Bernstein (1973), but others during summer were half the growth rate (fig.27). The body masses of quail presented in figure 26 include only chicks which continued to increase body mass during development. Quail which did not increase body mass in the first 10-15 days after hatching died.

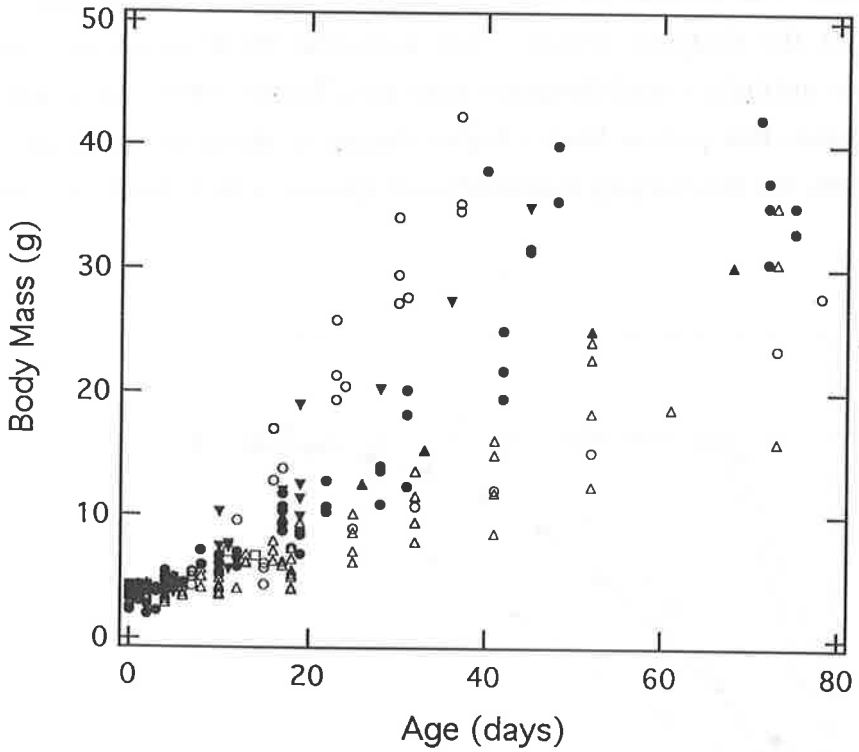

Fig. 26. Relationship between body mass and age for king quail. Quail which did not increase mass after hatching are not included. The month in which quail hatched are indicated by different symbols as follows: *Open circles*: January; *closed circles*: February; *open squares*: March; *open triangles*: October; *closed inverted triangles*: November; *closed triangles*: December.

Asymptotic body mass was between 30-45 g in quail. The highest growth rates (0.073 day^{-1}) were correlated with the highest asymptotes (45 g), which were attained at 35-40 days. The lowest growth rates (0.035 day^{-1}) were correlated with low asymptotes (30 g), which were reached at 70-80 days of age. The differences in body mass of quail were evident in the first 10 days after hatching (fig. 26). It was not possible to fit Gompertz growth functions to body mass for all chicks, because some were killed by adults or failed to increase mass and died. The relationship between growth and ambient temperature and the duration of daylight during the first 10 days was examined for all chicks which survived at least that period. An index of growth was calculated by dividing body mass at 10 days of age by initial mass. Body mass of chicks on day 1-2 was used as initial mass if mass on day of hatch was not known, and body mass at 10 days old was interpolated from measurements within 3 days before or after day 10 if mass on day 10 was not measured. Daily maximum T_a were averaged for the first 10 days after hatching for each chick. Growth rates of quail were significantly related to the duration of daylight (r^2= 0.265 $P<0.001$), but not related to the average maximum T_a during the 10 days (fig. 29). The increases in body mass over the first 10 days were directly related to the amount of daylight per day that was available, but were highly variable. The increases in body mass were up to three times hatchling mass.

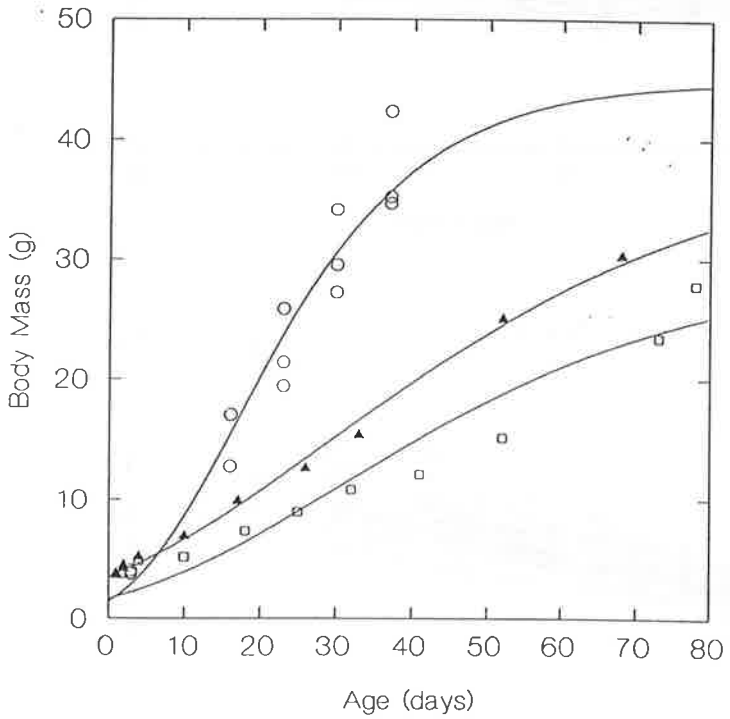

Fig. 27. The relationship between body mass and age of three separate quail broods hatched during December and January. Each point represents an individual quail. Gompertz growth curves for each brood were fitted (see text), and are indicated by solid lines. Asymptotic mass (A) and growth constants (K_G) for each brood are: *Circles*: A= 45g K_G= 0.073 day^{-1}; *triangles*: A= 40 g K_G= 0.035 day^{-1}; *squares*: A= 30 g K_G= 0.031 day^{-1}.

The earliest age at which quail fledged was 19 days, but most fledged at 25-28 days. Quail were between 7-30 g body mass at fledging, or 30-60% of adult mass. All quail were fully feathered at fledging and attained adult plumage shortly after fledging.

Relative growth rates (RGR) and absolute growth rates (AGR) were calculated as a function of body mass using the Gompertz growth equations obtained for king quail (figs. 30-31). RGR and AGR were also calculated for quail in a previous study (Bernstein 1973). RGR decreased with increases in body mass, but the time period over which it declined was longer for chicks with low K_G (fig. 30). AGR for quail with a K_G of 0.073 day^{-1} peaked 1.7 g day^{-1} at 17 g body mass, but quail with a K_G of 0.035 day^{-1} peaked at 0.55 g day^{-1} or 33% of the quail with high relative growth rates, at 10 g body mass (fig. 31).

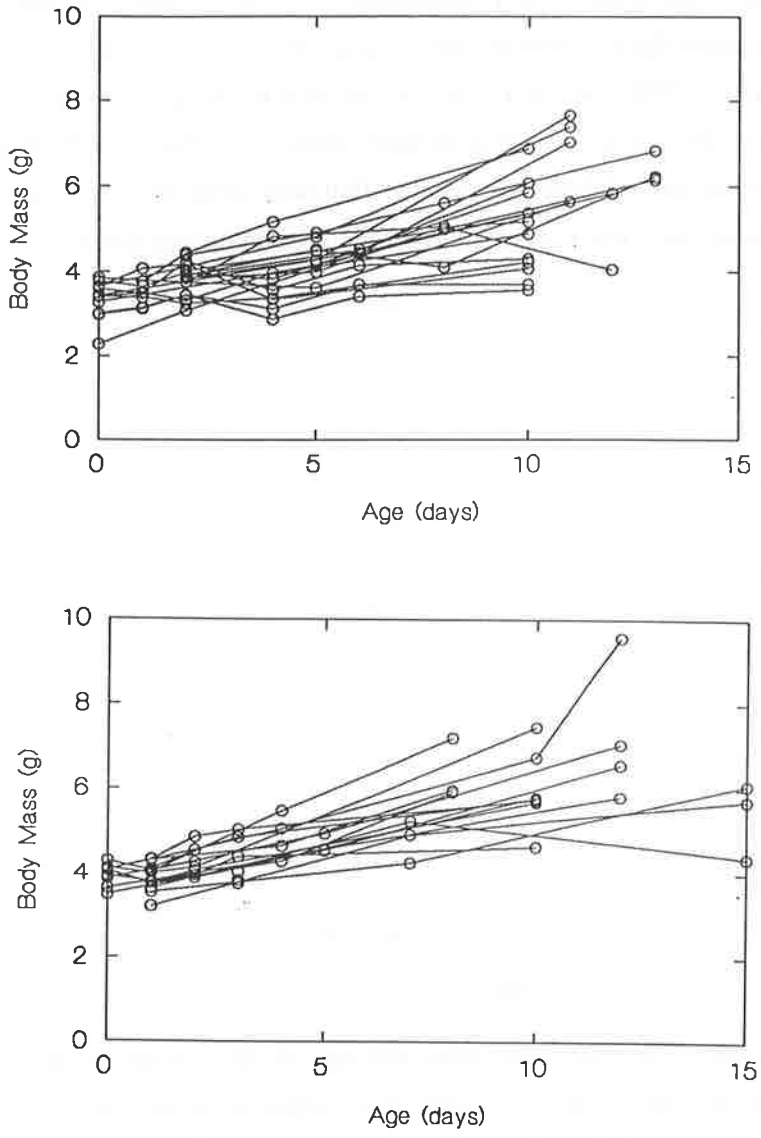

Fig. 28. Relationship between body mass and age of quail chicks during the first 15 days. Individual chicks are connected by lines to illustrate that some chicks never increased in body mass within this period.

Growth of quail body parameters were also variable at all ages, but significant Gompertz growth equations were fitted to all parameters except head width (HW), which could not be fitted (fig. 32, Table 3). Hatchling quail parameters were the greatest fraction of the adult parameter for HW, HL, Ta and To, but all were within the range of 34-57% (fig. 33). The highest growth rate of the parameters at 0.042 day^{-1} was for the Ha, which is correlated with the early age of fledging in precocial birds. Despite considerable variation in body mass between quail in the first 20 days after hatching, the growth of body parameters was similar for all quail in the same period.

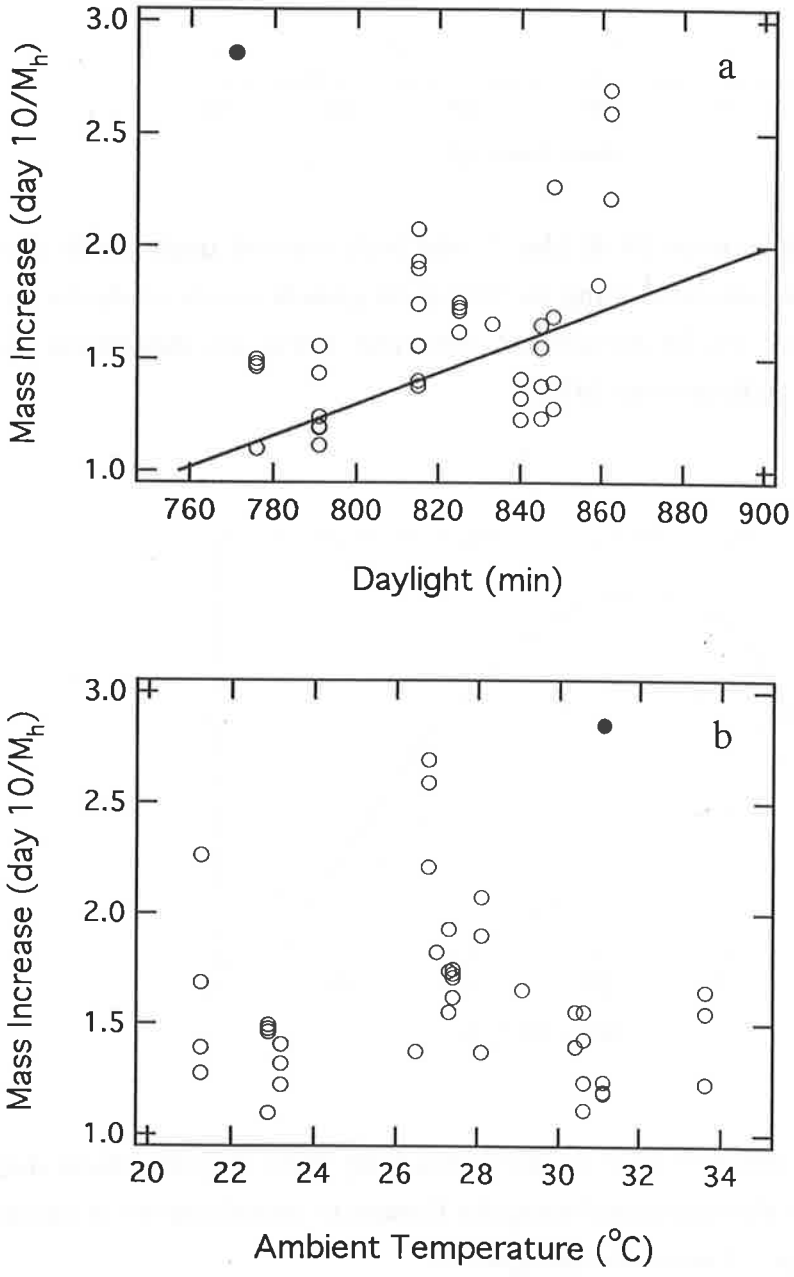

Fig. 29a. Relationship between body mass increase and available daylight per day for quail chicks over the first 10 days. Solid line indicates a significant regression (y = -4.302 + 0.007x; s_b= 0.002 r^2= 0.265 $F_{1,37}$= 13.328 P<0.001). *Filled circle* indicates an outlier which was not included in the regression. **b.** Relationship between body mass increase and mean maximum T_a during the first 10 days for the same chicks.

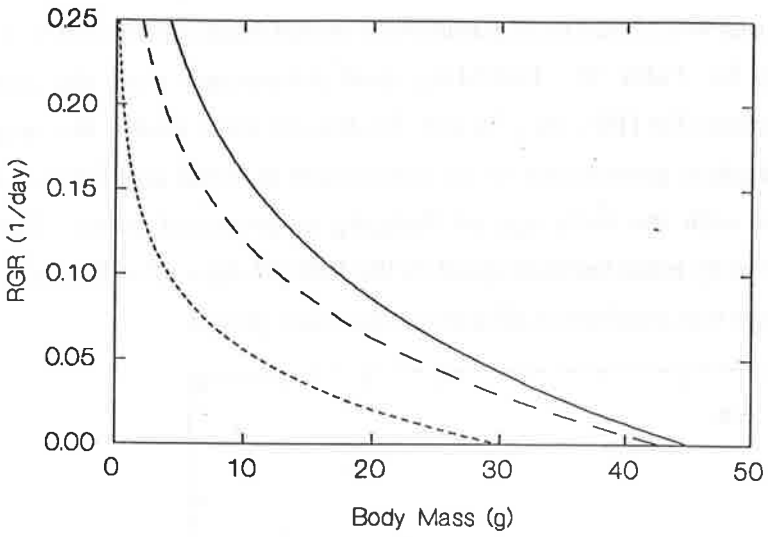

Fig. 30. Relationship between RGR (day^{-1}) and body mass of quail chicks during development. RGR was calculated using the Gompertz growth curves of chicks in the warm and cold groups (see text for definitions). *Solid line*: warm; *fine dashed line*: cold; *large dashed line*: chicks in Bernstein (1973).

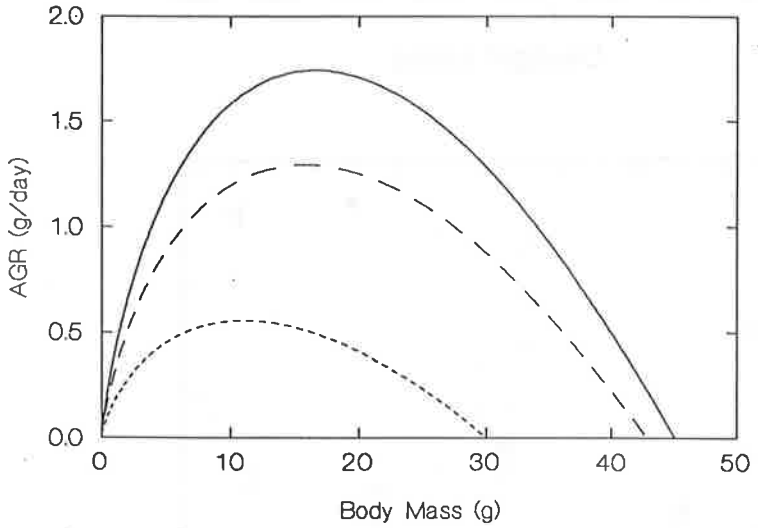

Fig. 31. Relationship between AGR (g day^{-1}) and body mass of quail chicks during development. AGR was also calculated using the Gompertz growth curves of chicks in the warm and cold groups . Lines same as figure 30.

Table 3. Fitted parameters of Gompertz growth curves for quail body parameters, where A is the asymptote (mm), K_G (day^{-1}) is the growth constant and w_i is the point of inflection (days)

Parameter	Abbreviation	A	K_G	w_i
Head Length	HL	28.0	0.030	-20.9
Head Width	HW	N/A		
Culmen	C	12.7	0.030	-0.5
Shoulder to Tail	ST	67.3	0.021	1.1
Hand	Ha	24.3	0.042	-0.2
Tarsus	Ta	23.8	0.023	-16.0
Toe	To	20.9	0.024	-24.1

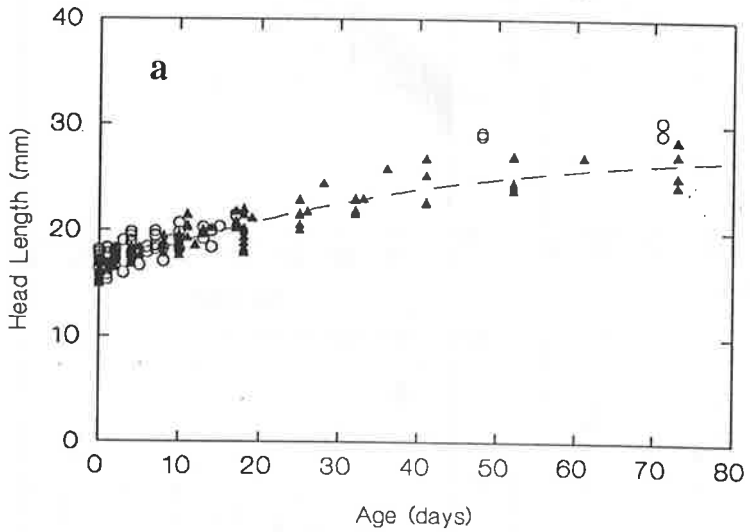

Fig. 32a-g. Growth of the following body parameters in king quail chicks as a function of age: a) Head Length; b) Head Width; c) Culmen; d) Shoulder to Tail; e) Hand; f) Tarsus; and g) Middle-Toe (mm). *Open circles*: warm group; *filled triangles and dashed line*: cold group. Gompertz growth functions for each parameter are listed in Table 3.

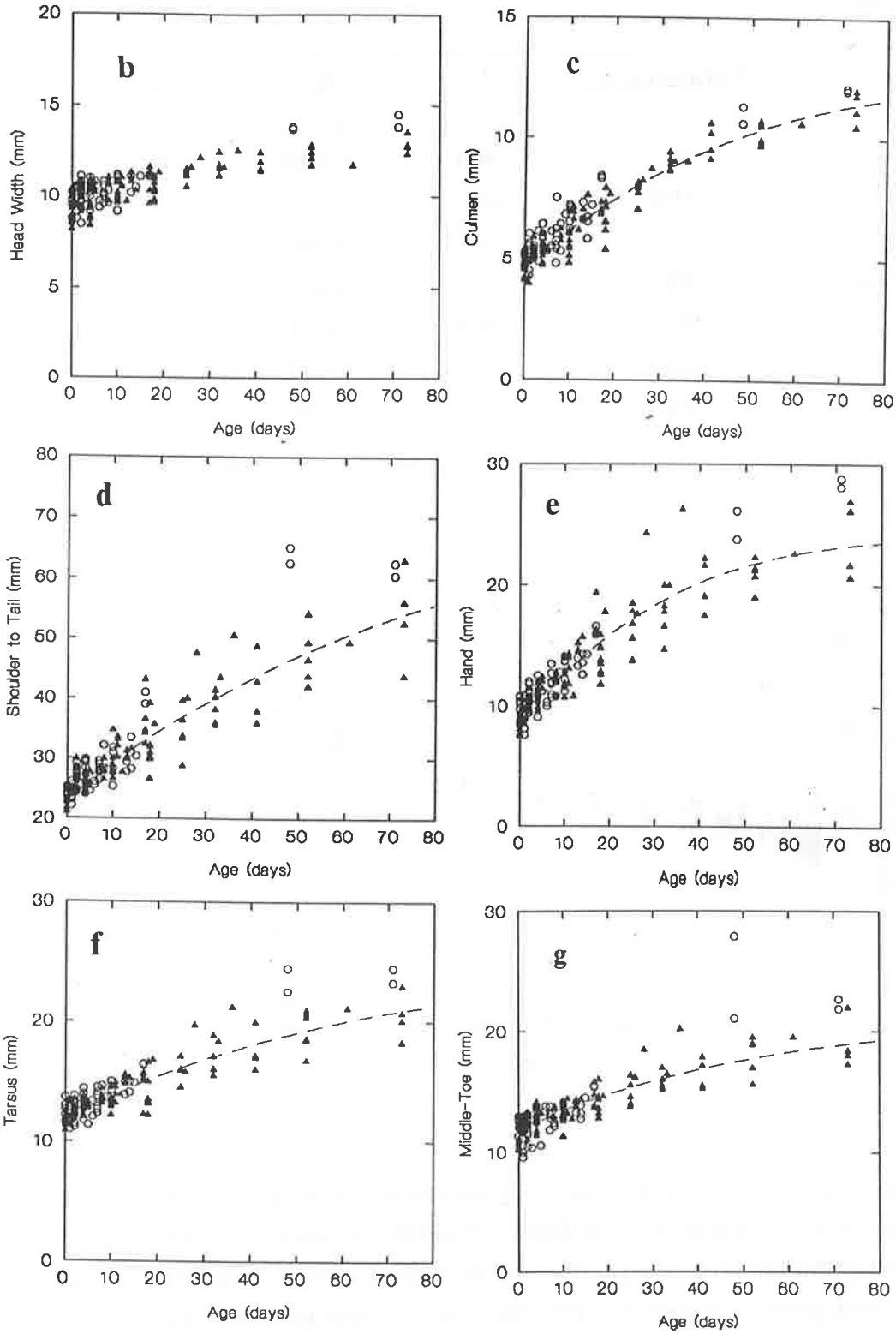

Fig. 32. continued from previous page.

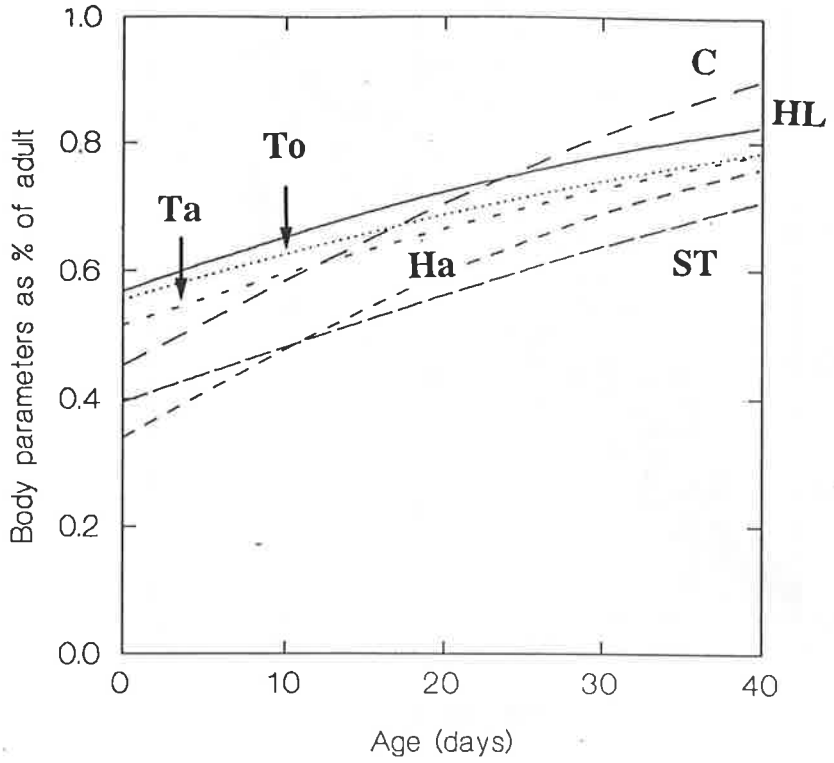

Fig. 33. The fraction of adult quail body parameters during development as a function of age (days). The same growth curves in figure 32 are expressed as a fraction of adult measurement. Symbols indicate parameters listed in Table 3 (p.161).

Posthatching growth of cockatiel

Cockatiel eggs hatched throughout the year in this study. The body mass of all cockatiel chicks increased to a maximum in most chicks between 25-40 days, but mass was variable at the end of the nestling period (fig. 34). Hatching was asynchronous and first hatched chicks were sometimes larger than second hatched chicks, and generally larger than third hatched chicks at all ages prior to fledging. Variability in chick crop contents could not be taken into account in figure 35, but generally the crops of chicks were all full during the day when measured. Asymptotic mass was between 65-95 g prior to fledging. The age at fledging was between 33-55 days for cockatiel, with a mean of 37 days in this study for those chicks which the day of fledging was known. The mean was similar to the 35 day nestling period previously reported for cockatiel (Saunders, Smith and Campbell 1984). The age at fledging was negatively correlated with body mass at fledging (fig. 35). Several smaller second or third hatched chicks were below average body mass at fledging, and were weak fliers. Chicks above 70 g at fledging were capable fliers.

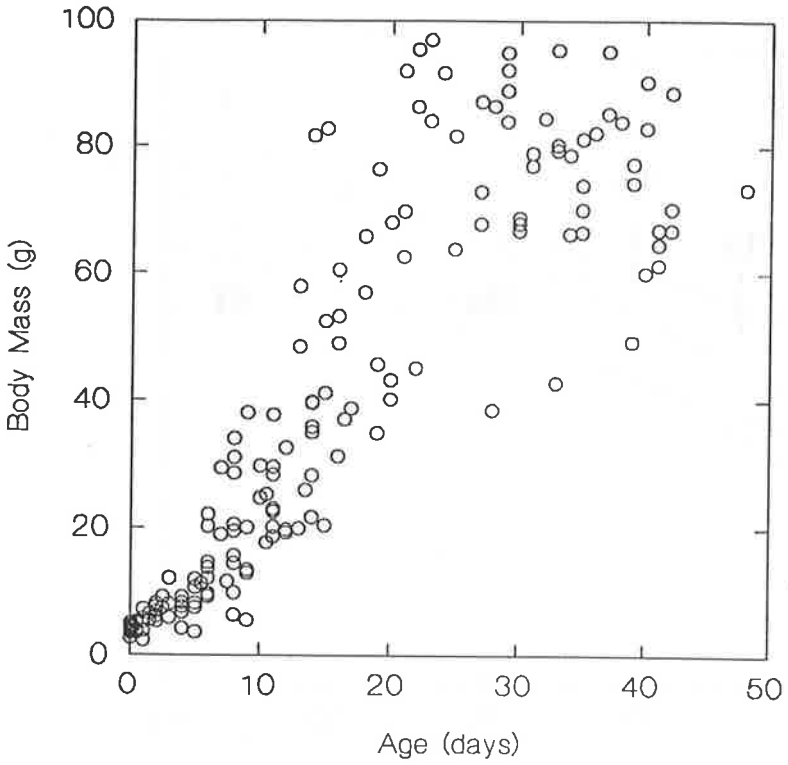

Fig. 34. Relationship between body mass of cockatiel chicks and age during development.

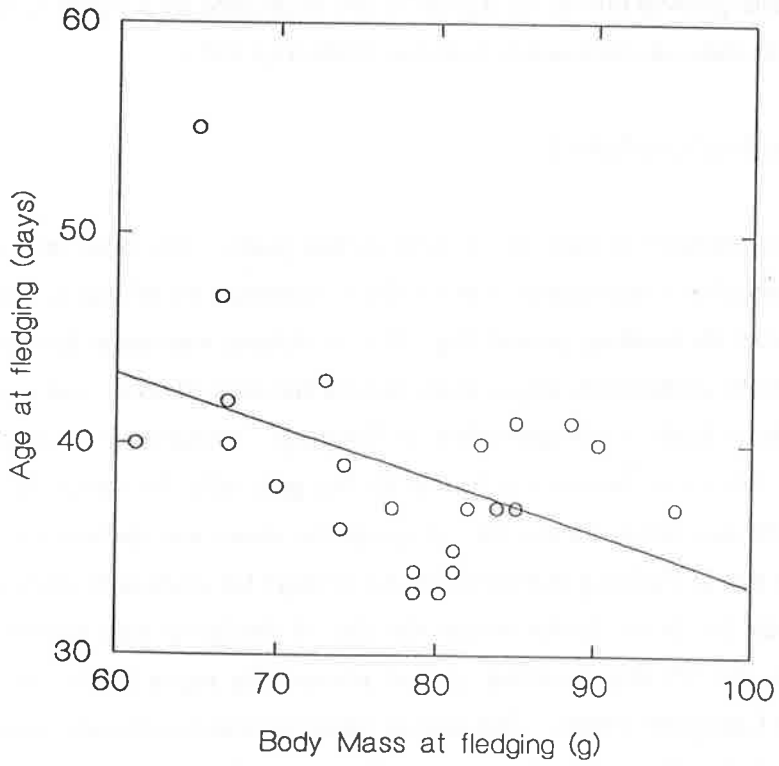

Fig. 35. Relationship between age at fledging (days) and body mass at fledging (g) in cockatiel. Only cockatiel for which the day of fledging was exactly known are included. A significant negative relationship is indicated by the solid line (Age= 57.5 - 0.23 Mass; (n=23) r^2= 0.203 $F_{1,18}$=4.582 P< 0.05).

Significant Gompertz growth curves were fitted to cockatiel body masses during development for individual broods. Growth curves were fitted to individual brood members when the variation in body mass within broods was marked (fig. 36). Relative growth rates were between 0.250 day^{-1} and 0.058 day^{-1} and asymptotic mass was positively correlated with growth rate. The average T_a that chicks experienced during the period before they reached asymptotic mass and the order of hatch was examined in relation to growth rate.

The fitted growth constants for individual cockatiel were negatively correlated with the mean maximum T_a over the first 20 days after hatching (of the first egg) (fig. 37). The 'warm' group typically had growth rates of about 0.209 day^{-1} and the 'cold' group had growth rates of about 0.101 day^{-1} (fig. 36). A significant multiple regression model explained 71.8% of the total variation in K_G ($F= 26.864$ $P<0.001$). Mean maximum T_a was the most significant variable ($F= 38.419$ $P<0.001$). The order of hatch was not significant in explaining variation, but the interaction term between order and mean maximum T_a was the next significant factor ($F= 6.079$ $P<0.022$).

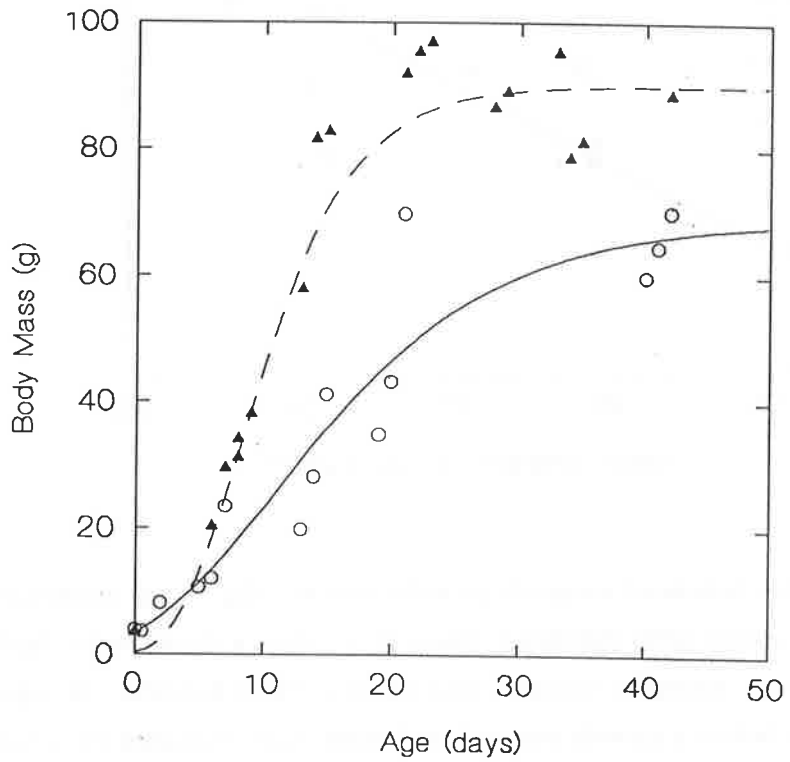

Fig. 36. Relationship between body mass (g) and age (days) for typical cockatiel chicks in the warm and cold groups (definitions in text). Fitted Gompertz growth curves are indicated by lines. *Circles and solid line*: brood of three chicks in cold group ($A= 69.3$ g $K_G= 0.101$ day^{-1} $w_i= 10.9$ days); *triangles and dashed line*: two broods of three chicks in warm group ($A= 90$ g $K_G= 0.209$ day^{-1} $w_i= 8.2$ days).

Second and third hatched cockatiel did not always grow more slowly at lower T_a than first hatched cockatiel. Body mass peaked between 20-30 days in the warm group and then declined before fledging in some cases. In the first 10 days after hatching, cockatiel chicks were brooded continuously during the day and night. Body mass was not different between groups in chicks less than 5-8 days of age (fig. 34). After 10 days of age cockatiel chicks were brooded intermittently for several days, and then not at all during the day. Body mass was higher in the warm group after day 8 compared to the cold group, which was attributed to the higher thermoregulatory costs of the unbrooded chicks after day 8.

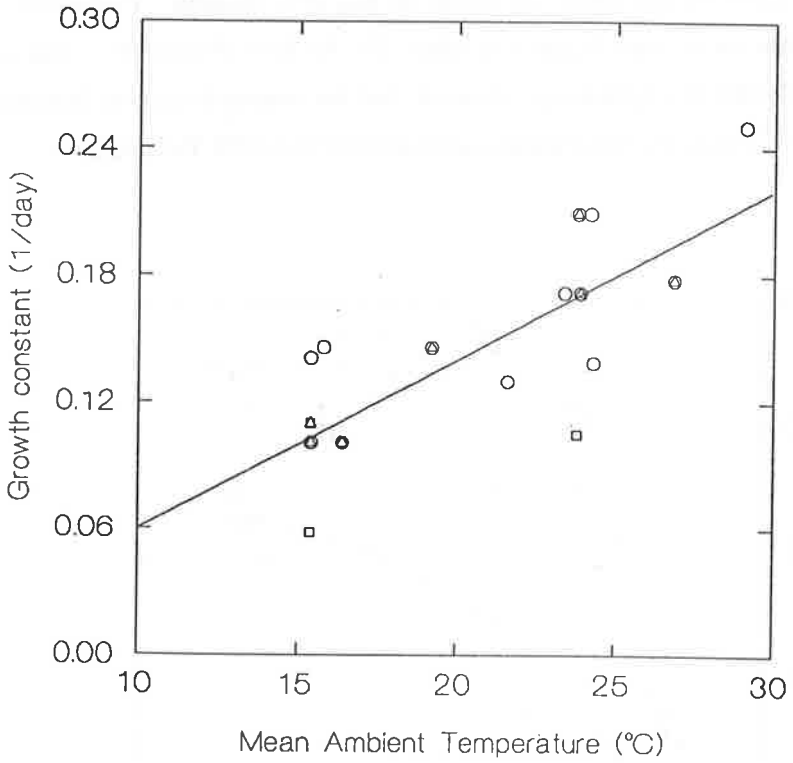

Fig. 37. Relationship between Gompertz growth constant (day^{-1}) and mean maximum T_a during the first 20 days after hatching. Each point represents an individual brood member. *Circles*: first; *triangles*: second; and *squares*: third hatched. A significant negative relationship between growth constant and mean T_a is indicated by a solid line (K_G= 0.008(mean T_a) - 0.02; r^2= 0.636 $F_{1,22}$= 38.419 P< 0.001).

RGR and AGR were calculated from the Gompertz growth equations for both warm and cold groups of cockatiel (figs. 38-39). The RGR of both groups decreased exponentially with age, but the RGR of the warm group was always higher than the cold group until immediately prior to fledging (fig. 38). AGR were 4.2 and 1.8 g day^{-1} at hatching for warm and cold groups respectively (fig. 39). AGR increased rapidly in the

warm group to a maximum of 11.2 g day^{-1} at a body mass of 30 g or 10-11 days of age, but the cold group increased less rapidly to a maximum of 3.9 g day^{-1} at a body mass of 26 g or 11-12 days of age.

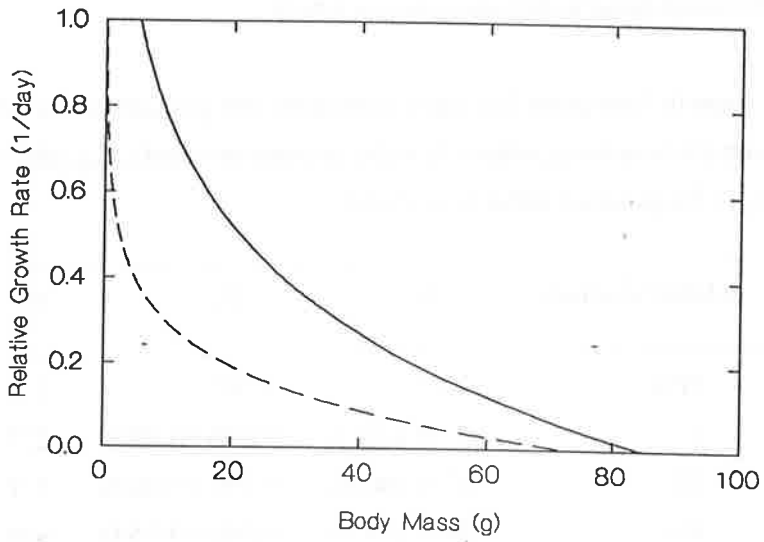

Fig. 38. Relationship between RGR (day^{-1}) and body mass of cockatiel chicks during development. RGR was calculated using the Gompertz growth curves of chicks in the warm (*solid line*) and cold (*dashed line*) groups.

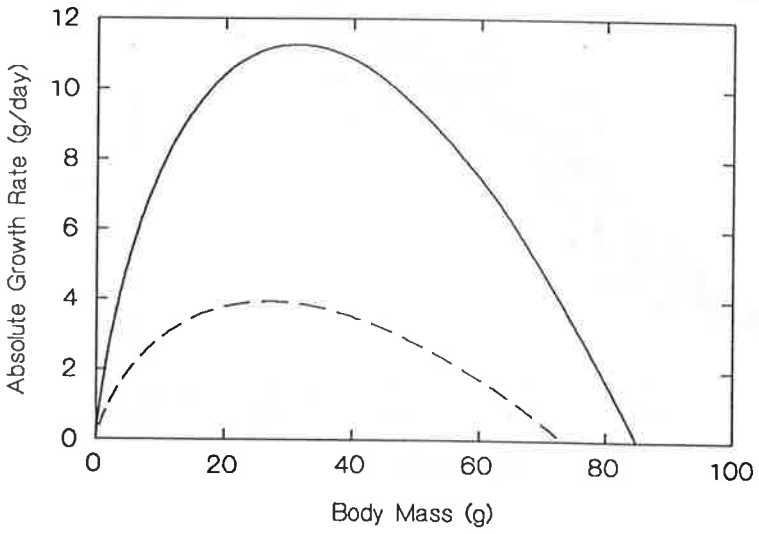

Fig. 39. Relationship between AGR (g day^{-1}) and body mass of cockatiel chicks during development. AGR was calculated using the Gompertz growth curves of chicks in the warm (*solid line*) and cold (*dashed line*) groups.

Gompertz growth equations were similarly derived for body parameters of cockatiel in the warm and cold groups (fig. 40a-f), and are summarised in Table 4. No significant differences in asymptotes were found between warm and cold for all body parameters, although all parameters were variable at all ages except head width. However, growth constants fitted to each parameter were significantly lower for the cold group in all parameters except head width and culmen length.

Table 4. Gompertz growth functions for each parameter are presented for the warm group and the cold group (in brackets), where A is the asymptote (mm), K_G (day^{-1}) is the growth constant and w_i is the point of inflection (days).

Parameter	Abbreviation	A	K_G	w_i
Head Width*	HW	24.1	0.081	-1.5
Culmen	C	17.8 (16.7)	0.056 (0.055)	-2.7 (-1.6)
Shoulder to Tail	ST	87.0 (80.4)	0.080 (0.060)	3.7 (3.2)
Hand	Ha	58.8 (63.8)	0.086 (0.054)	9.8 (14.2)
Tarsus	Ta	17.8 (17.1)	0.147 (0.102)	0.4 (0.1)
Toe	To	24.5 (24.3)	0.113 (0.076)	3.9 (5.6)

* warm and cold groups identical

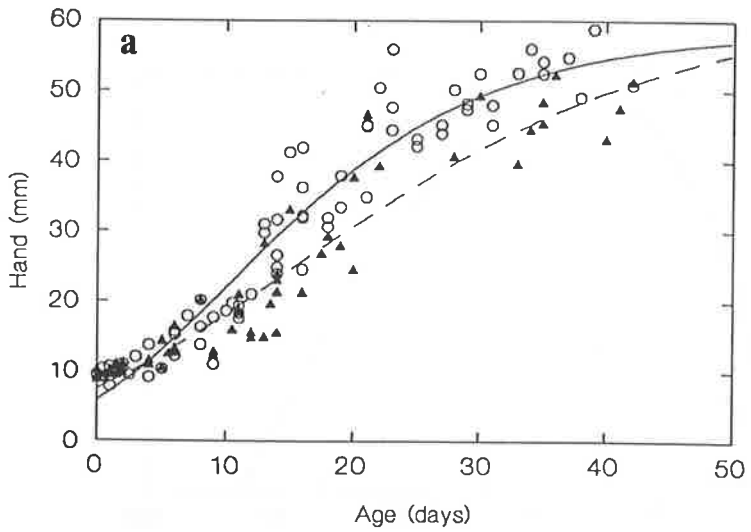

Fig.40 a-f. Growth of the body parameters in cockatiel as a function of age. Symbols indicate parameters listed in Table 4. *Open circles*: warm group; *filled triangles and dashed line*: cold group. (Continued on next page).

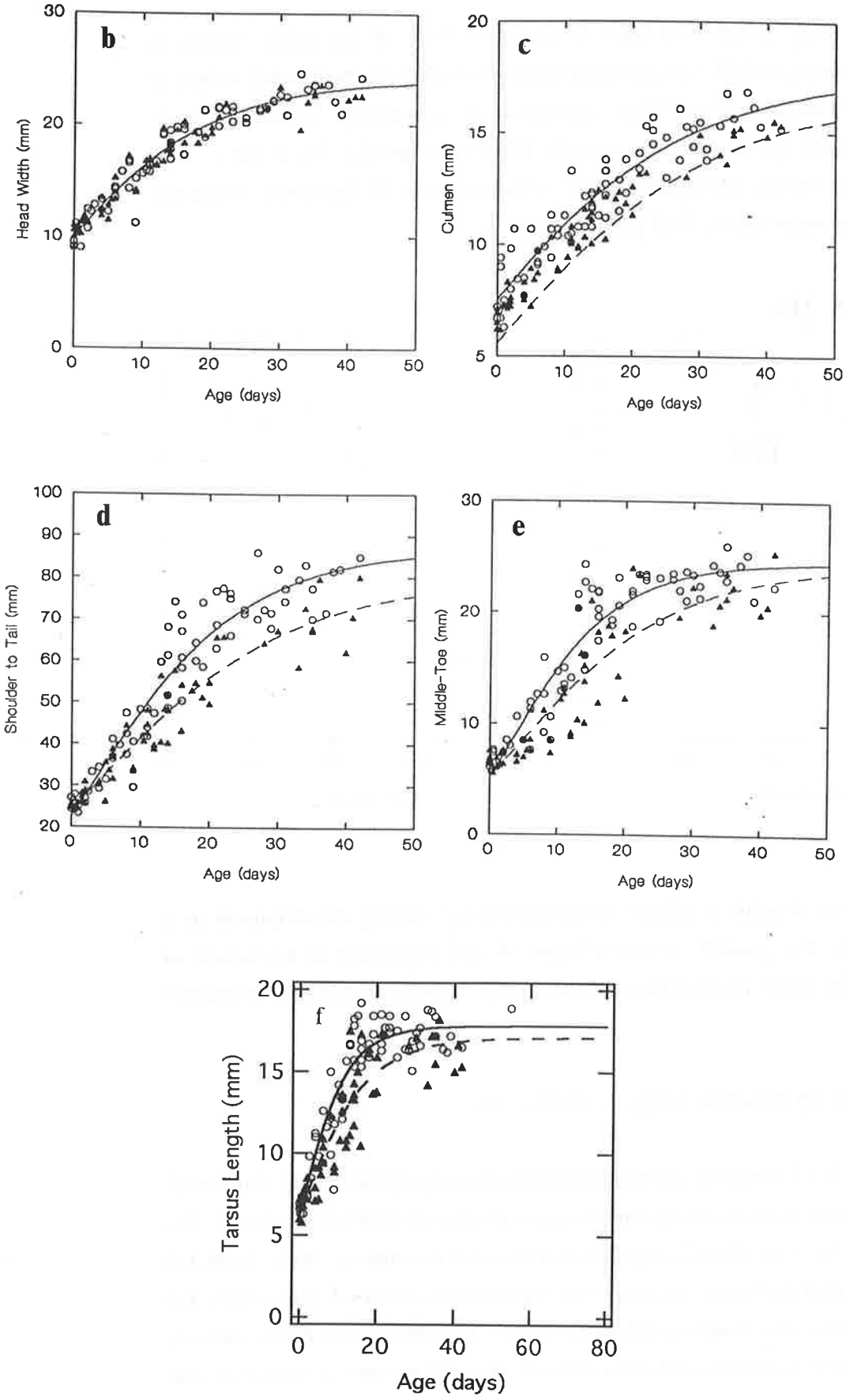

Fig. 40. Continued from previous page.

At hatching, body parameters were between 15-45% of the adult values in cockatiel (fig. 41). Tarsus, middle-toe and hand length exceeded the mean adult values at 20 days of age in the warm group and 30 days of age in the cold group. Growth of body mass plateaued at similar age to these parameters in both groups (fig. 34, p.163). The other body parameters reached asymptotic values approximately 10 days later. Only the head width grew at the same rate in both groups (fig. 41).

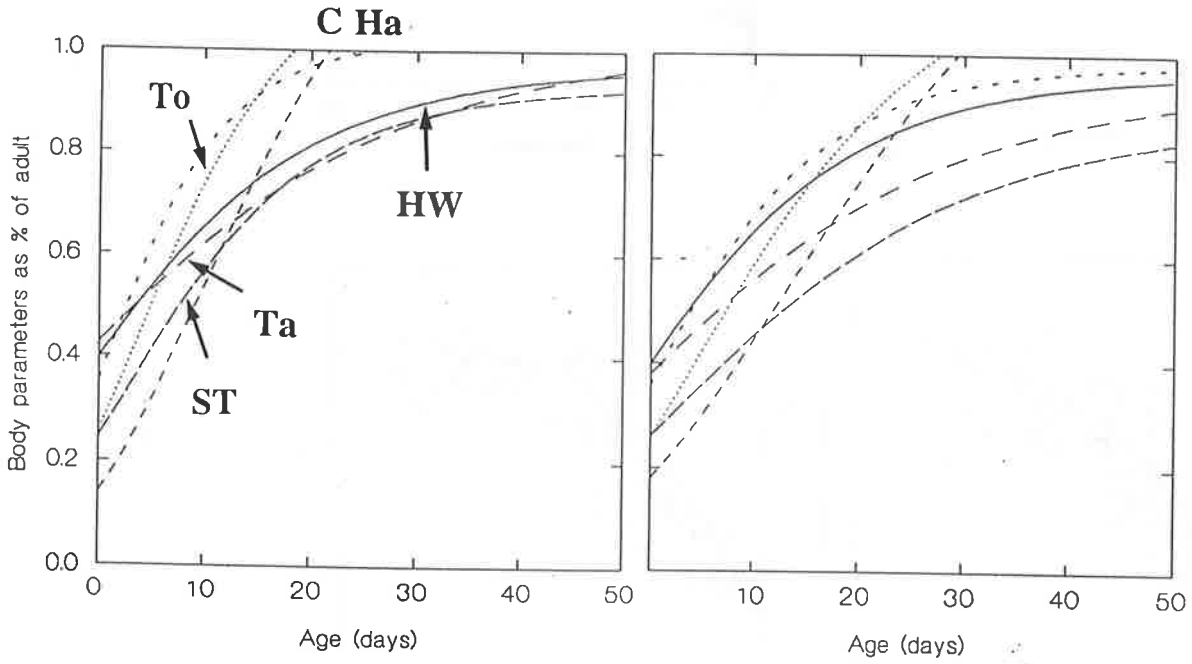

Fig. 41. The fraction of adult cockatiel body parameters during development as a function of age (days). The growth curves in figure 40 are expressed as a fraction of adult measurement in the warm (**a**) and the cold (**b**) group. Symbols indicate parameters listed in Table 4.

Allometric relations of posthatching growth rates

Available data for Gompertz growth constants and asymptotic body masses of psittaciform and galliform birds from the literature are presented with the results of this study in Table 5 (p.171). The relationship between K_G and asymptotic body mass for these orders is presented in figure 41, with the regressions obtained previously for altricial landbirds and precocial landbirds (Ricklefs 1973). Numbers in the figure indicate the species listed in Table 5, and the asterisks indicate the cold groups of cockatiel and king quail.

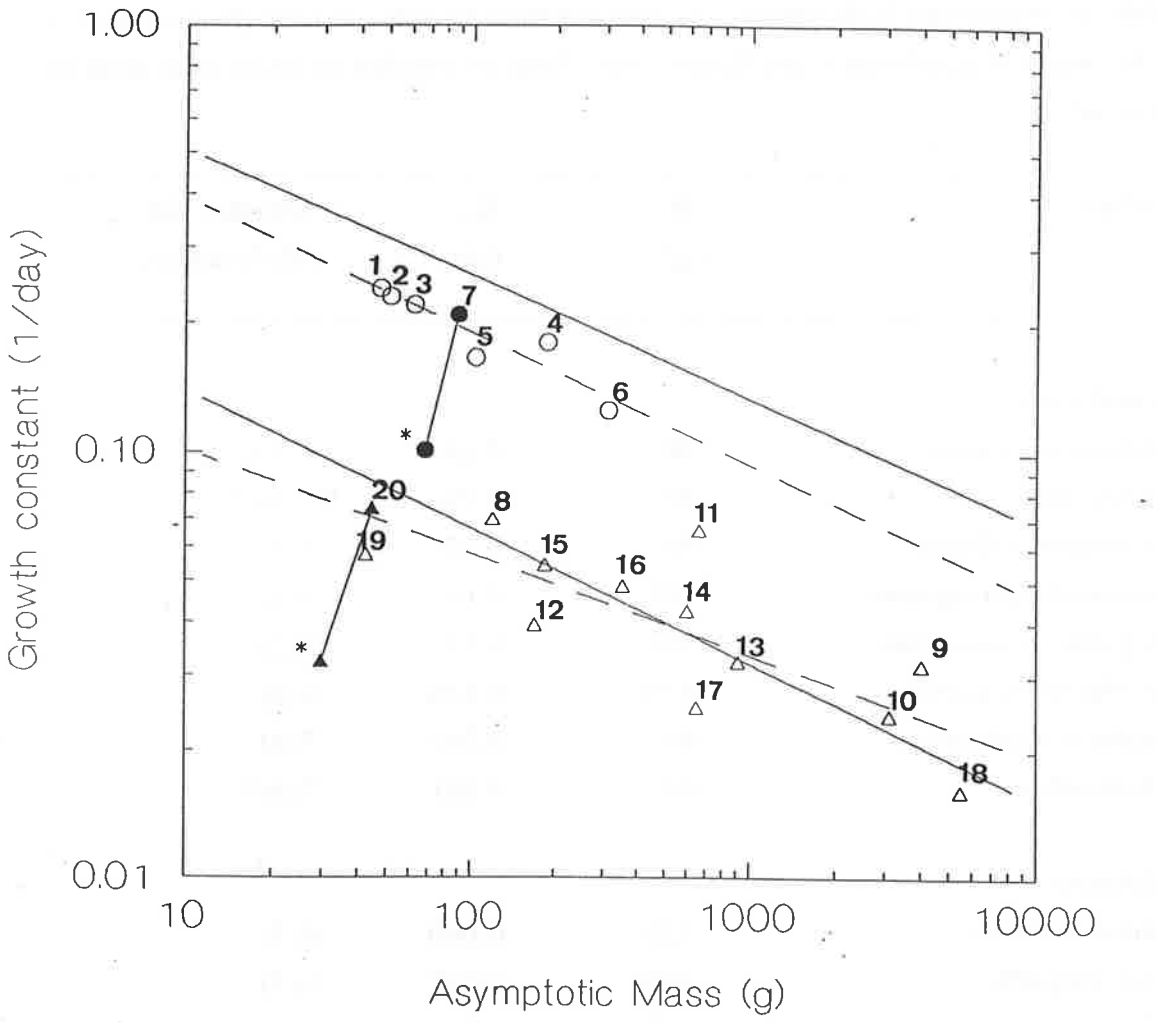

Fig. 42. Gompertz growth constants as a function of asymptotic body mass for species of Psittaciformes (*Circles*) and Galliformes (*Triangles*). Numbers refer to species listed in Table 5. *Filled circles*: cockatiel K_G for warm and cold* groups (fig. 36, p.165); *filled triangles*: king quail K_G for warm and cold* groups (fig. 28, p.158). *Upper and lower solid lines*: regression for Altricial Land Birds (log K_G= -0.069 - 0.289 log A) and Precocial Land-Birds (log K_G= -0.539 - 0.319 log A), respectively (Ricklefs 1973); *upper dashed line*: regression for Psittaciformes (eq. 3); *lower dashed line*: regression for Galliformes (eq. 4).

Table 5. Asymptotic body masses (A) and Gompertz growth constants (K_G) for species in the orders Psittaciformes and Galliformes. Species number refers to each point in figure 42.

Species	A (g)	K_G (day^{-1})	Species No. (Reference)
Psittaciformes:			
Agapornis personata	48	0.24	1 (1)
A. roseicollis	52	0.23	2 (1)
Bolborhynchus lineola	63	0.22	3 (1)
Enicognathus ferruginous	187	0.18	4 (1)
Myiopsittacus monachus	104	0.17	5 (2)
Eolophus roseicapillus	310	0.125	6 (3)
Nymphicus hollandicus	90	0.209	7 (4)
N. hollandicus *	69	0.101	7 (4)*
Galliformes:			
Coturnix coturnix	120	0.069	8 (1)
Tetrao urogallus	3940	0.032	9 (1)
Gallus domesticus	3050	0.024	10 (1)
Lagopus lagopus	650	0.065	11 (1)
Lophortyx californica	170	0.039	12 (1)
Phasianus colchicus	900	0.032	13 (1)
Bonasa umbellus	590	0.042	14 (6)
Cyrtonyx montezumae	185	0.054	15 (6)
Perdix perdix	350	0.048	16 (6)
Gallus gallus	640	0.025	17 (6)
Meleagris gallopavo	5410	0.016	18 (6)
Coturnix chinensis	43	0.057	19 (5)
C.chinensis	45	0.073	20 (4)
C. chinensis *	30	0.035	20 (4)*

1. Klaassen and Drent (1991); 2. Navarro and Bucher (1990); 3. Rowley (1990); 4. This study; 5. Calculated using data of Bernstein (1973); 6. Ricklefs (1973). * Indicates cockatiel and king quail chicks in the cold groups (see text).

New significant allometric relationships were found in this study between K_G and A for Galliformes (eq. 3) and Psittaciformes (eq. 4) based on the data presented in Table 5. The regression for Psittaciformes did not include the cockatiel cold group, and the regression for Galliformes did not include the king quail cold group because they were clearly outliers.

Galliformes:
$\log K_G = -0.756 - 0.240 \log A$ (eq.3)
($s_b = 0.051$ $r^2 = 0.664$ $F_{1,11} = 21.785$ $P<0.001$)

Psittaciformes:
$\log K_G = -0.101 - 0.310 \log A$ (eq.4)
($s_b = 0.055$ $r^2 = 0.863$ $F_{1,6} = 31.587$ $P<0.002$)

The slope of equation 3 for Galliformes is lower than that of Ricklefs' (1973) study, which included species belonging to several families in the orders Galliformes and Gruiformes. Growth records of small precocial species from other precocial orders are scant, but these limited data were examined here. Two small precocial species from the family Turnicidae (order Turniciformes, formerly Gruiformes) were included with two species from Rallidae (Gruiformes, Ricklefs 1973) for comparison of growth rates with the Galliform species (Table 5). Growth rates of *Turnix maculosa* and *T. melanogaster* were calculated from curves fitted to measurements of a few birds (n=2 and 1) raised in captivity ($K_G = 0.063$ and 0.075 day^{-1}; $A = 44.9$ and 42.6 g respectively) (p. 426 and 448, Marchant and Higgins 1993). The regression presented here (eq. 5) of growth rates on asymptotic mass for precocial land birds (from 3 orders), over a mass range of 40-7500 g, was significantly lower in slopes and elevation than the previous relationship based on birds larger than 100 g (ANCOVA $df = 26$ $t = 3.071$ $P<0.05$).

Precocial Land Birds:
$\log K_G = -0.724 - 0.253 \log A$ (eq. 5)
($s_b = 0.762$ $r^2 = 0.762$ $F_{1,16} = 51.274$ $P<0.001$)

Relationship between hatchling resting metabolism and growth rates

It has been shown that resting metabolic rate is correlated with relative growth rates after hatching, independent of body mass, in several phylogenetic groups (Drent and Klaassen 1989; Klaassen and Drent 1991). The relationship between deviations from allometric equations for growth rate and deviations in RMR_h were examined for Galliformes and Psittaciformes in this study. Posthatching growth rates and RMR_h were

available for a limited number of the species in the orders Galliformes and Psittaciformes (Species number 1-4, 7-13, 18-20 in Table 5). Residuals of the log-log regression (eq. 1 & 2) between RMR_h and M_h were plotted against the residuals of the log-log regression (eq. 3 & 4) between K_G and A (fig. 44). The relationship between RMR_h and growth constants, independent of body mass, was significant for Galliformes only (r^2= 0.501 $P<0.05$), and thus in this study, relatively high growth rates were correlated with high RMR_h. King quail in Bernstein's (1973) study had lower than expected growth rates and RMR_h, whereas the same quail in this study had higher than expected growth rates and RMR_h. The higher than expected growth rate of cockatiel was correlated with a higher than expected RMR_h, which was higher than all other RMR_h in parrots after taking into account hatchling mass, but there is insufficient data to determine if there is a significant relationship.

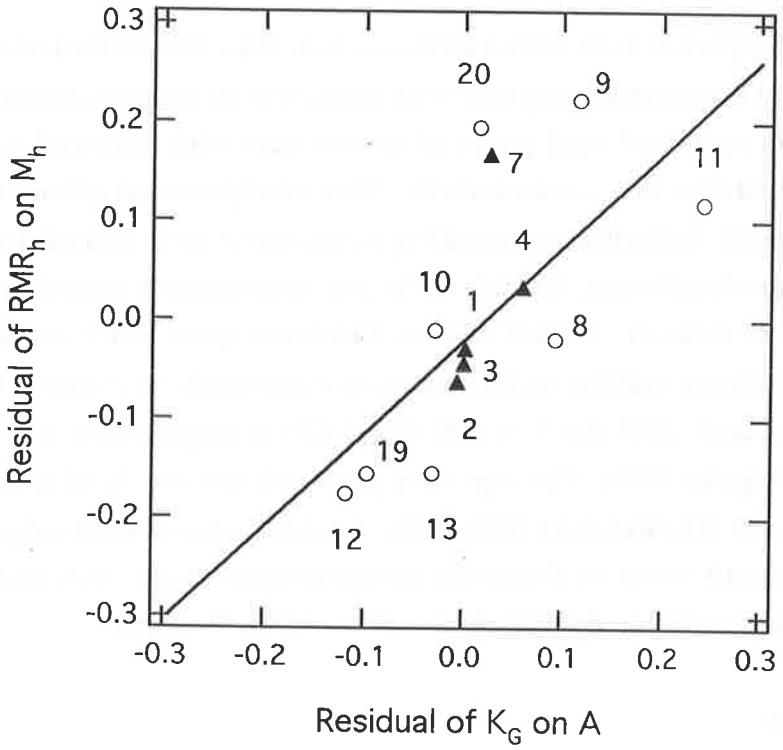

Fig. 43. Relationship between mass-independent RMR_h, and mass-independent growth constants for Galliformes and Psittaciformes. Numerals indicate species from figure 42. Solid line indicates a significant regression for Galliformes (y = -0.021 + 0.943x; s_b= 0.384 r^2= 0.501 $F_{1,11}$= 6.023 $P<0.05$).

Discussion

Hatchling Resting Metabolism

The hatchling resting metabolic rate (RMR_h) at thermoneutrality of king quail and cockatiel are both significantly higher than expected (36 and 47% higher, respectively) for all hatchling types on the basis of hatchling mass (fig. 1, p.134) (Klaassen and Drent 1991). Many altricial hatchlings have lower RMR_h than predicted by the regression for all hatchlings, but no simple relationship between hatchling type and RMR_h has been found (Klaassen and Drent 1991). Significant allometric relations between RMR_h and hatchling mass are presented here (eq. 1 & 2, p.133). The relation for Psittaciformes is not significantly different from the regression equation of Klaassen and Drent (in Table 2, 1991) with the inclusion of cockatiel hatchlings, but cockatiel are higher than all the other species reported when mass is taken into account. The same relation for Galliformes previously included the king quail, but the RMR_h of quail in this study is significantly higher than that value, but is within the 95% CI of the regression means for that group.

Hatchling maturity

The calculated ratio of mass-independent metabolic rate (MIM) of hatchlings to adults of the same species provides a measure of metabolic intensity which is essentially independent of body mass and phylogeny (Bucher 1986, 1987). The hatchling to adult ratio (MIM_h/MIM_A) for king quail and cockatiel hatchlings are 0.49 and 0.40 respectively, based on yolk-free hatchling mass. The ratio for king quail is higher than another small quail, *Coturnix coturnix* (0.43), and is similar to the ratios of much larger precocial galliforms and anseriforms (0.38-0.79) (Bucher 1986). The cockatiel ratio is noticeably higher than that reported for two other parrots (0.29 and 0.33) and altricial passerines, which indicates that the cockatiel hatchling is metabolically more precocial than other altricial birds (Bucher 1986). Larger numbers of species in each altricial group are required before any conclusions can be made about the relative degree of physiological precocity in hatchlings which are representative of these phylogenetic groups.

For convenience Bucher (1986, 1987) ignores variability in metabolic rates attributed to daily and seasonal cycles when determining adult MIM. It is likely that the RMR of most chicks undergo predictable daily cycles (Zeman and Gwinner 1993). Most chick RMR determinations are made during active phase of the day, and so the use of adult BMR during the rest phase in the daily cycle is potentially erroneous. The MIM ratio for king quail is 0.49 when calculated with the metabolic rates of hatchlings and adults in the α phase, but a value of 0.67 is obtained if the adult metabolic rate used is in

the ρ phase. The higher ratio would suggest a much higher degree of precocity than is warranted.

Hatchling metabolism and posthatching growth rates

Klaassen and Drent (1991) established an interspecific relationship between hatchling metabolism and posthatching growth rates in several orders. However, no significant interspecific relationship was found between hatchling metabolism and growth rates for Galliformes, and insufficient data were available for Psittaciformes. Significant relationships between growth rate and asymptotic mass (eq. 3 & 4, p.173), and between RMR_h and hatchling mass (eq. 1 & 2, p.133) are presented in this study. Deviations in RMR_h are positively correlated with deviations in growth rate for Galliformes only (r^2= 0.501 $P<0.05$). Both king quail and cockatiel have higher than expected RMR_h, which is correlated with high posthatching growth rates in Galliformes, but further psittaciform species are required to determine if a significant correlation exists (fig. 43, p.174). The yolk reserve of hatchling birds is variable between and within hatchling types, but larger yolk reserves are associated with increasing precocity (Carey, Rahn and Parisi 1980; Ar et al. 1987; Sotherland and Rahn 1987; Vleck and Vleck 1987). Although yolk reserves in hatchlings are not metabolically active (Steen and Gabrielsen 1986), yolk does increase the metabolic rates of hatchlings (Klaassen et al. 1987). However, it is unlikely that yolk reserves contribute to the correlation between RMR_h and growth rate (Klaassen and Drent 1991). King quail in Bernstein's (1973) study were smaller than the hatchlings in this study, but are likely to have similar proportions of yolk reserves. In contrast to quail in this study, the hatchlings in Bernstein's study have lower than expected RMR_h (both studies within 95% CI of regression mean) and growth rates, and so yolk reserves are unlikely to explain these intraspecific differences (fig. 6, p.140). It is interesting to note that RMR_h for quail in both studies reflect differences between adult quail in both studies. The metabolic rates of non-passerine embryos at PIP stage also are correlated with the BMR of the incubating adult (Hoyt and Rahn 1980; Paganelli and Rahn 1984).

It is suggested here and in subsequent discussion (refer to p.178), that the discrepancy between results obtained for king quail in this study and that of Bernstein (1973), are not attributable to artefact, but warrant further investigation into the effect of ambient temperature on growth during both incubation and posthatching periods. RMR_h of quail in this study are higher than the regression mean for Galliformes (fig. 1, p.134), but at the pre-internal pipping stage of incubation, $\dot{V}O_2$ of quail in this study is identical to the allometric predictions for all hatchling types (Section 3.2, fig. 6 p.82). The MIM value of hatchling quail are also similar to that of larger precocial hatchlings.

Relationship between hatchling state and endothermy

The development of temperature regulation in altricial and precocial birds occurs in stages which may be detected by measuring $\dot{V}O_2$ during gradual cooling (Tazawa et al. 1988b; Whittow and Tazawa 1991; Olson 1992). Stage 1 is characterised by the lack of thermogenic responses, and $\dot{V}O_2$ varies with T_a during cooling (T_b=T_a, Arrhenius-limited). Stage 2 represents incipient endothermy, when chicks are capable of modest thermogenic responses during cooling and metabolic intensity is high (T_b falls, but $T_b > T_a$). Finally, stage 3 is full blown homeothermy with sustained thermogenic responses (T_b=T_a).

The timing of the three stages to homeothermy varies across the altricial-precocial continuum. Precocial species pass through incipient endothermy (stage 2) during the latter part of incubation, prior to external pipping, and develop thermogenic responses (stage 3) in the paranatal period before hatching (Tazawa et al. 1988; Kuroda et al. 1990; Nichelmann et al. 1994a). After hatching the thermogenic responses improve rapidly in precocial birds, especially in Anseriformes (Kuroda et al. 1990). Altricial birds are Arrhenius-limited during incubation and after hatching (Kuroda et al. 1990). Altricial birds enter incipient endothermy mid-way through the nestling period, and finally acquire thermogenic responses late in the nestling period (Olson 1992). Semi-altricial and semi-precocial hatchlings are thought to have developmental times for the acquisition of homeothermy which are intermediate between precocial and altricial species. The semi-precocial noddy, *Anous stolidus*, and the wedge-tailed shearwater, *Puffinus pacificus*, are Arrhenius-limited throughout incubation, but pass into incipient endothermy at hatching, and stage 3 soon after that (Matsunaga et al. 1989; Mathiu et al. 1992).

The development of thermogenic responses in king quail appears to be later than other larger precocial species, with many chicks exhibiting incipient endothermy only after hatching (Stage 2). King quail chicks (0-1 days) with dry down are variable in their $\dot{V}O_2$ during gradual cooling (fig. 2, p.135) (Bernstein 1973). Some chicks are capable of thermogenesis equivalent to almost twice RMR at 5-10 °C below the thermoneutral point, whereas other chicks can only maintain $\dot{V}O_2$ at constant levels during cooling. However, between 2-6 days of age king quail acquire thermogenic responses (Stage 3) (fig. 2-3). The delay in acquisition of thermogenic responses may in part be attributed to a shorter incubation period in king quail than predicted by egg mass for other precocial species (Section 3.2, p.77) (Dietz and van Kampen 1994).

The development of temperature regulation in the cockatiel at least, appears to be as precocial as the king quail. Cockatiel hatch at stage 2, and maintain constant $\dot{V}O_2$ during gradual cooling to T_a 25 °C (fig. 12, p.145). Cockatiel RMR_h is higher than expected for parrot hatchlings (fig. 1, p.134) and hatchlings of all developmental types (Klaassen and Drent 1991). Thermogenic responses are present in some hatchlings, but rapidly develop in all chicks within several days (fig. 13, p.146). Another parrot,

Agapornis roseicollis, also has thermogenic responses early in the nestling period, but it is not possible to discern if the hatchlings have incipient endothermy in that study (Bucher and Bartholomew 1986). A more severe cooling test was used by those authors in comparison to this study. Parrots appear to enter stage 2 at hatching or soon after, but the timing of the transition to stage 3 is variable, but earlier than described for other altricial birds (Kuroda et al. 1990; Olson 1992).

Development of resting and peak metabolism in king quail

The hatchling king quail has 66% of the predicted mass-specific RMR for an adult bird of the same mass (fig. 6, p.140) (Aschoff and Pohl 1970). This is comparable to the range of values for other galliform hatchlings (40-72% Dawson, Bennett and Hudson 1976), and quail RMR in this study is double the RMR of quail in Bernstein's (1973) study (32%).

Quail chicks are unable to maintain constant T_b during gradual cooling until body mass reaches 7-10 g (10-12 days old; fig. 10, p.142). The RMR of chicks exceeds the predicted RMR of an adult bird of the same mass at 4-5 g (fig. 6), but PMR is not different from RMR and is insufficient for thermoregulation. At 7-10 g body mass PMR is maximal during development and chicks can thermoregulate. Chicks in Bernstein's study did not exceed the predicted adult RMR until 7-10 g. The pattern of development of RMR in quail is the same in both studies, however the highest RMR is achieved at a lower body mass in this study after a two fold increase from hatching. It is possible that intermittent periods of low T_a may have stimulated greater improvements in thermoregulatory abilities of chicks in this study. Cold acclimation increases the PMR, but not the RMR of bantam chicks relative to that of control chicks (Aulie 1977; Aulie and Grav 1979). Ducklings from eggs incubated at normal incubation T_a, but then exposed to low T_a during the first 10 days after hatching, use physiological thermoregulatory mechanisms such as shivering, in comparison to ducklings raised at optimal T_a during the same period, which used behavioural thermoregulatory mechanisms, and consequently $\dot{V}O_2$ is 20% higher at 10 °C in the low T_a group (Nichelmann et al. 1994b). Thus cold acclimation of king quail may explain the larger increases in RMR from hatchling levels in this study compared to Bernstein (1973), but this needs to be verified in controlled experiments.

The mean BMR of adult quail at thermoneutrality in Bernstein (1971) is 1.7 mL O_2 $g^{-1}h^{-1}$ (α phase), 1.59-2.03 mL O_2 $g^{-1}h^{-1}$ ($\rho-\alpha$ phases, Table 1, p.202) in this study and 1.47 mL O_2 $g^{-1}h^{-1}$ (ρ phase) in Roberts and Baudinette (1986). The value reported by Bernstein (1971) may in fact be elevated due to the stress associated with cutaneous evaporation measurements during metabolism measurements, but both chick and adult RMR quail appear to be lower than the values in this study. However, the adult BMR of quail in this study is comparable to that of Roberts and Baudinette (1986), and therefore

systematic error in any of $\dot{V}O_2$ measurements in this study seems unlikely.

An important distinction needs to be made between this study and Bernstein's (1971, 1973) studies, which relates to the different conditions in which chicks were raised. In this study, T_a was not controlled, and many chicks were exposed to potentially low T_a during foraging, whereas in Bernstein's studies, chicks fed and developed in a thermoneutral environment (35 °C). Experiments with domestic ducks eggs by Nichelmann et al.(1994b), conclude that low T_a during incubation and early posthatching periods both stimulate higher $\dot{V}O_2$ of chicks in the early posthatching period. Ducklings from eggs incubated at a low T_a of 34.5 °C, for the last 7 days of incubation, have higher T_b after cold exposure at 10 °C, and 35% higher $\dot{V}O_2$ than ducklings incubated at the normal incubation temperature (Nichelmann et al. 1994b).

Body mass of quail chicks changes little in the first week after hatching period, and changes in insulation during this period are minor. The greatest improvements in temperature regulation exhibited by quail initially are most likely the result of greater thermogenic powers by increased phosphorylative enzyme levels and or better nervous or hormonal control of heat production. Other studies have been unable to separate which factors contribute the most to the improvements in thermoregulatory abilities of precocial chicks in the first days after hatching (Spiers, McNabb and McNabb 1974; Hissa et al. 1983). The RMR of quail chicks increases significantly in the first 4-6 days, after the yolk reserve has been utilised (by about 3 days), and so the increases in RMR reflect either improvements in the thermoregulatory control mechanisms or biochemical maturation of skeletal muscles (Marsh 1980). Similar changes in RMR occur in the Japanese quail between 3-5 days after hatching (Spiers, McNabb and McNabb 1974).

After the initial increases in RMR in young quail chicks (<10 g), to levels in excess of the estimated RMR for an adult bird of similar body mass (fig. 5, p.139), the RMR of chicks decreases with increasing body mass at a rate that is significantly steeper than the same relationship between RMR and body mass for adult birds (chick regression b= -0.50 (95% CI of b is -0.34 to -0.66); adult b= -0.28 (Aschoff and Pohl 1970)). The decrease in RMR as body mass increases reflects the lower heat production required to maintain adult T_b at thermoneutrality as the surface area to volume ratio decreases (Bernstein 1973; Hissa et al. 1983). However, the steeper slope of the relationship between RMR and body mass for chicks also reflects changes in the thermal conductance of the skin and plumage of the chicks. Initially the thin skin and neonatal down of the youngest chicks has a high thermal conductance, but later this down is replaced by contour feathers, and thermal conductance decreases to levels similar to allometric predictions for adult birds.

The ability of small chicks to maintain constant Tb below the TNZ is dependent on its ability to increase its metabolism above RMR (factorial metabolic scope = PMR/RMR). The factorial metabolic scope of hatchling quail is variable between individuals 1.0-1.5, and lower than in other galliform species, ranging between 2.0-2.5

(Dawson, Bennett and Hudson 1976; Hissa et al. 1983). The thermogenic scope (mW g^{-1}) of chicks increases with body mass, reaching a maximum at 10 g, and then decreases in parallel with RMR with increasing body mass (fig. 8, p.141).

Development of resting and peak metabolism in cockatiel

The RMR_h of cockatiel hatchlings is 42% of the adult parrot RMR at the same body mass (fig. 17, p.148) (Williams et al. 1991). In comparison *Agapornis roseicollis* hatchlings have only 25% of the predicted adult parrot RMR at the same body mass (Bucher 1983). RMR of cockatiel increases within days after hatching, and exceeds the predicted RMR of adult parrots at 9 g. Even though the chicks are poorly coordinated and still blind, PMR starts to increase above RMR at 10 g. PMR of cockatiel increases further and remains maximal throughout the nestling period, whereas RMR declines with increasing body mass (fig. 16, p.148). Despite the fact that the cockatiel lack feathers and have only sparse down at this body mass, RMR decreases because of a more favourable surface area to volume ratio, but remains higher than that of adult parrots of equivalent body mass. The changes in RMR of cockatiel during development are similar to those of precocial birds (Aulie 1976, 1977; Bernstein 1973; Hissa et al. 1983), but unlike those of altricial passerines (Dawson and Evans 1957, 1960; Williams and Prints 1986; Olson 1992). However, precocial and semi-precocial birds hatch with relatively high factorial metabolic scopes (PMR/RMR) of 1.5-2.5, and so PMR decreases in parallel with RMR as body mass increases (Dawson, Bennett and Hudson 1974). The metabolic scope of cockatiel hatchlings is about 1.0-1.5, but the thermogenic scope increases after hatching and reaches a maximum at about 20 g (fig. 19, p.151). With increasing body mass the metabolic scope increases linearly because RMR decreases with mass, whilst PMR remains constant.

Temperature regulation in king quail and cockatiel

The body temperature (T_b) of brooded quail hatchlings is lower than other galliform birds, which is attributed to the smaller mass (Myhre and Steen 1979). However, it is higher than the T_b of many larger precocial charadriiform hatchlings which have lower a degree of homeothermy at hatching as a result of a higher thermal conductance and lower resting metabolism (Myhre and Steen 1979; Visser 1991).

Quail chicks at 6 days of age are able to maintain significant temperature gradients between themselves and the environment at T_a >15 °C, but not below 15 °C (fig. 10, p.142). This ability to maintain high T_b for short periods is also supported by a significant decrease in brooding time of quail chicks at this age (Chapter 5 fig. 13, p.208). At T_a between 15-20 °C, the T_b of the smaller chicks is less than 25 °C, physical coordination is lost, and chicks no longer shiver or vocalise. However, all chicks

rewarm without any ill-effects to their development at this age. Between 10-12 days of age chicks are able to regulate at higher T_b over the same T_a range as younger chicks, but the T_b of smaller chicks declines below 33 °C at T_a 15 °C (fig. 10). Chicks 10-12 days old regulate T_b between 35-41 °C above T_a 20 °C. The level of T_b at this age is positively correlated with body mass. Chicks regulate T_b at adult levels over the whole T_a range (8-36 °C) by 17-18 days of age, except when body mass is less than 10 g. Even after the chicks have fledged, chicks with low body mass for their age (fig. 26, p.156) regulate T_b at lower levels (fig. 11, p.143). Such fledglings are not brooded during the day during cold exposure, but are seen to huddle with siblings and adults frequently, and thus may achieve higher T_b than individual chicks.

The T_b of brooded cockatiel chicks at 2-3 days of age is between 34-37 °C (Chapter 5 fig. 5, p.201), which is comparable to the T_b of other altricial hatchlings (Myhre and Steen 1979). The T_b of brooded chicks approaches adult T_b at the end of the brooding period (10-13 days, body mass 20-30 g), but is variable between individuals (Chapter 5 fig. 5). Most chicks older than 18 days of age are homeothermic over the range 5-36 °C when body mass is between 50-90 g (fig. 21, p.152). Chicks in the warm group are heavier and achieve homeothermy at 18 days of age, but the body mass of chicks in the cold group is dependent on T_a during the nestling period, and some chicks only become homeothermic after their feathers have opened and they prepare to leave the nest.

During periods of parental absences chicks are able to huddle with siblings. The T_b of an individual chick that huddles is dependent on T_a, age, body mass, number of siblings. At T_a 10-25 °C the T_b of huddled chicks increases directly with the body mass of the individual chick, and with the total brood mass (fig. 22). In general a chick of 20-25 g can achieve adult T_b in broods of 2-4 chicks during cold exposure.

Achievement of Homeothermy

Physiological homeothermy is acquired earlier by king quail in this study than in a previous study (Bernstein 1973) (10 and 20 g respectively; fig. 24, p.154). However, the difference between studies in the timing of effective homeothermy is not as pronounced, at 5-7 g in this study and 7-10 g in Bernstein (1973). The time taken to reach this body mass is between 7-15 days in this study, depending on growth rate, and 10-13 days in Bernstein's study. The earlier achievement of effective homeothermy in some quail in this study is the result of larger increases in body mass, and secondly increases in RMR which are related to body mass (fig. 5, p.139). Thus the time of the year that quail chicks hatch is an important factor in determining the growth rate and therefore the age at which quail reach homeothermy. The energetic burden to parents of brooding chicks is expected to be higher when chicks hatch at the beginning or end of the breeding season (October and March). Shorter periods of daylight and low T_a result in

lower growth rates and a higher brooding frequency (see Chapter 5).

The degree of effective homeothermy of many altricial and precocial chicks have been compared using the criteria of Dunn (1975, 1976). Visser and Ricklefs (1993) present an allometric relation based on the data of Dunn (1975) between the mass at effective homeothermy (75% of adult ability) in altricial birds and fitted asymptotic mass. The predicted mass at effective homeothermy in cockatiel is 48.5 g for an asymptotic mass of 90 g. However, the actual mass (20 g) is less than half that predicted. Physiological homeothermy in cockatiel is achieved at 20-40 g (fig. 24). However, the age at which cockatiel reach this critical body mass is between 8-30 days depending on T_a during the posthatching period. Thus chicks which hatch during spring-summer (warm group) are homeothermic at the end of the brooding period. In contrast altricial passerines achieve physiological homeothermy near the end of the nestling period (Dunn 1975, 1976).

Coordination of developmental and physiological traits

The acquisition of significant insulation during development in altricial birds is believed to be coincident with sudden and rapid improvements in the thermogenic capacities of skeletal muscles (O'Connor 1975a; Webb 1993). The close coupling of physiological and morphological developmental traits is believed to be a prerequisite for prevention of body cooling, because as tissues mature, temperature sensitivity of those tissues to low T_a increases. However, cockatiel chicks increase their thermogenic scope early in development, when they only have sparse down on the dorsal and lateral surfaces of their bodies. Cockatiel are already homeothermic before their feathers start to become unsheathed at 25 days of age (starting with the primaries). Parental attentiveness decreases rapidly after 10-11 days of age, at which point chicks weighing more than 40 g are homeothermic. Regardless of body mass all brood members benefit by brood huddling behaviours. During parental absence the upright postures of these parrot chicks makes close contact between the naked ventral surfaces of their body masses possible. Under these circumstances cockatiel chicks would benefit from improved heat transfer between brood members in the absence of unsheathed feathers (Webb and King 1983b).

Growth of king quail

The increase in quail body mass in the first 10 days is positively correlated to the time available for foraging during the day (fig. 29a, p.159). In the first three days chicks do not increase body mass appreciably, but the yolk reserve is replaced by tissue mass within this period (fig. 26 & 28). Increases in body mass of chicks less than 5 days old is low because all chicks are brooded 50-80% of the daylight time (Chapter 5 fig. 12, p.208). After 5 days of age, brooding time decreases and chick foraging time increases.

Foraging time is negatively correlated to T_a in quail chicks (Chapter 5, fig. 13), but variation in chick body mass is not significantly related to T_a (fig. 29b). However, it appears that longer foraging time may compensate for the thermoregulatory costs incurred by chicks at low T_a. The effects of wind and exposure to incident solar radiation on foraging times and chick body mass are not considered here because these factors were not uniform between enclosures. However, the growth rates of some chicks may increase due to the benefit of basking behaviours at low T_a, and may confound a significant relationship between growth rate and T_a.

King quail have sub-tropical and temperate natural distributions in northern and eastern Australia and in South-East Asia (Marchant and Higgins 1993). The locality of this study (Adelaide) is at a higher latitude than the southern limits of their natural distribution, and in early spring (September - October) quail experience low T_a. Quail which experience low T_a and wet weather during the first days after hatching do not increase body mass and subsequently die. In this study the highest chick mortality is during early spring. Under these conditions chicks are brooded for 70-80% of the day, even after their thermoregulatory abilities improve (day 5-6) (Chapter 5 fig. 12, p.208). Precocial shorebird chicks fail to meet their energy requirements when brooded for longer then 75% of the day under cold and wet conditions, and subsequently die (Bientema and Visser 1989).

Growth of body parameters are less variable than body mass between chicks (fig. 32, p.161-162). The growth rates of the hand are higher than other parameters, which is consistent with early fledging in precocial development (figs. 32-33) (Ricklefs 1973, 1979b). The age of chicks at fledging is generally between 25-28 days, which is similar to the age reported by Bernstein (1973). Exceptionally, some chicks with the highest growth rates fledged earlier at 19 days of age.

The RGR and AGR of quail which experience longer periods of daylight in summer (December-January) are three times higher at the inflection point of growth than those of quail which hatch in early spring (September-October) (fig.30-31). Quail in the cold group (low growth constants) did not reach adult body mass at fledging, although other body parameters grew to asymptotic values at that point. Such quail with low growth rates reach adult mass at 80-100 days or three times longer than the normal development time. The development time of Arctic tern chicks, *Sterna paradisaea*, increases with decreasing growth rates, and the probability of slow growing tern chicks surviving to fledging is low (Klaassen and Bech 1992). However, quail chicks which fledge at sub adult body mass are independent and may have greater chance of survival than semi-precocial terns.

Growth of cockatiel

The body mass of cockatiel chicks is highly variable in chicks older than 4-5 days (fig. 35, p.164). Asymptotic mass is reached between 20-35 days but is variable. Variability in body mass at all ages during development is common in parrots (Bucher 1983; Navarro and Bucher 1990). In this study the greatest source of variation in chick body mass is attributed to variability in T_a during the nestling period (fig. 37). Growth rates of cockatiel are positively correlated with the average maximum T_a during the first 20 days after hatching. The variability in body mass increases after several days, and the differences are greatest after 10 days of age. Brooding during the day is intermittent when the first hatched chick is 9-10 days old and ceases at 12-13 days (see Chapter 5). Chicks incur thermoregulatory costs dependent on T_a at several days of age when unbrooded (figs. 13-14, p.146). However the $\dot{V}O_2$ of brooded chicks <8-9 days old is 50% of the unbrooded $\dot{V}O_2$ at thermoneutrality, when T_a is between 10-37 °C (Chapter 5). Chicks 9-13 days old, and between 20-30 g are brooded less effectively than younger chicks and $\dot{V}O_2$ increases as T_a decreases during brooding, but remains lower than unbrooded chicks of the same age (Chapter 5 fig. 4, p.197). When brooding bouts become intermittent after 10 days from the first egg hatching, more energy is allocated to thermoregulation by chicks. The thermoregulatory costs of chicks increases further when brooding is stopped altogether, and therefore the energy available for growth decreases in chicks which experience low T_a (fig. 37, p.166).

The order of hatch is not a significant factor in explaining the variation in chick body mass, but the interaction term between order of hatch and mean maximum T_a during the first 20 days is significant ($F= 6.079$ $P<0.022$). At the end of the brooding period third hatched chicks are between 2 and 4 days younger than the first hatched chicks. As the mean T_a decreases, the growth rates of all chicks decreases, but the growth rate of the youngest chicks decreases at a steeper rate from first or second hatched chicks when the age difference between siblings is greatest (fig. 37). Therefore third hatched chicks incur thermoregulatory costs earlier in their development than older siblings. However, the growth rates within broods which experience high T_a during the nestling period are little different. It is not known if the intraspecific variability of body mass in other parrots also reflects differences between individual chicks in thermoregulatory costs (Bucher 1983; Navarro and Bucher 1990).

The RGR and AGR of cockatiel chicks are highest during the brooding period when the parents contribute to the cost of temperature regulation (fig. 38-39, p.167). The highest AGR at the inflection point is coincident with the age when the brooding period of cockatiel becomes intermittent, and at a body mass when the efficiency of parent-chick heat transfer starts to decline (see Chapter 5). Although a causal relationship between the increased thermoregulatory costs and the decline in AGR with age is not implied here. The AGR of cockatiel chicks which experience higher T_a during development in spring or

summer is three times higher than the AGR of chicks which hatch in winter.

The growth rates are higher for all body parameters of the warm group in comparison to the cold group, except head width (fig. 40, p.168-169). Head width is indistinguishable between groups of chicks throughout development. The asymptotes of all other parameters are similar between groups, with considerable overlap in values at all ages (fig. 40 and Table 3, p.161). Growth of leg parameters are faster than all other parameters in cockatiel, with asymptotic values being reached between 10 and 15 days of age in all chicks (fig. 41). Increases in leg skeletal musculature are important for the early development of thermogenesis and locomotion (Dawson, Bennett and Hudson 1974; Aulie 1976; Aulie and Grav 1976; Ricklefs 1979b; Marsh and Wickler 1982; Aulie and Tøien 1988). Cockatiel chicks are not active in the nest early in their nestling period, but the rapid improvement in the coordination of leg muscles in the first days, above that of other muscle groups indicates more mature functional capabilities of the leg muscles. The relative contributions of muscle groups to heat production in parrots is not known. In altricial passerines the rapid improvements in thermogenesis are correlated with rapid increases in the mass of pectoral muscles late in the nestling period (Marsh and Wickler 1982; Choi, Ricklefs and Shea 1993).

Growth rates in altricial and precocial birds

Ricklefs (1979a) suggests that 3-4 fold differences in posthatching growth rates between altricial passerines and precocial birds may be attributed to differences in maturity of function at hatching. Mature muscle function is believed to be incompatible with high relative growth rates because tissue differentiation is correlated with the accumulation of solids (Ricklefs 1979a; Ricklefs and Webb 1985; Visser and Ricklefs 1993). Instantaneous growth rates of passerines are highest early in their posthatching development, when maintenance costs are low and prior to the development of thermogenic responses (Dawson and Evans 1957, 1960; Olson 1992). Thermogenesis is not present in passerines until late in development after large increases in muscle mass have taken place (Ricklefs and Webb 1985). In contrast, precocial chicks have mature muscle function at hatching and high maintenance costs, and are capable of thermogenic responses. In addition the energy allocation hypothesis predicts that less of the metabolisable energy intake is allocated to growth in active chicks (Dawson and Evans 1957, 1960). Precocial chicks therefore expend more energy during foraging than nidicolous altricial chicks.

Posthatching growth rates of king quail and cockatiel in the warm groups are in close agreement with allometric expectations for each phylogenetic group (eq. 3 & 4, p.173). K_G of king quail in this study and in Bernstein's (1973) study are lower than the predicted by the relationship for precocial land birds (fig. 42, p.171) (Ricklefs 1973). However, the previous allometric relationship for precocial land birds was derived for

species of Galliformes and Gruiformes with asymptotic masses greater than 100 g. The inclusion of king quail and other smaller precocial species (*Turnix* spp.) significantly reduces the slope of this relationship for precocial land birds (ANCOVA $t= 3.071$ $P<0.05$). A new relationship between growth rate of Galliforms and asymptotic mass (eq. 5, p.173) is suggested for precocial land birds (Galliformes, Gruiformes and Turniciformes). Thus the differences in growth rates between precocial and altricial birds increases with decreasing asymptotic mass. The lower growth rates of small precocial birds in these orders appears to support a greater dependence on parental brooding after hatching which limits their energy intake. In addition small precocial chicks may allocate more energy to the development of heat production capacities after hatching to balance the higher rates of heat loss. The relative growth rates of small precocial Charadriiform birds are significantly higher than Galliform birds over a similar asymptotic mass range (Visser 1991; Visser and Ricklefs 1993). The PMR of hatchlings of both orders are identical at the same body mass, and so the higher growth rates cannot be explained by a greater independence of hatchlings from parental brooding (Visser and Ricklefs 1993). However, Charadriiform birds lay eggs and produce hatchlings which are approximately double the mass of those Galliform birds (Rahn, Paganelli and Ar 1975; Visser 1991). Charadriiform birds hatch as a relatively larger fraction of the asymptotic mass and therefore a smaller growth increment is required to reach adult body mass than in galliform birds.

The pattern of energy allocation in the cockatiel offers an alternative explanation for the growth rates of all parrots, which are intermediate between other altricial and precocial birds. Lack (1968) suggests that the absence of selective pressures of predation on cavity-nesting parrots has resulted in low growth rates in comparison to open-nesting altricial birds. The early development of endothermy and thermogenic responses in the cockatiel (fig. 13, p.146) and the parrot, *Agapornis roseicollis* (Bucher and Bartholomew 1986) limits the energy available for growth, and consequently their growth rates are lower than other altricial birds. However, in spite of their precocious development of temperature regulation, parrots have higher growth rates than precocial land birds (fig. 42). Parrots are brooded continuously early in their development, during which time the parents make contributions to the cost of temperature regulation. Additionally parrot chicks utilise brood huddling behaviours during parental absences and do not expend energy foraging. All three factors represent energy savings for the chicks, and consequently parrot growth rates are higher than precocial birds of similar mass.

Intraspecific relationship between RMR, PMR and growth rate in king quail and cockatiel

The growth rates of both quail and cockatiel which were used to determine $\dot{V}O_2$ were intermediate between the highest and lowest growth rates found in this study. The RMR of hatchlings is significantly related to posthatching growth rates between species (Drent and Klaassen 1989; Klaassen and Drent 1991). However, no intraspecific relationship between RMR and residual body mass exists in king quail and cockatiel (fig. 7, p.140-141 and fig.17, p.148). Despite large variations in body mass at any given age, the RMR of chicks with negative residual body masses are determined by mass rather than age, and such chicks are equally capable of elevating metabolism during cold exposure. Similarly no correlation exists between deviations in PMR and growth rate in the king quail, but a significant correlation exists in cockatiel weighing more than 9 g, but the regression coefficient is very low, and therefore is not very convincing that a biologically relevant relationship exists (fig. 17). The PMR of cockatiel chicks with negative residual body masses is marginally higher than expected for their body mass. The variability in residuals of PMR decreased with age, and it is suggested that young chicks with low body mass have high PMR on the basis of body mass, but similar to expectations for their age. Klaassen and Bech (1992) also found no intraspecific correlation between RMR or PMR and growth rate in Arctic terns, *Sterna paradisaea*, but chicks lower than 25% of the average body mass have significantly lower RMR and PMR. In king quail and cockatiel, age is initially important in explaining variation in metabolic rates, but after RMR and PMR reach maximal levels, body mass is more important in explaining variation. Therefore it is concluded that no correlation exists between either resting metabolism or maximal metabolism during cold exposure and growth rate during development in king quail and cockatiel.

CHAPTER 5

Oxygen consumption of Adults and Chicks during Brooding

Introduction

Parental energy expenditure during incubation has been the subject of debate since Kendeigh (1963) first published his biophysical model of incubation costs. In his estimations of energy expenditure it was assumed that all thermal requirements of incubation must be met in addition to that of daily energy expenditure of the parent. The later model of King (1973) assumed that all or a large fraction of the heat generated by the adult was available to meet incubation requirements. Since these studies, other deterministic models have been produced to indirectly estimate energy expenditure during incubation (Walsberg and King 1978a, b; Walsberg 1983), and they concluded that incubating adults should be able to reduce heat loss through nest insulation and thus save energy. Other studies of incubating birds suggest that nests can offer considerable thermal benefits in comparison to birds outside the nest by reducing the surface area of the bird exposed to radiative and convective heat losses (Calder 1973; Kern and van Riper 1984).

There are direct measurements of parental energy expenditure during the incubation period of small birds, which demonstrate that the metabolic demands to meet the thermal requirements of incubation are significantly higher than non-incubating birds at T_a below the TNZ (Biebach 1979, 1981, 1986; Vleck 1981; Drent, Tinbergen and Biebach 1985; Haftorn and Reinertsen 1985; Weathers 1985; Williams 1991). In addition to increased energy expenditure during steady-state incubation, birds returning to the nest after inattentive periods increase heat production to rewarm the chilled clutch (Biebach 1986).

Embryonic respiration throughout most of the incubation period makes insignificant contributions to the total $\dot{V}O_2$ during incubation, and so total respiration typically is not corrected for the oxygen consumed by clutches (Vleck 1981), but after hatching, the relative contribution of broods to $\dot{V}O_2$ during brooding becomes significant. When estimating the energy cost of brooding, therefore, it is necessary to account for heat production by the chicks.

Only one study has determined the importance of parental heat transfer to the maintenance of chick T_b during brooding (Webb 1993). With the exception of megapodes, hatchlings of all developmental types require parental brooding immediately after hatching (Booth 1984). However, the energetic demands associated with this early brooding and the thermoregulatory control of brooding have not been studied. There are two reasons why it is important to address these questions. It is well recognised that the high thermal conductances and low rates of heat production of hatchlings of small birds prevent homeothermy at T_a below thermoneutrality, independent of the hatchling developmental type (Whittow and Tazawa 1991). Consequently, small hatchlings may require extensive additional heat input to prevent lethal declines in body temperature. Secondly, many non-altricial hatchlings leave the nest soon after hatching, and are

brooded without the benefits of nest insulation. The increased thermal gradients between adults and chicks and the environment is expected to increase the costs of brooding to adult birds.

This study investigates the brooding $\dot{V}O_2$ of king quail and cockatiel. Only the female quail incubates the eggs, but both male and female brood the chicks. In the cockatiel both sexes incubate the eggs and brood the chicks. The king quail has one of the smallest recorded precocial hatchlings (about 3-4 g) (Bernstein 1971, 1973), and the altricial cockatiel hatchling is a similar mass. However, the brooding requirements are likely to differ between species. The cockatiel and other closely related parrots are brooded constantly throughout the day for at least the first week after hatching (Kavanau 1987; Rowley and Chapman 1991; Smith 1991), in nest hollows that may offer thermal benefits to the brood and adults. In contrast, adult quail and their precocial hatchlings do not remain at the nest, and may experience greater heat losses to the environment. Quail chicks also forage independently of their parents, during which time they may have considerable thermoregulatory costs.

Broodpatches develop early in the egg-laying period of female king quail and are maintained up until the chicks fledge, but its role in brooding has not been studied. It is not known if cockatiel develop a broodpatch during breeding. Brooding periods are quantified with respect to T_a, age and body mass of chicks, to determine if chick and adult foraging times are constrained during low T_a.

Materials and Methods

Measurements

$\dot{V}O_2$ of adults and chicks of king quail and cockatiel were measured continuously using an open-flow respirometry system (see Chapter 2). Dry air was passed through calibrated flowmeters (SA-18 Fischer & Porter, Hatboro, Pennsylvania) at a flow rate of 800-1000 mL min^{-1} before entering the metabolism chamber. All metabolic measurements with adult quail were conducted in 1L plexiglass chambers during both α (day) and ρ (night) phases of the circadian cycle. All metabolic measurements of non-brooding adult cockatiel were conducted in cylindrical PVC metabolism chambers (150 mm diameter; 4.7L) fitted with dowel perches. Brooding $\dot{V}O_2$ of cockatiel measurements were conducted in modified plywood nestboxes, the entrance-hole of which was sealed by a piece of plywood containing the incurrent air line and excurrent air line was fitted close to the bottom of the box. Brooding $\dot{V}O_2$ of cockatiel was only measured during α (day) phase of the circadian cycle. All measurements were performed under a fluorescent light in a constant temperature cabinet during the α phase, but without the light on during ρ phase. Quail and cockatiel were placed in chambers 30 minutes prior to commencing

$\dot{V}O_2$ measurements, which was always sufficient time for the birds to reduce activity. Quail were postabsorptive 3.5-4 h at the start of measurements. $\dot{V}O_2$ measurements of non-brooding adult cockatiel were made with birds postabsorptive for 3.5-4 h. However, cockatiel were not postabsorptive during brooding measurements, both adult and chicks were removed from the nest after the chicks were fed mid-morning. Ambient Temperature (T_a) was lowered stepwise at a rate of 5 °C per 20 min, starting at 30-35 °C, and a minimal stable $\dot{V}O_2$ was calculated over a 5-10 min interval at the end of each period of exposure to each T_a (5% variation or less). Each adult quail was exposed to five or six different T_a within this range on any one day.

Adult core temperature (T_b) was measured after each $\dot{V}O_2$ measurement run, by inserting a precalibrated 36 ga. copper-constantan thermocouple to a depth of 1cm into the cloaca of adult birds, and reading from a digital thermometer (Fluke Model 52). Chick T_b was measured in the same manner with a 40 ga. thermocouple. The birds were weighed before and after each $\dot{V}O_2$ measurement. The relationship between thermal conductance and T_a below thermoneutrality was examined in non-brooding and brooding quail. Minimal 'wet' thermal conductance (C_{wet}: mL O_2 $g^{-1}h^{-1}C^{-1}$) of individual quail was calculated according to the Scholander model (Scholander et al. 1950) using the mean recorded T_b of adult quail in each phase of the day, over the T_a range 5-30 °C.

Experimental procedure

Non-brooding $\dot{V}O_2$

Adult quail were measured during both the breeding season and the non-breeding season. Non-brooding metabolism includes all $\dot{V}O_2$ of adult quail measured in the absence of chicks, and is separated into categories of breeding and non-breeding quail. Non-brooding measurements of $\dot{V}O_2$ were made during July to September of 1990 and 1991 in the ρ phase, and during September to March of 1991-92 and September to October of 1992 in the α phase. The non-breeding group were compared with the breeding group for differences in α phase metabolism. During the breeding season, the $\dot{V}O_2$ of non-brooding quail was not measured during ρ phase to limit disturbances to the birds.

Measurements of non-brooding $\dot{V}O_2$ of cockatiel were made during July to September of 1990 and 1991 in the ρ phase, and during September to March of 1991-92 and September to October of 1992 in the α phase. The non-breeding cockatiel group were then compared with the breeding group for differences in α phase metabolism. During the breeding season, non-brooding cockatiel $\dot{V}O_2$ was not measured during ρ phase to limit disturbances to the birds. The presence or absence of a broodpatch was recorded for each quail and cockatiel during the breeding season.

Brooding $\dot{V}O_2$

Adult quail were combined with their broods in the same chamber and $\dot{V}O_2$ measured during December to March 1991-92 and October to November 1992. Measurements of brooding $\dot{V}O_2$ were often made simultaneously with non-brooding (non-breeding and breeding) $\dot{V}O_2$ measurements during these periods. The chambers lacked any nest insulation, and were considered to be similar to the conditions under which chicks were brooded by adult quail in the outdoor aviaries. During brooding measurements the adults' behaviour was observed through the transparent metabolism chambers.

Adult cockatiel were combined with their broods in the same nestbox (metabolism chamber) and $\dot{V}O_2$ measured during July to November 1992 and November 1993. Measurements of brooding $\dot{V}O_2$ were often made simultaneously with non-brooding (non-breeding and breeding) $\dot{V}O_2$ measurements during these periods. The next box-chambers contained potting mix and was not considered to offer any significant nest insulation, and were considered to be similar to the conditions under which chicks were brooded by adult cockatiel in the outdoor aviaries. Behavioural observations were not possible during measurements, but nest boxes were inspected at the end of measurements to determine if the chicks were indeed brooded by the adult cockatiel.

The contribution of the chicks to $\dot{V}O_2$

The contribution of the brood to the total oxygen consumed during brooding was assessed by measuring the $\dot{V}O_2$ of broods under a heated taxidermic mount during the α phase. This mount was designed to simulate the brooding conditions under a brooding adult. A hollow shell was constructed from fibreglass to the same shape and dimensions as the thoracic region of a typical female king quail and adult cockatiel. Plumage and skin, head, legs and wings of a dead female adult birds were stretched over the surface of the mount, with the wings mounted slightly outstretched from the sides of the mount to approximately achieve the same degree of insulation offered by a brooding adult. This also allowed the chicks to adopt normal brooding behaviour. Temperature controlled water was circulated through the mount via two tubes. The temperature within the mount was recorded by a sealed copper-constantan thermocouple and was maintained at 38-40 °C over the whole T_a range, which was equivalent to recorded skin temperatures on the ventral surface of adult quail and cockatiel (this study), and was 2-4 °C higher than thermoneutral point for king quail chicks (Bernstein 1973).

The number and age of quail chicks in a brood were recorded during $\dot{V}O_2$ measurements with the heated mount. Quail chick $\dot{V}O_2$ was calculated as the $\dot{V}O_2$ of the whole brood divided by the number in the brood. Measurements of quail brood $\dot{V}O_2$ under the heated mount were made with a brood of 5 chicks (1 day old), brood of 2 (1 day old), brood of 4 (8 days) and a brood of 3 chicks (16 days). Measurements of brooded cockatiel chick $\dot{V}O_2$ under the heated mount were made each time with one chick only in the chamber, using chicks of age 2, 3, 6, 8, 8, and 11 days. The $\dot{V}O_2$ of artificially brooded chicks was compared with chicks measured in metabolism chambers without brooding (by parent or heated mount) (20-40 °C for unbrooded chicks and 10-40 °C for brooded). Measurements using the same adult quail and broods were limited to one run every other day throughout this study to avoid developmental delays in chick growth associated with recurrent fasting during the day.

Time budgets for brooding quail

The time adult quail spent brooding chicks was estimated for daylight hours by videorecording behaviour in one aviary. Brooding was continuous during the night. A videorecording system was used to record activity in a restricted area of one aviary (1.5m × 1.5m), so that the area filmed filled the field of view of the camera. Activity was recorded continuously for 9 h per day in the absence of observers, but on several occasions only 6 h were recorded on the same day. Proportion of time during the day that parent quail spent brooding (% brooding time) was calculated from these records. Brooding activity was recorded in the posthatching period of 1-18 days with between 4-6 recording days (each 6 or 9 h) per brood. Age of chicks on videorecording days was not always the same because hatching dates were close together. Four broods of chicks were used for brooding time measurements. T_a was recorded at 10 min intervals continuously in the shade of the recording area using a copper-constantan thermocouple and a Squirrel Datalogger 1203 (Grant Instruments, Cambridge U.K.) during all videorecording days.

Results

Brooding behaviour of king quail and cockatiel

After hatching, quail chicks usually initiate brooding by tunneling under the wings and to a lesser extent the legs of both parents. Chicks under adults press their bodies against apteria present in those regions, whilst the adult adopts a crouching posture with fluffed ventral feathers. The apteria under the wings of king quail (both parents) are permanent throughout the year and there is a seasonal reduction in plumage

and down between the legs and the thorax. Adult female quail are rarely seen to sit directly over the chicks to facilitate contact with the broodpatches for any length of time. Brooding is intermittent throughout daylight hours, but continuous during the night. The highly developed quail hatchlings do not become fully homeothermic until fledging at 25-28 days and so have an extended brooding period (Bernstein 1973).

Cockatiel brood their chicks under the thorax initially, until the chicks become too large and are then generally brooded under the wings. Chicks have upright postures after several days and press either their dorsal or lateral surfaces against the adult during brooding. However, cockatiel do not appear to form typical broodpatches, which are highly vascularised and oedematous, but some feather loss from the ventral surface of breeding adults may occur.

The $\dot{V}O_2$ of brooded quail chicks less than 5 days old

The mass-specific $\dot{V}O_2$ of the two broods under the heated mount were lower than the $\dot{V}O_2$ of chicks of similar age when not in the presence of a heated mount at $T_a < 35$ °C (fig. 1). At T_a 30-35 °C, the broods in the chamber with the mount were found to intermittently seek the warmth of the mount, and were frequently restless and often calling at the start of experiments. Below T_a 30 °C, broods were usually continuously brooded by the heat mount, with the exception of brief periods away from the mount. The metabolism of chicks brooded by the mount was independent of T_a over the range 10-40 °C, with little variation in $\dot{V}O_2$ about the mean of 2.93 mL O_2 $g^{-1}h^{-1}$ (two broods N=18). Broods in the presence of the heated mount, but not brooded by the mount, had higher $\dot{V}O_2$ (3.00-3.90 mL O_2 $g^{-1}h^{-1}$) than brooded chicks, but within the range of $\dot{V}O_2$ of quail chicks measured without the mount in the chamber. The $\dot{V}O_2$ of all unbrooded chicks was significantly higher than the $\dot{V}O_2$ of brooded chicks and more variable (ANOVA $F_{1, 68} = 14.894$ $P< 0.001$).

The unbrooded $\dot{V}O_2$ of newly hatched chicks (0-1 days) increased as T_a decreased in some birds, but not others (2.40-5.50 mL O_2 $g^{-1}h^{-1}$) (fig. 1). The $\dot{V}O_2$ of unbrooded chicks at T_a <30 °C was higher than that of chicks when brooded by the mount. The total $\dot{V}O_2$ of broods during brooding $\dot{V}O_2$ measurements with adult quail was calculated using the initial brood mass multiplied by a $\dot{V}O_2$ of 2.95 mL O_2 $g^{-1}h^{-1}$.

The $\dot{V}O_2$ of brooded quail chicks 6-17 days old

Chicks intermittently seek brooding from parents at T_a >30 °C, and chicks only sought the warmth of the heated mount when T_a <30 °C. The $\dot{V}O_2$ of the brood of chicks at 8 days of age increased linearly from 6.00 mL O_2 $g^{-1}h^{-1}$ at 35 °C to 8.00 mL O_2 $g^{-1}h^{-1}$ at 18 °C when unbrooded but in the presence of the heated mount (fig. 2). The brood of

chicks at 16 days of age were brooded only intermittently T_a >28 °C, and their $\dot{V}O_2$ was between 4.0-4.5 mL O_2 $g^{-1}h^{-1}$. Both broods were brooded continuously by the heated mount below T_a 18 and 28 °C respectively, with a mean $\dot{V}O_2$ of 5.86 ± 0.34 mL O_2 $g^{-1}h^{-1}$ (N=12). The brood at 8 days of age were unbrooded by the mount at a T_a >18 °C because they were initially unsettled. The $\dot{V}O_2$ of chicks (>10 days of age) increased in the absence of the heated mount at T_a<35 °C (fig. 2). Chicks at 6 days of age, failed to increase $\dot{V}O_2$ at low T_a (15-20 °C) and maintained a high $\dot{V}O_2$ at a mean of 5.54 ± 0.48 mL O_2 $g^{-1}h^{-1}$ over a T_a range of 17-32 °C (n=3, N=15), similar to chicks at age 4 days between T_a 25-35 °C (fig. 1-2). Subsequently, a $\dot{V}O_2$ of 5.80 mL O_2 $g^{-1}h^{-1}$ was used to calculate brood (>5 days of age) $\dot{V}O_2$ contributions to adult brooding $\dot{V}O_2$ below T_a 35 °C. Broods did not seek the warmth of the heated mount above T_a 30 °C as $\dot{V}O_2$ was sufficiently high for heat production to equal heat loss.

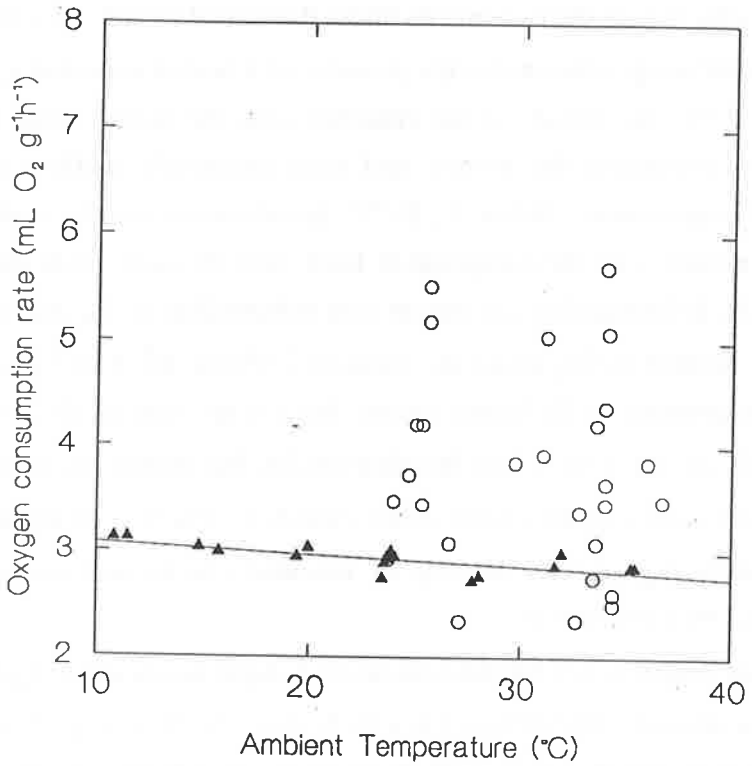

Fig. 1. Relationship between $\dot{V}O_2$ and T_a in chicks <5 days of age. *Filled triangles and solid line*: chicks brooded under a heated taxidermic mount (two broods, N=18; mean mass= 3.66 ± 0.50g); *open symbols*: chicks not brooded by mount and other chicks not in the presence of the mount (*circles*: 0-1 days old, and *triangles*: 4 days old) (12, 52; mean mass= 3.86 ± 0.60g).

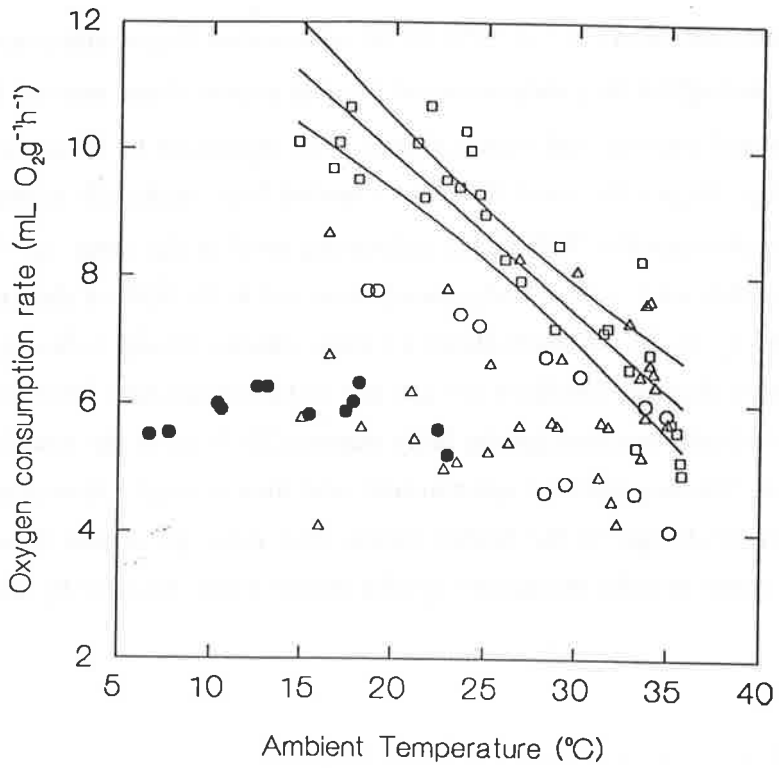

Fig. 2. Relationship between $\dot{V}O_2$ and T_a in quail chicks 6-17 days of age. *Filled circles*: chicks brooded under a heated taxidermic mount (two broods, N= 18; mean mass= 6.519 ± 1.729 g); *open circles*: unbrooded chicks in the presence of the mount (same two broods, 12); *triangles*: chicks (day 6-10) not in the presence of the mount (8, 34; mean mass= 5.257 ± 0.859 g); *squares and solid line*: chicks (day 11-17) not in the presence of the mount (4, 28; mean mass= 9.541 ± 1.661 g).

The T_b of hatchlings and chicks one day of age which were measured immediately after parental brooding were 36.6 ± 0.9 °C (SD) (body mass 3.93 ± 0.32 g n=14) (fig. 3). Chick T_b increased to 37.9 ± 0.8 °C (body mass 4.29 ± 0.56 g n=8) during parental brooding in chicks 3-6 days of age. During short-term cold exposure (<30 min at T_a 15-30 °C), the T_b of unbrooded chicks declined in a poikilothermic manner in chicks less than 12 days of age (fig. 10, p.142). Homeothermy was achieved in king quail between 15-18 days of age at a body mass of 7-10 g.

The $\dot{V}O_2$ of brooded cockatiel chicks less than 11 days old

The $\dot{V}O_2$ of chicks brooded by the heated mount was always lower than unbrooded chicks between 2 and 11 days of age at T_a 10-35 °C (fig. 4). The $\dot{V}O_2$ of unbrooded and brooded cockatiel chicks increased in the first five days after hatching (fig. 4; and fig. 13, p.146). At thermoneutrality the $\dot{V}O_2$ of brooded cockatiel chicks was typically 50% of the unbrooded rate of chicks of the same age with the exception of the brooded chick which was >20 g body mass. The $\dot{V}O_2$ of brooded chicks (<20 g) was

independent of T_a between 10-35 °C, at 50% of the unbrooded $\dot{V}O_2$ at thermoneutrality. One brooded chick during the $\dot{V}O_2$ measurement became exposed and was no longer in contact with the heated mount, and consequently $\dot{V}O_2$ increased to levels similar to unbrooded chicks (fig. 13, p.146), until the chick crawled back under the mount, where upon the chick's $\dot{V}O_2$ decreased to 70% of the unbrooded level at the same T_a. The $\dot{V}O_2$ of brooded chicks, which were ≥ 20 g body mass, increased to 70-80% of the unbrooded level as T_a decreased to 10 °C. Observations of these chicks during brooding by the heated mount revealed that the chicks were too big to be completely brooded by the heated mount. When chicks reached similar body masses (20-30 g) in the nest, brooding by the parents during the day became intermittent and then ceased. However, it was considered that the rigid design of the heated mount may have prevented these chicks from achieving the same benefit as smaller chicks which were brooded by the heated mount.

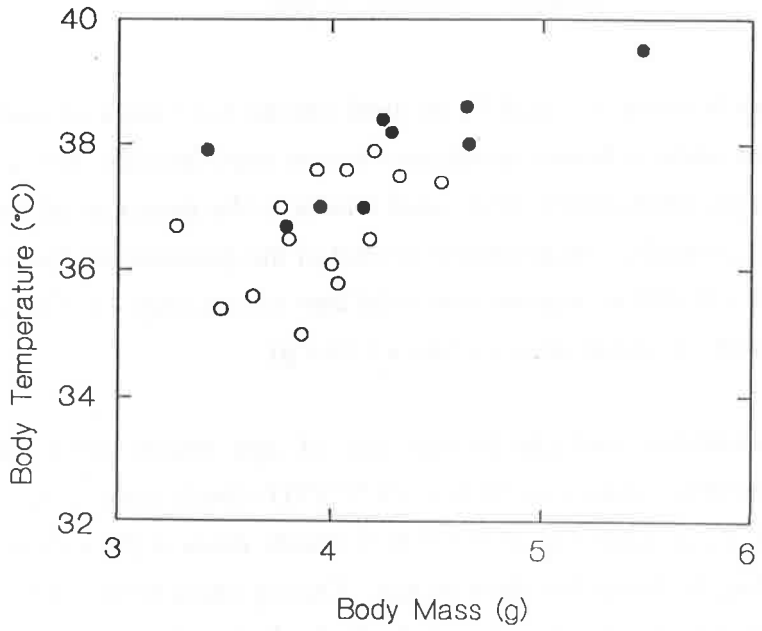

Fig. 3. The body temperature of brooded king quail chicks less than 6 days old in relation to body mass. *Open circles*: 0-1 days old (n=14); *filled circles*: 3-6 days old (n=9).

The contributions of chicks to $\dot{V}O_2$ during parental brooding was determined using chick mass and a mass-specific $\dot{V}O_2$ of 50% of the unbrooded level at thermoneutrality. Specifically, the following $\dot{V}O_2$ were used: hatchlings 0.9 mL O_2 $g^{-1}h^{-1}$, chicks at 2-3 days were 1.9-2.2 mL O_2 $g^{-1}h^{-1}$ and chicks ≥ 5 days of age were 2.5 mL O_2 $g^{-1}h^{-1}$.

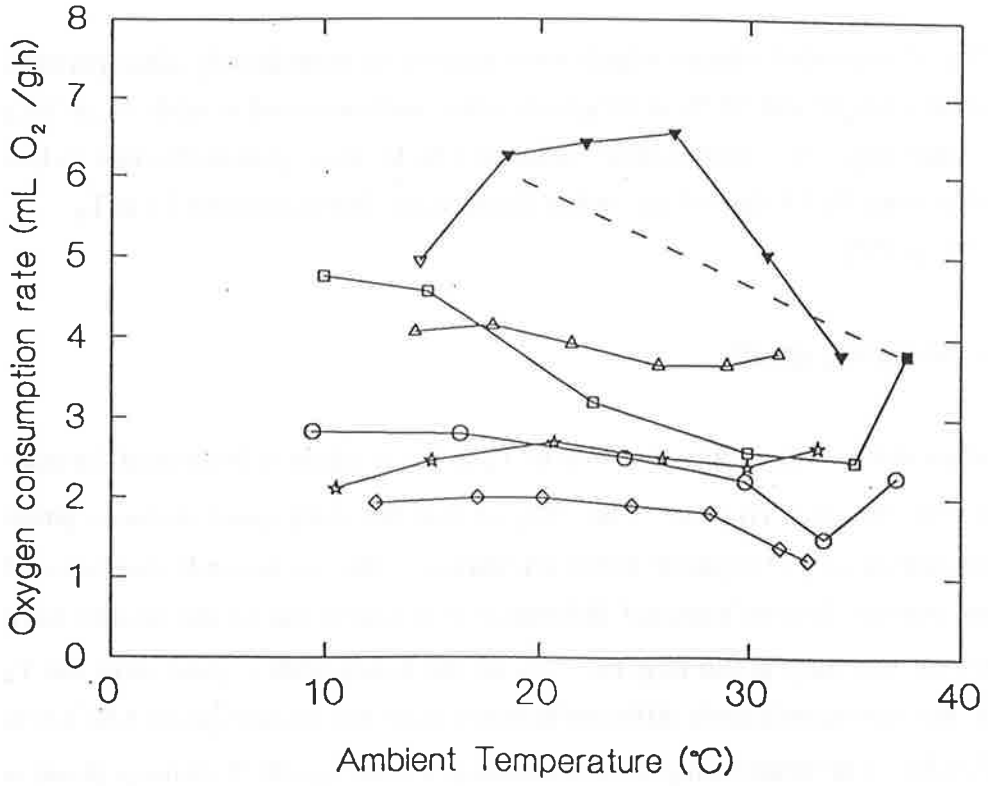

Fig. 4. Relationship between $\dot{V}O_2$ and T_a for individual cockatiel chicks in the presence of a heated mount between T_a 10-37 °C. *Open symbols*: chicks brooded by the heated mount; *closed symbols*: unbrooded chicks in the chamber with a heated mount. Individual chicks are connected by unique symbols and a solid line. *Diamond*: chick 2 days of age (8.14 g); *circle*: 3 days of age (12.08 g); *star*: 6 days of age (11.44 g); *square*: 8 days of age (28.64 g); *triangle*: 11 days of age (18.67 g); *inverted triangle*: 8 days of age (13.36 g). *Dashed line* indicates $\dot{V}O_2$ of unbrooded chicks >5 days of age in the absence of a heated mount (refer to fig. 13, p.146).

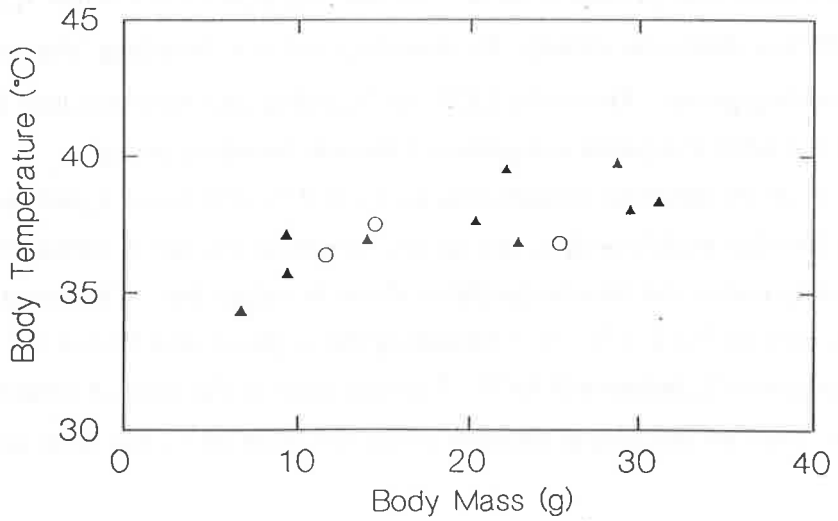

Fig. 5. Body temperature of brooded cockatiel chicks in relation to body mass. Chicks were between 3 and 13 days of age. *Open*: chicks under heated mount, *filled symbols*: parental brooding.

The T_b of cockatiel chicks which were measured immediately after parental brooding was between 35 and 37 °C at 10 g body mass, and increased to adult T_b at 30 g (12-13 days old) (fig. 5). Unbrooded cockatiel chicks were poikilothermic below thermoneutrality until 10-13 days of age, when chicks were able to regulate T_b at T_a >15 °C (fig. 21, p.152).

$\dot{V}O_2$ *of non-brooding quail*

The relationship of non-brooding $\dot{V}O_2$ to T_a in the α phase is presented for non-breeding and breeding quail (fig. 6). The $\dot{V}O_2$ of non-breeding quail in the α phase could not be statistically compared between seasons, due to limited numbers of measurements, but no obvious seasonal difference was found and so the results were pooled as the non-breeding group (fig. 6). $\dot{V}O_2$ of the non-breeding quail over the T_a range 8-36 °C was not significantly different between male and female quail (ANCOVA $F_{1,93}$= 0.805 N.S.). The relationship of non-breeding $\dot{V}O_2$ to T_a <28 °C in the ρ phase is presented in figure 8, for comparison with brooding quail. The biphasic regression technique (Yeager and Ultsch 1989) was not able to distinguish a lower critical temperature in either breeding or non-breeding quail (α & ρ phases). Previously the TNZ was defined as 28-35 °C for the king quail (Roberts and Baudinette 1986), therefore for the purposes of comparing between groups, 28 °C was defined as the lower critical temperature (LCT) in this study. Below T_a 28 °C, the relationship between $\dot{V}O_2$ and T_a was not significantly different between breeding and non-breeding quail (fig. 6). Above T_a 28 °C, there was a significant elevation in SMR of breeding quail in relation to non-breeding quail (2.03 ± 0.29 (N=34) and 1.62 ± 0.35 mL O_2 $g^{-1}h^{-1}$ (22): t-test $t_{1,54}$= -5.128 P< 0.001). Below thermoneutrality, the breeding and non-breeding $\dot{V}O_2$ were pooled as the non-brooding group. Above the LCT, the breeding and non-breeding $\dot{V}O_2$ were not pooled, but considered separate categories of the non-brooding group.

The mean T_b of seven breeding females was 41.1 ± 0.7 °C (N=24) at T_a between 10-35 °C. Breeding females with broodpatches showed a similar degree of variation in mean T_b as non-breeding males and females (n=38) without broodpatches. The mean T_b of non-breeding quail was 41.6 ± 1.1 °C (N=110) during the α phase and 40.6 ± 1.2 °C (N=42) during the ρ phase at T_a between 5-38 °C. The similarity in the level of observed T_b suggests that there were no permanent changes in the set-point of T_b for both sexes and breeding states.

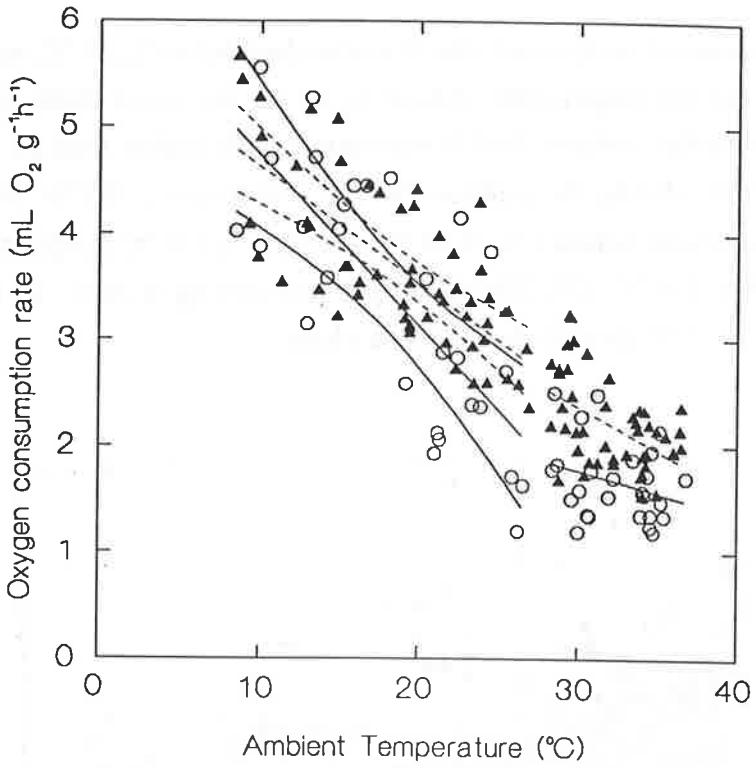

Fig. 6. Relationship between non-brooding $\dot{V}O_2$ and T_a of breeding and non-breeding adult quail (± 95% CI) in the α phase. *Circles and solid lines*: non-breeding (n=7, N=55); *triangles and dashed lines*: breeding (13, 119). Regressions of $\dot{V}O_2$ on T_a <28 °C: breeding $\dot{V}O_2 = 5.718 - 0.109\ T_a$ (s_b= 0.013 r^2= 0.535); non-breeding $\dot{V}O_2 = 6.337 - 0.161\ T_a$ (s_b= 0.028 r^2= 0.575). The slopes and intercepts of these relationships were not significantly different for breeding and non-breeding quail below T_a 28 °C (ANCOVA $F_{1,81}$= 3.630 N.S. in slopes, t= -0.461 N.S. in intercepts).

$\dot{V}O_2$ *of non-brooding adult cockatiel*

The relationship between non-brooding $\dot{V}O_2$ and T_a below 29 °C was significant during the α and ρ phases (fig. 7). Non-brooding $\dot{V}O_2$ below T_a 29 °C was higher during the α phase than the ρ phase, but there was no significant difference in the slope or intercepts of the relationships (ANCOVA F= 0.632 N.S. in slope, t= 0.749 N.S. in intercept). The variability in non-brooding $\dot{V}O_2$ during the α phase was analysed by stepwise multiple regression which included categories of body mass, sex and breeding status. The final model explained 66.0% of total variation in $\dot{V}O_2$. T_a explained 61.8% of variation in $\dot{V}O_2$ (F=138.956 P<0.001). Sex explained a further 2% of variation (F= 4.894 P<0.03). The interaction term sex × T_a and breeding status were not significant in explaining variation alone, but in the final model both explained a further 1.1% each (F= 2.810 and 2.662 N.S.). The biphasic regression technique (Yeager and Ultsch 1989) was not able to distinguish a lower critical temperature in non-brooding $\dot{V}O_2$, but it was

considered for the purposes of comparison that $\dot{V}O_2$ increased below T_a 29 °C, and it was accepted as the lower critical temperature. Above T_a 29 °C, the mean SMR of 2.24 ± 0.45 mL O_2 $g^{-1}h^{-1}$ during the α phase (N=41) was significantly higher than the mean of 1.63 ± 0.16 mL O_2 $g^{-1}h^{-1}$ during the ρ phase (N= 54) (t-test $t_{1,93}$= -8.376 P<0.001). The mean T_b of adult cockatiel between T_a 5-25 °C was 42.1 ± 1.0 °C (n=20, N=32) in the α phase and 39.6 ± 1.6 °C (20, 20) in the ρ phase during winter. In summer cockatiel T_b was 40.3 ± 1.2 °C (N=28) during the α phase.

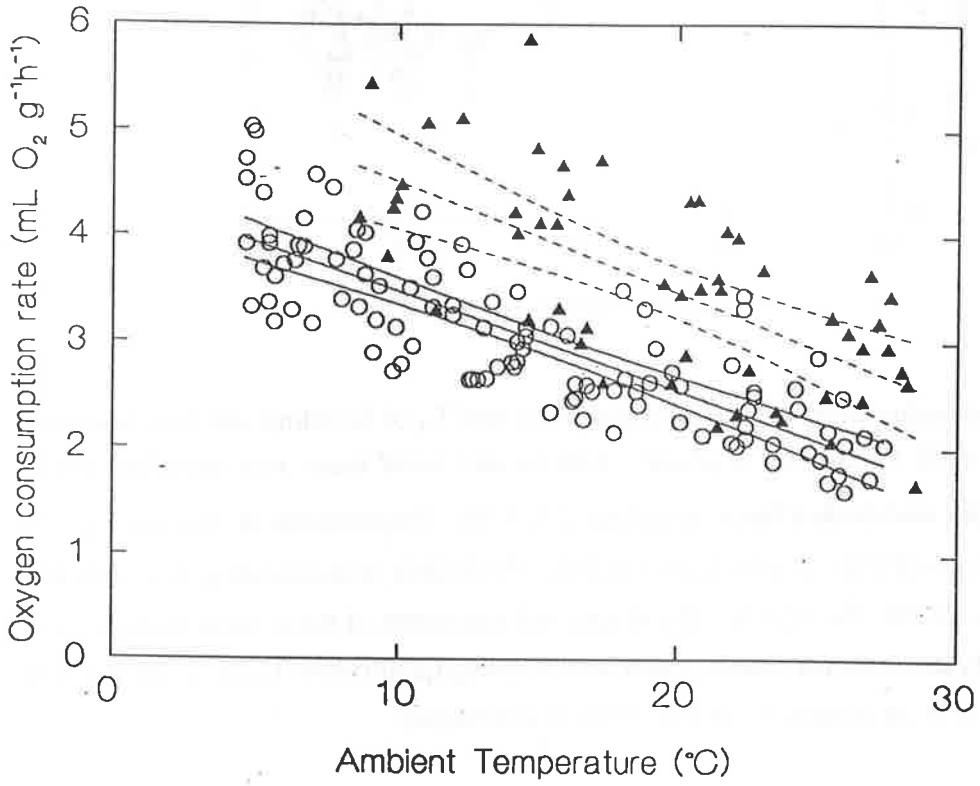

Fig. 7. Relationship between $\dot{V}O_2$ and T_a <29 °C for non-brooding adult cockatiel during the α and ρ phases of the circadian rhythm (± 95% CI). *Circles and solid lines*: ρ phase ($\dot{V}O_2 = 4.356 - 0.092T_a$; s_b= 0.005 r^2 = 0.700 (n=18) $F_{1,151}$= 348.058 P< 0.001); *triangles and dashed lines*: α phase ($\dot{V}O_2 = 5.546 - 0.104T_a$; s_b= 0.013 r^2 = 0.447 (n=12) $F_{1,51}$= 41.224 P< 0.001).

$\dot{V}O_2$ *of brooding adult quail*

Total $\dot{V}O_2$ of each brood was subtracted from the $\dot{V}O_2$ measured during parental brooding. The relationship between $\dot{V}O_2$ and T_a for brooding quail was separated into two groups, T_a <28 °C and T_a between 28 and 36 °C, for comparison with the non-brooding quail. Linear regressions of the relationship of $\dot{V}O_2$ on T_a <28 °C were not

significantly different between α and ρ phases for brooding quail ($F_{1,122}$= 2.933 N.S.), and so the common regression for both phases pooled was compared with non-brooding $\dot{V}O_2$ (fig. 8). Below T_a 28 °C, brooding $\dot{V}O_2$ was significantly higher in slope and intercepts than both non-brooding $\dot{V}O_2$ in α and ρ phases. In the T_a range 30-36 °C, non-brooding quail were within their thermoneutral range and $\dot{V}O_2$ was at a minimum. Within the same range of T_a brooding $\dot{V}O_2$ was significantly higher than all non-brooding groups except breeding quail (α phase) (Table 1, p.204).

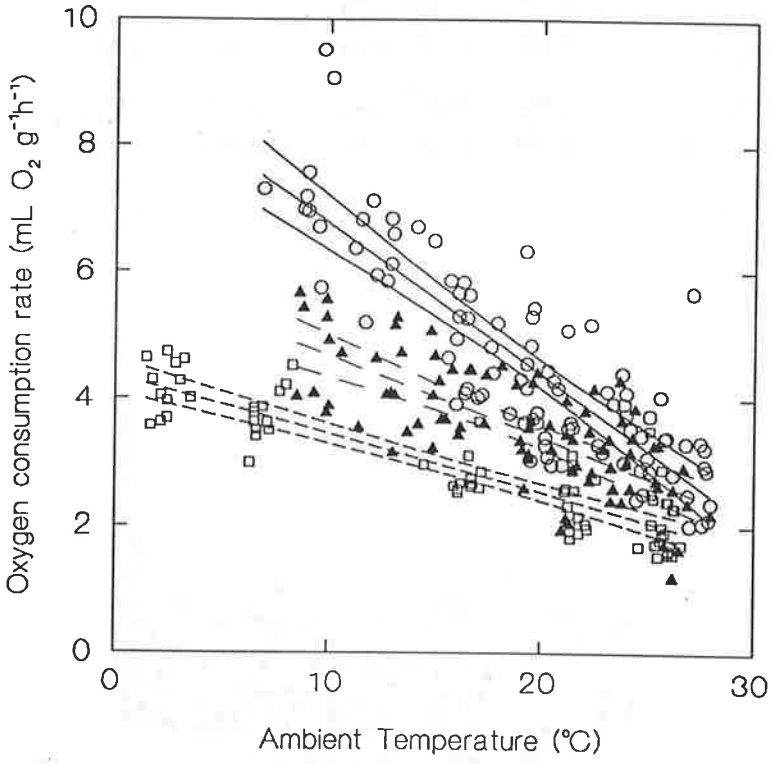

Fig. 8. Relationship between $\dot{V}O_2$ and T_a <28 °C for brooding and non-brooding quail (± 95% CI). *Open circles and solid line* : brooding in α and ρ phases (n=8), $\dot{V}O_2$ = 9.150 - 0.234 T_a (s_b= 0.016 r^2= 0.712 $F_{1,77}$= 185.732 P< 0.001); *filled triangles and large dashed line* : non-brooding in α phase (20), $\dot{V}O_2$ = 5.936 - 0.127 T_a (s_b= 0.013 r^2= 0.517 $F_{1,83}$= 88.797 P< 0.001); *open squares and fine dashed line* : non-brooding in ρ phase (20), $\dot{V}O_2$ = 4.360 - 0.092 T_a (s_b= 0.006 r^2= 0.789 $F_{1,71}$= 265.577 P< 0.001). The brooding regression was significantly different in slope and intercept from non-brooding α phase (ANCOVA $F_{1,158}$= 23.947 P< 0.001) and non-brooding ρ phase (ANCOVA $F_{1,146}$= 75.251 P< 0.001).

Table 1. Comparisons of brooding $\dot{V}O_2$ with non-brooding at T_a 28-36 °C. Brooding quail were pooled for α and ρ circadian phases, and non-brooding quail were separated into groups based on breeding condition and circadian phase. Mean $\dot{V}O_2$ (± SD) of each non-brooding group were compared with the brooding quail by t-test, and significance was accepted at $P< 0.05$. $\dot{V}O_2$ are presented in mL O_2 $g^{-1}h^{-1}$.

	mean $\dot{V}O_2$	SD	(N)	*t*	P
Brooding	2.06	0.61	(35)		
α Non-brooding (breeding)	2.03	0.29	(34)	0.335	N.S.
(non-breeding)	1.62	0.35	(22)	3.474	0.001
ρ Non-brooding (non-breeding)	1.59	0.20	(35)	4.374	0.001

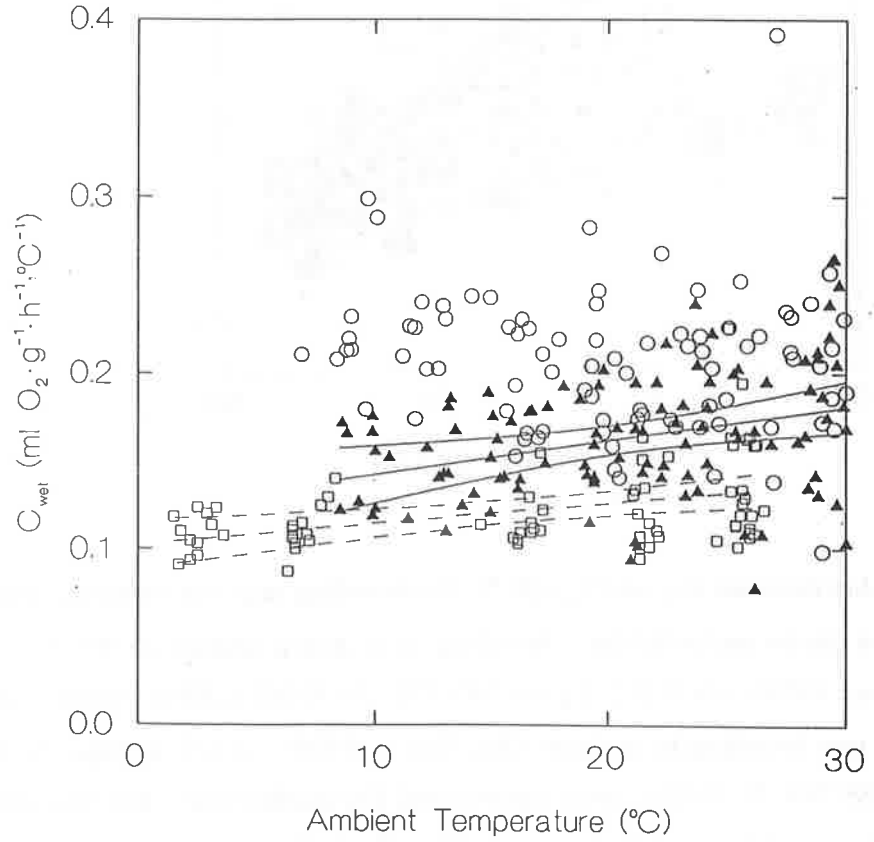

Fig. 9. Relationship between C_{wet} and T_a <28 °C for brooding and non-brooding quail (± 95% CI). *Open circles*: brooding quail in α and ρ phases (n=8), relationship N.S.; *filled triangles and solid line*: non-brooding quail in α phase (20), C_{wet}= 0.123 - 0.002 T_a (r^2= 0.114 $F_{1,104}$= 13.428 P< 0.001); *open squares and dashed line*: non-brooding quail in ρ phase (n=20), C_{wet}= 0.103 - 0.001 T_a (r^2= 0.176 $F_{1,71}$= 15.154 P< 0.001).

Extrapolation of the relationship of $\dot{V}O_2$ on T_a<28 °C, to the T_a axis exceeded the measured T_b of brooding and non-brooding king quail in this study. C_{wet} was calculated assuming a constant T_b for both brooding and non-brooding (α phase) groups of 41.6 °C, and 40.6 °C for the non-brooding (ρ phase) group. C_{wet} of adult quail increased significantly from ρ phase non-brooding, to α phase non-brooding and the brooding group (0.122 ± 0.024, 0.163 ± 0.036 and 0.207 ± 0.041 mL O_2 $g^{-1}h^{-1}°C^{-1}$ respectively ANOVA $F_{1,263}$= 116.429 P< 0.001) (fig. 9). C_{wet} of non-brooding quail was higher than predicted for non-passerine birds of similar mass (0.104 ± 0.001 mL O_2 $g^{-1}h^{-1}°C^{-1}$; Aschoff 1981), but similar to the values reported by Roberts and Baudinette (1986) (0.120 ± 0.002 mL O_2 $g^{-1}h^{-1}°C^{-1}$). In the non-brooding quail groups C_{wet} decreased with T_a, but in the brooding group C_{wet} appears to increase below 15 °C. Though no significant relationship was found between C_{wet} and T_a for brooding quail.

The relationship between brooding $\dot{V}O_2$ and T_a over the range 8-36 °C, was not different between males and females in this study despite considerable dimorphism in body mass (mean adult mass of females (n=6) = 50.18 ± 4.37 g and males (n=2) = 44.35 g), but small numbers of birds prevented testing for significant differences. The brooding $\dot{V}O_2$ of quail with 4-5 chicks was significantly elevated above the $\dot{V}O_2$ of quail brooding 1-2 chicks (fig. 10). Brood mass was found to have a significant influence on C_{wet} of adult quail (ANCOVA $F_{1,\ 93}$ = 9.827 P< 0.001) and therefore contributed significantly to the explained variation in the thermal conductance of brooding quail below T_a 28 °C.

A stepwise multiple regression model found that T_a explained most variation (82%) in brooding $\dot{V}O_2$ (F= 58.994 P< 0.001). However, the age of broods (F= 11.012 P< 0.001) and brood number (F= 18.912 P< 0.001) were significant in explaining further variation in $\dot{V}O_2$, as were the interaction terms between brood mass and T_a, brood number and T_a (F= 8.390 P< 0.01 and F= 22.493 P< 0.001). $\dot{V}O_2$ of quail brooding chicks was not significantly different between age groups with respect to changes in T_a (F= 0.067 N.S.). The combined brood mass was not significant in the final model (F= 0.015 N.S.), but the interaction term of brood number with T_a was significant. Brood number was more important in explanation of variability in $\dot{V}O_2$ than combined brood mass, since chick mass was variable during development.

$\dot{V}O_2$ *of brooding adult cockatiel*

Total $\dot{V}O_2$ of each cockatiel brood was calculated on the basis of chick body mass and was subtracted from the $\dot{V}O_2$ measured during parental brooding. Brooding $\dot{V}O_2$ was measured on seven occasions with broods of 1-4 chicks aged between 1 and 11 days old. The relationship between $\dot{V}O_2$ and T_a was separated into two groups, T_a <29 °C and T_a between 29 and 35 °C. Below T_a 29 °C, brooding $\dot{V}O_2$ was not significantly different in

slope or intercepts than non-brooding $\dot{V}O_2$ during the α phase (fig. 11). The relationship between brooding $\dot{V}O_2$ and Ta <29 °C was as variable as non-brooding $\dot{V}O_2$ during the α phase. The brooding $\dot{V}O_2$ of one adult cockatiel with a brood of three chicks, two of which were 8 and 9 days old (34.0 and 38.1 g respectively), was lower than the brooding $\dot{V}O_2$ of other cockatiel and non-brooding $\dot{V}O_2$ (stars, fig. 11). The lower $\dot{V}O_2$ of the brooding adult with large chicks was attributed to the benefits of huddling behaviours, as large chicks (25-30 g) were not able to fit completely under the wings of the brooding adult. SMR of brooding cockatiel at T_a >29 °C was not significantly higher than the mean SMR of non-brooding cockatiel during α phase (mean 2.23 ± 0.64 mL O_2 $g^{-1}h^{-1}$ (N=14); $t_{1,53}$= -0.391 N.S.).

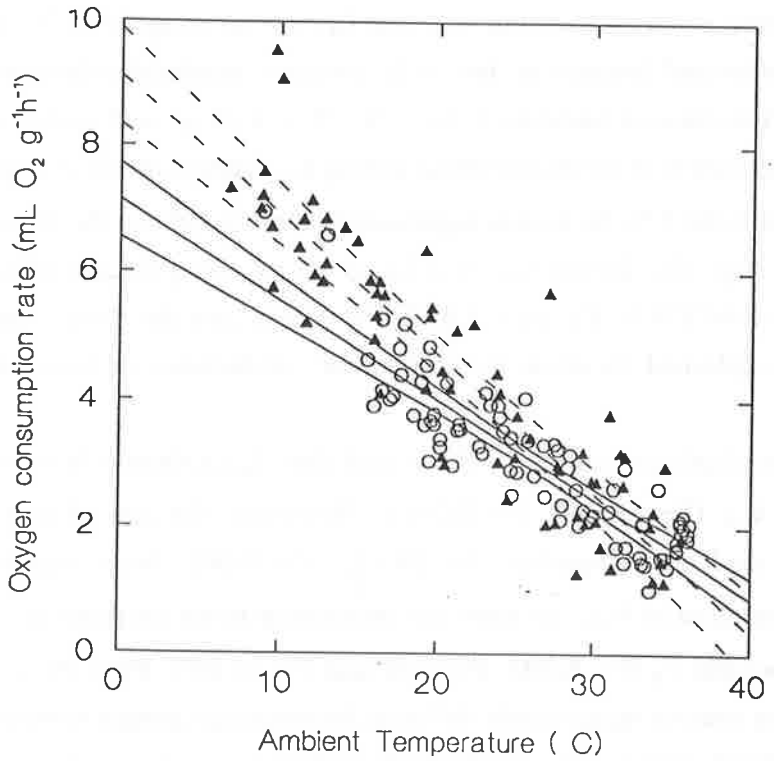

Fig. 10. Relationship between $\dot{V}O_2$ and T_a for quail brooding chicks between 0 and 17 days over a T_a range of 5-36 °C with brood numbers of 1-2 and 4-5 chicks. *Circles and solid line*: quail brooding 1-2 chicks (N=81); *triangles and dashed line*: quail brooding 4-5 chicks (N=67). The relationships were significant for both groups (1-2 chicks: $\dot{V}O_2$ = 7.134 - 0.156 T_a (s_b= 0.009 r^2= 0.806 $F_{1,79}$= 328.302); and 4-5 chicks: $\dot{V}O_2$ = 9.119 - 0.219 T_a (s_b= 0.013 r^2= 0.808 $F_{1,65}$= 273.209)). The relationships of $\dot{V}O_2$ on T_a were significantly different in slope and intercept between groups (ANCOVA $F_{1,146}$= 15.626 P<0.001).

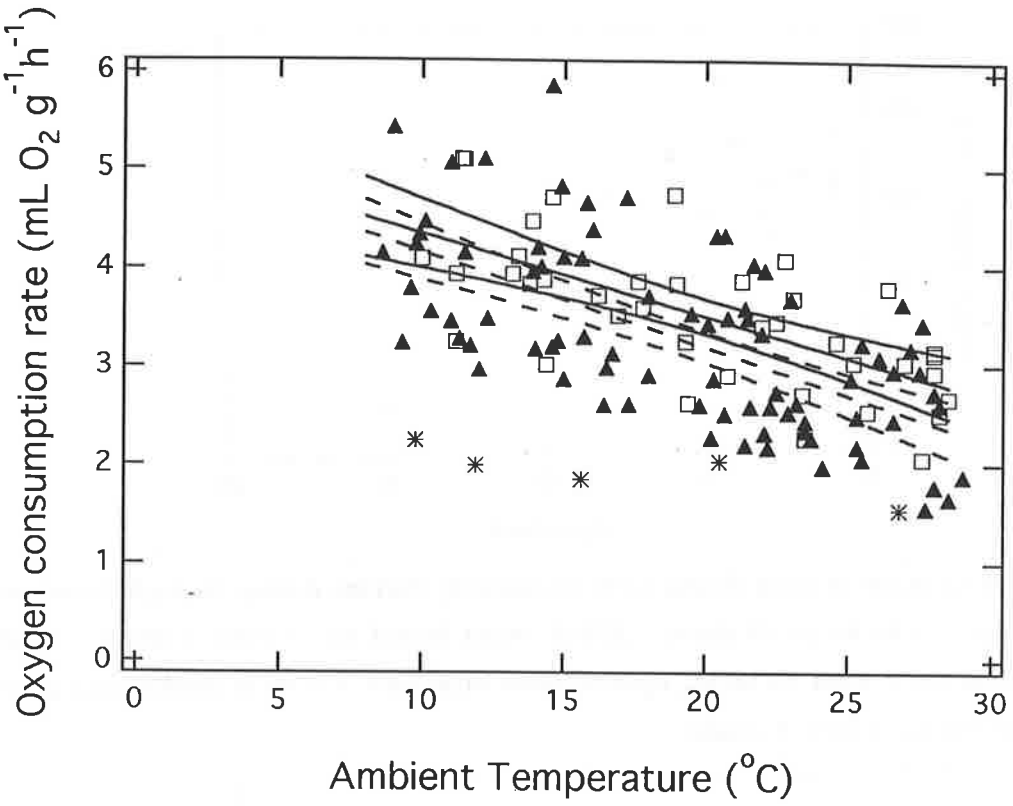

Fig. 11. Relationship between $\dot{V}O_2$ and T_a <29 °C for non-brooding and brooding adult cockatiel (± 95% CI). *Triangles and dashed lines*: non-brooding $\dot{V}O_2$ during α phase ($\dot{V}O_2 = 5.546 - 0.104T_a$; $s_b = 0.013$ $r^2 = 0.447$ (n=12) $F_{1,51} = 41.224$ $P < 0.001$); *squares and solid lines*: brooding $\dot{V}O_2$ during α phase ($\dot{V}O_2 = 5.186 - 0.084T_a$; $s_b = 0.015$ $r^2 = 0.453$ $F_{1,37} = 30.604$ $P < 0.001$); *stars*: brooding $\dot{V}O_2$ of one cockatiel with a brood of large chicks (see text p.204). The slopes and intercepts of these relationships were not significantly different (ANCOVA $F_{1, 83} = 0.434$ N.S.).

Percentage brooding time of quail

The percentage brooding time for 4 pair of quails and their broods (3-6 chicks) averaged 64% for chicks one day old, and decreased non-linearly with age until chicks were no longer brooded at 15-18 days of age (fig. 12). Chicks <5 days of age were brooded 50-75% of the time, and chicks >10 days of age were brooded <50% of the time. Brooding time (%) was negatively correlated with mean T_a of each hour during daylight for all chicks prior to reaching homeothermy (fig. 13). Hours in which quail were basking in direct sunlight were not included because operative temperature (T_e) was not known. Brooding times were only calculated for daylight hours in which quail were observed to be in shade. Brooding times of chicks <5 days of age were significantly longer in brooding times at T_a >18-20 °C than chicks >5 days of age (fig. 13). At T_a 18-20 °C, chicks of all ages prior to reaching homeothermy were brooded between 55-85% of the time. Brood no.1 (filled circles in fig. 12) experienced inclement weather and T_a

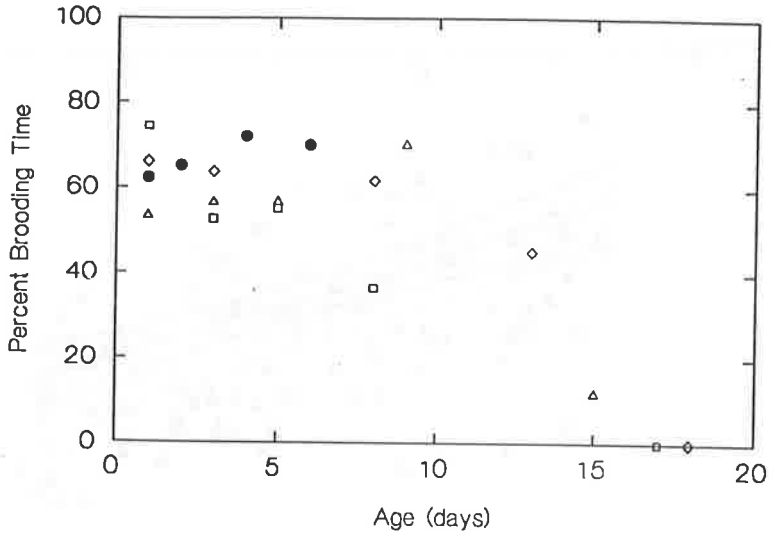

Fig. 12. Percentage of time chicks were brooded by parents during daylight hours in relation to age of chicks (0-18 days). *Filled circles* brood no. 1 with 4 chicks, *open triangles* brood no. 2 with 6 chicks, *open squares* brood no. 3 with 6 chicks, and *open diamonds* brood no. 4 with 4 chicks.

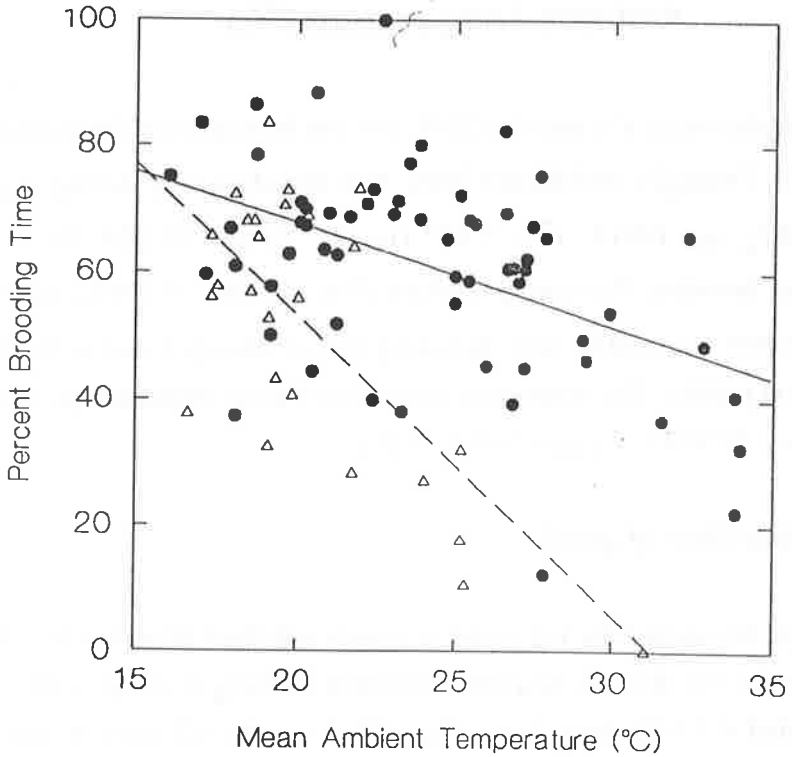

Fig. 13. Brooding time (% of each hour) in relation to mean air temperature during each hour of the daylight period recorded prior to chicks reaching homeothermy. *Circles and solid line*: chicks < 5 days of age; *triangles and dashed line*: chicks >5 days of age. Relationships for both age groups were significant: (<5 days) brooding time (BT) = 100.12 - 1.62 T_a (s_b= 0.409 r^2 = 0.207, $F_{1,60}$= 15.670 $P < 0.001$) and (>5 days) brooding time (BT) = 148.27 - 4.75 T_a (s_b= 0.957 r^2 = 0.506, $F_{1,25}$= 24.625 $P < 0.001$). The relationships of BT on T_a were significantly different in slope and intercept between groups (ANCOVA $F_{1,85}$= 9.880 $P< 0.002$).

18 °C during the daytime after hatching and were brooded 75% of the time up to 4 days of age. With reduced foraging time these chicks never gained mass and they died presumably as a direct result of exposure. In contrast, brood no.3 experienced T_a > 25 °C after one day of age and were brooded < 50% of the day, which allowed the chicks to forage for longer and thus increase body mass and reach homeothermy before 17 days of age.

Discussion

Metabolism of brooded and unbrooded quail chicks

The development of thermoregulatory abilities of unbrooded chicks in this study is similar to the patterns reported for the same species (Bernstein 1973). Chicks between hatching and day 3 maintain constant $\dot{V}O_2$ or are capable of minor increases as T_a decreases over the T_a range 20-35 °C (fig. 1, p.196). However, after day 3, chicks have higher $\dot{V}O_2$ at thermoneutrality than younger chicks, and increase $\dot{V}O_2$ above minimal levels at T_a lower than 35 °C. Thermoneutral and maximal $\dot{V}O_2$ during cold exposure increase in unbrooded chicks until 11-17 days of age, when chicks are able to maintain high T_b (fig. 2-3, p.197-198). The improvements in heat production capabilities are initially the result of increases in mass-specific metabolism rather than increases in body mass, because mass changes little during this period. However, increases in mass are likely to be partly responsible for the more rapid increases in heat production after 8 days of age. Chicks which experience continual low T_a during their early development have lower body mass in comparison to chicks which experience high T_a during the day, which in consequence delays the age at which they become homeothermic (fig. 8, p.202). Quail become fully homeothermic when body mass is 7-10g, which coincides with 15-18 days of age. The acquisition of homeothermy is at an earlier age than reported by Bernstein (1973), but at similar body masses, which is attributed to higher levels of heat production at thermoneutrality and during cold exposure. Brooded quail chicks are less variable in their $\dot{V}O_2$ at any T_a, and maintain $\dot{V}O_2$ at levels identical to that found for unbrooded chicks at thermoneutrality because the parents contribute to the costs of temperature regulation (fig. 1-2).

Metabolism of brooded and unbrooded cockatiel chicks

The increases in $\dot{V}O_2$ at thermoneutrality in both unbrooded and brooded cockatiel chicks in the first five days after hatching is attributed primarily to increases in mass-specific metabolism, rather than body mass, even though body mass doubled in that period. Further improvements in the thermoregulatory abilities of cockatiel chicks older than five days is primarily attributed to increases in body mass, because the slope of the

relationship between $\dot{V}O_2$ and T_a below thermoneutrality did not change with age, but the T_a at which PMR was elicited decreases with body mass (Table 2, p.144 and fig.20, p.151). Cockatiel chicks reach 30 g between 8 and 13 days in summer and are no longer brooded effectively by adults, remaining partly exposed during brooding. However, at the end of brooding period cockatiel chicks are homeothermic (fig. 21, p.152).

$\dot{V}O_2$ *of non-brooding adult quail*

King quail females retain fully developed broodpatches for considerable periods after their chicks hatch. Both breeding and non-breeding females are able to brood chicks, but non-breeding quail only rarely brood other quail's chicks. $\dot{V}O_2$ of breeding quail is 31% higher within the TNZ than non-breeding quail (Table 1, p.204). In contrast to the studies of Brummermann and Reinertsen (1991, 1992) with breeding bantam hens, the increases in SMR of breeding quail are not correlated with the presence of broodpatches, since male do not have broodpatches. In quail the increase in SMR is not correlated with extra heat loss through the broodpatch, but may represent a seasonal change in metabolism associated with increased allocation of energy to reproduction.

$\dot{V}O_2$ *of non-brooding adult cockatiel*

Below the TNZ the $\dot{V}O_2$ of non-brooding cockatiel is highly variable between individuals, and as a result the difference in $\dot{V}O_2$ between α and ρ phases is not significant (ANCOVA $F=0.632$ N.S., intercept $t=0.749$ N.S). However, the difference between phases of the day below T_a 29 °C is on average between 30 and 51% (fig. 7, p.202), which is similar to other species (Aschoff and Pohl 1970). In contrast $\dot{V}O_2$ at T_a >29 °C is less variable and the difference between phases in SMR is significant (t-test $t_{1,93}=-8.376$ $P<0.001$).

$\dot{V}O_2$ *of brooding adult quail*

The $\dot{V}O_2$ of brooding quail in the TNZ (T_a >30 °C) is not significantly higher than that of breeding king quail which are not brooding chicks (Table 1). Thus no additional heat production is required of parent quail to maintain high chick T_b at T_a >30 °C However, at T_a <28 °C, the $\dot{V}O_2$ of brooding quail increased with decreasing T_a with a significantly higher slope (C_{wet}) than in non-brooding quail during both α and ρ phases (fig. 5, p.199). Brooding metabolism is not increased significantly during the α phase in comparison to ρ phase, reflecting a suppression of the circadian rhythm of metabolism in comparison to non-brooding quail (Aschoff 1981). The maintenance of high nocturnal metabolism suggests that thermosensor inputs from the peripheral regions of skin in

contact with the chicks might act as a feedback control of chick T_b. Brummermann and Reinertsen (1991, 1992) have suggested that inputs from broodpatch thermosensors of incubating bantams take a higher priority than many other peripheral sensors in the central processing of information for the regulation of body temperature.

With the increases in body mass and $\dot{V}O_2$ of quail chicks during early development, the adult brooding response might be expected to diminish as the broods develop, resulting in higher contributions of the broods to heat production and gradual reductions in adult $\dot{V}O_2$ during brooding. However, this is not the case in brooding quail. The $\dot{V}O_2$ of quail brooding chicks 6-17 days of age is not significantly different from $\dot{V}O_2$ of quail brooding chicks 0-5 days of age, despite significant increases in heat production capabilities of the older unbrooded chicks. The cost of brooding per unit time remains high, and as a consequence, the cost of brooding chicks at low T_a would remain an energetic burden until fledging. However, the time chicks spend unbrooded increases after 5 days of age (fig. 9, p.204). Brood contributions to $\dot{V}O_2$ remain at minimal levels similar to the thermoneutral point despite improvements in thermoregulatory capacities (fig. 1-2, p.196-197). Therefore it is suggested that when brooding is initiated, the lower skin T_b of chicks stimulates a thermoregulatory feedback mechanism resulting in increased parental heat production. The age of the broods does not affect the parental contribution to the cost of temperature regulation.

Brooding behaviour in quail adults is stimulated by the behaviour of the chicks. Chicks seek the warmth of adults when their body temperature decreases, and the adults respond by crouching close to the ground and fluffing their ventral and lateral feathers. It is similarly suggested that the broodpatch in quail is not required to brood chicks, and when present, does not perform any role in maintaining a suitable thermal environment. Changes in parental behaviour during the transition from incubation to brooding, by brooding their chicks under the wing, instead of the broodpatch suggests that the changes are adaptive to avoid trampling broods whilst maintaining a suitable brooding environment (Evans 1992).

It has been suggested that the role of male parents may be less effective during incubation and brooding when they lack broodpatches (Skutch 1962), and that males simply cover their broods to reduce their heat loss (Jones 1971). Contact between the broodpatch of female white-crowned sparrows (*Zonotrichia leucophrys*) and the brood and parental heat production are both important for the transfer of heat to the brood (Webb 1993). Male king quail brood chicks equally as well as female quail without ever forming broodpatches. The increased metabolism of male and female quail during brooding is therefore not correlated with functional changes as a result of the presence of broodpatches. Thus brooding appears to be under a tactile or thermoregulatory feedback control distinct from the feedback loop believed to be responsible for the regulation of egg temperature via the broodpatch (Gabrielsen and Steen 1979; Haftorn and Reinertsen 1985; Tøien et al. 1986; Tøien 1989). However, chick T_b similarly appears to be

controlled as an energetic extension of the adult's body, as previously hypothesised for the control of egg temperature (Drent 1975; Haftorn and Reinertsen 1985). This means that the thermal conductance of brooding quail is regulated at constant high levels, but thermal conductance in non-brooding quail decreases at T_a below TNZ (fig. 6, p.201).

$\dot{V}O_2$ *of brooding cockatiel*

Unlike king quail, the brooding $\dot{V}O_2$ of cockatiel is not significantly higher than that of non-brooding cockatiel between T_a 10-36°C (fig. 11, p.207). Breeding cockatiel do not form distinct broodpatches like female king quail, but sometimes feather loss is noted. Webb (1993) suggests that parental-offspring contact is important for heat transfer during brooding, but heat flow to the offspring is reliant on the absence of insulation or that the insulative coat of feathers or down be compressible. The $\dot{V}O_2$ of cockatiel chicks during brooding is minimal, but high chick T_b are maintained during brooding periods (fig. 5, p.199). However, the chick T_b set-point is not as high as king quail in the first days after hatching. During the brooding period the essentially naked cockatiel chicks (sparse down on dorsal surfaces) continually lose heat through their ventral surfaces to the nest environment. Heat is able to flow from the adult to the chicks by direct contact because adult T_b is higher than the chick (6-8 °C lower). It is suggested here that heat input from brooding cockatiel is more effective than that of brooding quail to their chicks because cockatiel chicks are naked. As a consequence brooding cockatiel do not need to increase heat production to maintain constant chick T_b at a level which is lower than the quail chick.

Parental energy expenditure during breeding

Direct measurements of the metabolism of small birds incubating clutches of 4-5 eggs suggest that incubating metabolism is elevated 20-30% at air temperatures below thermoneutrality (Biebach 1979, 1981, 1986; Vleck 1981; Drent et al. 1985; Weathers 1985). However, at air temperatures within the TNZ, $\dot{V}O_2$ of incubating birds is not significantly higher than that of non-incubating birds within a nest. The ecological relevance of comparing non-incubating and incubating birds under the same environmental conditions has been questioned, since many non-incubating birds do not occupy nests, and therefore are exposed to potentially lower air temperatures outside of the insulation of the nest (Walsberg 1983). King quail, like many precocial birds, leave the nest soon after the clutch hatches, and consequently lose the thermal benefits of nest insulation. The energy expenditures increase below thermoneutrality when measured in the absence of nest insulation, and at the same time the relative proportions of time spent brooding increases as T_a decreases, despite their relative inactivity during brooding bouts.

In contrast to the quail, the cockatiel does not have an elevated metabolism below the TNZ whilst brooding. It is suggested here that this difference may reflect a lower chick T_b set-point, and therefore the parental contribution to thermoregulation is lower, and a more effective heat flow during brooding because of the absence of significant insulation in cockatiel chicks. Further measurements of $\dot{V}O_2$ of chicks and adults in altricial species are required to test this idea.

Implications for brooding quail and their young

Adult quail brood chicks on average 65% of daylight hours during the first five days after hatching (fig. 8, p.203). For the first days after hatching, chicks are reliant on their internal yolk stores during prolonged brooding periods. Small body mass and poor thermoregulatory abilities limit the foraging times of chicks during the first five days, but after day 5 foraging time is inversely related to T_a (fig. 9, p.204). These changes in chick dependency on parental brooding are also common to small precocial hatchlings of shorebirds (Visser and Ricklefs 1993). Parental contributions to the cost of temperature regulation are an energetic saving for chicks, but the time spent brooded is not available for foraging. The costs of temperature regulation increase as body mass decreases. Consequently the energy available for tissue synthesis to small chicks may be limited by the need to be brooded at low T_a, and high thermoregulatory costs during foraging. In this study broods which experienced continual low T_a during the early development did not grow.

The $\dot{V}O_2$ of a brooding adult is 0-42% higher than a non-brooding quail at a T_a range of 18-35 °C during the day (calculated using the equations in fig. 8, p.203). At night, when non-brooding quail are inactive and chicks are brooded constantly, the $\dot{V}O_2$ of brooding quail is 96-98% higher than a non-brooding quail at T_a 10-15 °C . During daylight hours an adult with a brood of 4-5 chicks would have about 35% of the time available to a non-brooding quail, to obtain sufficient food to meet the metabolic demands of brooding and other daily activities. Therefore it is concluded that the parental contribution to chick temperature regulation is an energetic burden to the parent. Furthermore, if they experience continual low T_a, then the chicks may fail to grow and chick mortality will increase.

CHAPTER 6

Conclusions from this study

Conclusions

The previous chapters of this thesis introduce the extent of our knowledge on avian development, and then discusses where further research is required and the specific aims of this study. Comparisons are made between two species of bird, the king quail (*Coturnix chinensis*) and the cockatiel (*Nymphicus hollandicus*), which have different developmental modes during incubation and posthatching periods, and their development is compared with established allometric relationships. However, each chapter addresses separately either development in the incubation or posthatching periods of these species. This concluding chapter serves to restate the questions examined in this study, and relate the findings from the incubation period to that of the posthatching periods, in order to appreciate the continuous process of development. It also highlights where these findings differ significantly from previous assumptions concerning avian development.

Allometric comparisons of development in birds

Allometric comparisons of the characteristics of developmental modes in avian orders are complicated by the fact that the majority of altricial species are small birds, and precocial species are often several magnitudes larger. Valid allometric comparisons of any energetic variable should ideally always be made with species of similar or overlapping mass ranges because metabolism is highly size dependent. Even in recent literature investigating developmental patterns in birds, there are few comparisons between species which satisfy this criterion, and so this work represents an improvement in its comparison of two species of similar body mass. Furthermore, because it is now accepted that phylogeny may also explain a significant amount of variation in physiological variables (Bucher 1987; Drent and Klaassen 1989; Klaassen and Drent 1991), and for this reason this study makes allometric comparisons of metabolism and growth rate of developing king quail and cockatiel with species (young and adult) from their respective orders for which data are available.

Comparing growth and developmental rates in young birds

It is convenient to use categories in defining hatchling developmental types based principally on morphological and behavioural criteria, put forward by Nice (1962), but many of these characters give no indication of the underlying physiological maturity of developing birds. Reference to only a single point in the developmental sequence, such as the hatchling may lead to erroneous conclusions concerning the developmental patterns of physiological functions. It is demonstrated here for the first time in the cockatiel, that some species with altricial hatchlings have a higher degree of precocity during their early development than previously recognised. It is apparent from this study that the cockatiel

hatchling lacks the ability to increase heat production significantly during cooling, but it is able to sustain heat production for short periods, and rapidly develops its thermogenic powers soon after hatching, a finding that would otherwise be overlooked if only one part of the overall development was considered.

The egg and embryonic development

The king quail invests significantly more energy in a smaller egg than the cockatiel, principally in a larger fraction of yolk solids. In spite of the small egg mass, egg composition of king quail eggs is similar to allometric predictions, based in general on much larger precocial species (Table 4, p.52) (Sotherland and Rahn 1987). Similar to the eggs of other parrots (Bucher 1983), cockatiel eggs contain a larger yolk fraction, and therefore more energy, than do other altricial species. The composition of cockatiel eggs also agrees well with allometric predictions, based on yolk content of eggs (Sotherland and Rahn 1987).

Typically altricial species have lower costs of embryonic development than precocial species (Vleck and Vleck 1987). Hatchling energy content is similar in both species, and agrees well with allometric predictions based on egg mass for precocial and altricial species, respectively. The cost of development of king quail is similar to that of other precocial species, and is higher than that of the cockatiel, but the cost of development of the cockatiel is higher than expected of altricial species, because more energy is initially invested in their eggs (Ar et al. 1987). The cockatiel hatchling also has double the amount of energy remaining as yolk reserve than predicted for altricial species. However, both the cockatiel and the king quail hatchling tissues have a lower than average energy density, as a result of a low rate of accumulation of solids during incubation, in comparison to much larger species investigated by Ricklefs (1987), which is attributed to the earlier precocity of embryonic tissues of both species.

The relationship between egg mass, embryonic metabolism, growth and incubation period in these small species shows significant deviations from the developmental patterns previously described by many authors for precocial and altricial species, respectively. The incubation period of the king quail (16.5 days) and cockatiel (19-21 days) are shorter and longer than predicted, respectively, on the basis of egg mass (Table 1, p.72), but it is emphasised here that, although in general altricial species have shorter incubation periods than precocial species, significant deviations from predicted incubation periods occur within and between many avian orders with the same hatchling developmental types. The incubation period of the cockatiel is identical to predictions based on the relationship between incubation period and egg mass for parrots only, and thus the longer than expected incubation of cockatiel in comparison to all altricial species is partly attributed to phylogeny. The best agreement with observed incubation periods for both species is obtained by the alternative model of Ricklefs (1987), using parabolic

growth equations to empirically derive growth rates of avian embryos (Chapter 3.2).

Typically two patterns of development of metabolism are used to describe most avian embryos, which distinguishes altricial and precocial modes of development. The $\dot{V}O_2$ of precocial and altricial embryos increases exponentially during incubation, but the rate of increase of $\dot{V}O_2$ in precocial embryos declines, and then $\dot{V}O_2$ plateaus at the end of the incubation period before pipping. Similarly, embryo mass increases exponentially throughout incubation in both precocial and altricial species, but the growth rate of precocial embryos declines at the end of incubation (Hoyt et al. 1978; Vleck et. al. 1979; C. Vleck et al. 1980; D. Vleck et al. 1980; Bucher 1983; Bucher and Bartholomew 1984; Ricklefs 1987). It was predicted in this study that small precocial embryos had less time to mature during incubation, because incubation period decreases with egg mass, and that embryos hatched before $\dot{V}O_2$ reached a plateau at the end of incubation. The observed pattern of development of $\dot{V}O_2$ in the king quail increases exponentially throughout most of incubation without reaching a plateau, but the rate of increase in $\dot{V}O_2$ is less steep during the last 10% of incubation (fig. 4, p.79). The rate of increase in embryo mass also decreases later in the incubation period of king quail than other larger precocial species (fig. 1, p.105). Thus king quail appear to hatch earlier in the developmental sequence, but there is no obvious lack of maturity in hatchlings, with the exceptions of low energy density of hatchling tissues and the absence of thermogenic responses in some quail hatchlings. The developmental pattern of cockatiel embryonic $\dot{V}O_2$ is not exponential throughout the whole incubation period like the pattern described for other altricial species (Vleck, Hoyt and Vleck 1979; Hoyt and Rahn 1980), but in fact shows a significant decline in the rate of increase of $\dot{V}O_2$ at the end of incubation (fig. 5, p.80). The rate of increase in embryo mass decreases at the end of the incubation period of cockatiel unlike other altricial species (fig. 2, p.106). However, the developmental patterns described for king quail and cockatiel in this study reinforces the general conclusion of other recent studies, that all avian embryos may be described by the same developmental pattern for metabolism or growth, but species vary in the point along that developmental sequence at which they hatch (Bucher 1987; Sotherland and Rahn 1987; Vleck and Vleck 1987). The growth rates of king quail and cockatiel embryos declines relatively early in the incubation period, which is attributed to the earlier differentiation of embryonic tissues. Both species also have higher metabolic intensities during the second half of incubation in comparison to other altricial species, which is thought to reflect the higher maintenance costs of maintaining more metabolically active tissues (Bucher and Bartholomew 1984; Hoyt 1987; Vleck and Vleck 1987).

The results of this study suggest for the first time that in some altricial species such as the cockatiel, the development of thermoregulation is not entirely a posthatching event. Sustained $\dot{V}O_2$ during short-term gradual cooling by cockatiel embryos, suggests that the embryos have incipient endothermy before hatching (fig. 16, p.92), which is

attributed to the longer incubation period. Despite these differences from previously described patterns of development of metabolism, growth and the duration of incubation, for king quail and cockatiel, the $\dot{V}O_2$ of both species at the pre-internal pipping stage of incubation is identical to allometric predictions for all hatchling types based on egg mass (fig. 6, p.82).

An alternative developmental strategy in altricial birds

The results presented here suggest that parrots have developmental strategies which are dissimilar to the patterns previously described for altricial passerines. Parrots are similar to other altricial birds in that they hatch blind, poorly coordinated and with only sparse down on their dorsal surfaces (Bucher 1983). The timing of maturational events, such as the early development of thermogenic responses, delayed acquisition of insulation relative to the acquisition of homeothermy, in combination with high hatchling resting metabolic rates are unlike the characteristics previously ascribed to altricial birds in general. However, with the exception of the cockatiel (fig. 1, p.134), the resting metabolic rate of many parrot hatchlings examined to date are below that of precocial hatchlings of similar body masses. Cockatiel hatch with incipient endothermy and improve their thermoregulatory abilities gradually after a period of rapid growth, unlike precocial species. For the cockatiel, the rapid acquisition of homeothermy is correlated with changes in parental attentiveness during the posthatching period. peak metabolic rate is elevated above resting metabolic rate at 20 g body mass, whilst the chicks are still brooded and the adult contributions to the cost of thermoregulation are substantial. But with further increases in body mass the chicks out grow the parent's ability to adequately brood the chicks, and brooding is reduced. Later the insulation of chicks improves when all feather tracts are present and the plumage becomes unsheathed late in the development of cockatiel, which is similar to other altricial groups of birds (O'Connor 1975a; Webb 1993). However, it is not suggested here that the cockatiel is exceptional in respect to having a more precocial pattern of development of thermoregulation. The cockatiel is thought to have arisen from an ancient lineage of *Cacatua* stock in Central Australia (Schodde 1984), and its pattern of development of physiological functions may more closely resemble extant *Cacatua* species, than other species of parrots mainly from the South American continent.

Development of thermoregulation and growth in small precocial birds

It is well known that precocial species allocate energy preferentially to thermoregulation earlier in their posthatching development than many altricial species. However, this observation is based primarily on large species, while the relationship between the development of thermoregulation and growth of small precocial birds has

been ignored. It is suggested here that small precocial hatchlings require greater parental energy contributions towards the cost of thermoregulation than larger precocial species, because of their higher rates of heat loss and low rates of heat production. Therefore posthatching growth rates of small precocial species are lower (eq. 5, p.173) than previously considered by Ricklefs (1973), who examined predominately larger species. King quail hatch with high levels of resting metabolism (fig. 1, p.134), but their thermoregulatory abilities are weak (fig. 2, p. 135), and it is considered here that at hatching embryos are in a state of transition from incipient endothermy to true endothermy (Tazawa et al. 1988b). Growth rates of quail are initially low because of brooding requirements, but increase after five days of age when their thermoregulatory abilities improve (fig. 3, p. 136 and fig. 28, p.158). The lower growth rates of small precocial species in comparison to altricial species of similar asymptotic mass are attributed to the early development of thermoregulation in precocial species. Improvements in thermoregulatory abilities are attributed to both increases in peak and resting metabolic rate after hatching, to levels exceeding that of adult birds of the same mass (fig. 5-6, p.139-140).

Oxygen consumption rates of adults and chicks during brooding

Previously it was believed that parental heat transfer to eggs or chicks was only possible through a specialised broodpatch, and that birds lacking broodpatches only reduce heat loss from the eggs during incubation or chicks during brooding. The role of the broodpatch during brooding is examined, and for the first time the parental contribution to body temperature regulation of hatchlings is quantified for small birds in this study. Parental energy expenditure during incubation is elevated above non-incubating levels at low T_a in small birds, but the energy expenditure of parent birds during brooding periods and thermoregulatory control of brooding have not previously been examined. High thermal conductances and low rates of heat production of hatchlings of small birds prevent homeothermy at T_a below thermoneutrality, independent of hatchling type (Whittow and Tazawa 1991). Consequently small hatchlings may require extensive additional heat input to prevent lethal declines in T_b. The $\dot{V}O_2$ of brooded quail chicks is maintained at a constant level as T_a decreases, in contrast to the increases in $\dot{V}O_2$ observed in unbrooded chicks (fig. 1-2, p.196-197). Quail chicks are brooded extensively during daylight hours, and foraging appears to initially limit posthatching growth during the first five days, but foraging time subsequently improves and is inversely related to T_a (fig. 12-13, p.208). The $\dot{V}O_2$ of brooding male and female adult quail is equally elevated above the $\dot{V}O_2$ of non-brooding quail at T_a below TNZ, but brooding $\dot{V}O_2$ within the TNZ is not significantly elevated (fig. 8, p.203 and Table 1, p.205). Brooding $\dot{V}O_2$ is constant during the day and night, indicating a temporary suppression of the circadian rhythm of metabolism. Parental heat contribution to chick

temperature regulation is achieved by increasing parental thermal conductance by a feedback control similar to that for the control of egg temperature via the broodpatch. However, it suggested in this study that heat from the brooding quail originates mainly from permanent apteria under the wings and legs of the parent, rather than from the broodpatch, as assumed in other studies.

As in the quail chicks, the $\dot{V}O_2$ of brooded cockatiel chicks is maintained at constant levels as T_a decreases below the thermoneutral point. However, $\dot{V}O_2$ rises in unbrooded chicks older than 2-3 days of age (fig. 3, p.198). Chicks are brooded constantly for 9-10 days by either parent, after which brooding becomes intermittent, and then ceases during daylight hours after several more days. Brooding $\dot{V}O_2$ of cockatiel below the TNZ is not significantly different from non-brooding $\dot{V}O_2$ during the day (fig. 11, p.207). Thus for the cockatiel, brooding is not a period of increased energy expenditure for adults, and chicks make considerable energy savings due to parental heat contributions and reduced activity costs within nest hollows.

The apparent differences in cost of brooding chicks to adult quail and cockatiel is attributed here to the lower body temperature maintained during brooding by the cockatiel chick compared to that of the more precocial king quail chick, and secondly, more efficient heat transfer from the brooding parent to the essentially naked cockatiel chick. In contrast to the cockatiel, quail chicks have a downy coat at hatching, and develop contour feathers earlier in their development, before the end of the brooding period. Thus parental energy expenditure during brooding is likely to vary between species with different hatchling types, dependent on factors including the level of body temperature of chicks, the presence of insulative coats and the resting heat production level of the chick.

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In brief, this thesis indicates that phylogeny explains a significant amount of the variation in the growth rates and developmental patterns of avian embryos, in addition to the amount of energy and water initially invested in eggs, incubation period and hatchling developmental type. Because there are phylogenetic differences between species in the amount of energy in eggs, egg mass and incubation period, there is continuous variation in the patterns of development of metabolism and embryonic growth, rather than a dichotomy of altricial and precocial extremes of development usually envisaged in the literature. The precocial king quail has a similar hatchling mass to that of the altricial cockatiel, but more energy is utilised by the king quail during incubation, which is attributed to the early development of mature function in precocial species. After hatching more of the metabolisable energy of the king quail is allocated to thermoregulation and activity than the cockatiel and altricial species in general, and posthatching growth is

limited by the greater brooding requirement of small precocial hatchlings than larger species. However, the cockatiel and other parrots allocate more energy than altricial species to thermoregulation in the early posthatching period, and consequently growth rates of parrots are intermediate between precocial and other altricial species.

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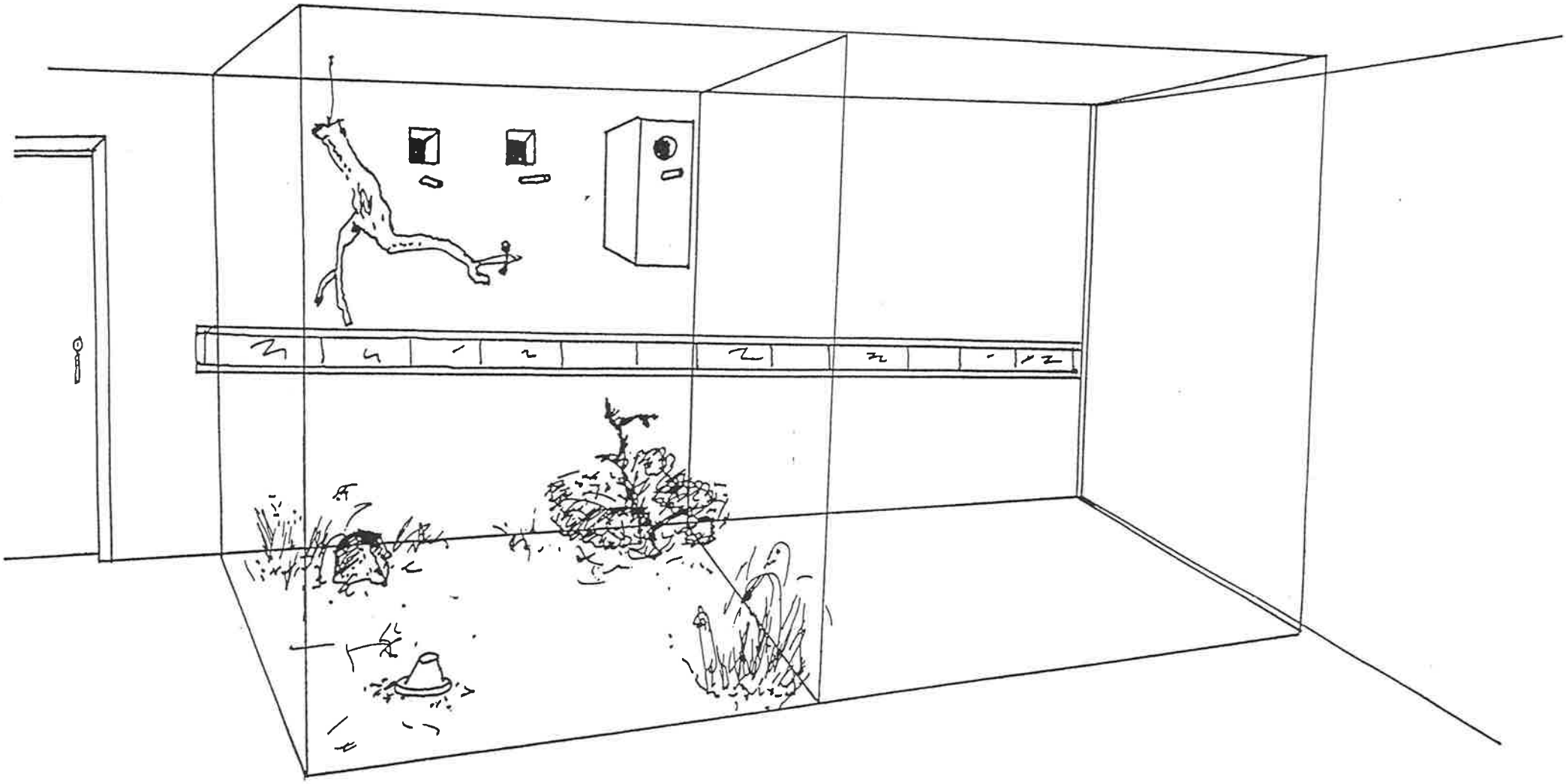
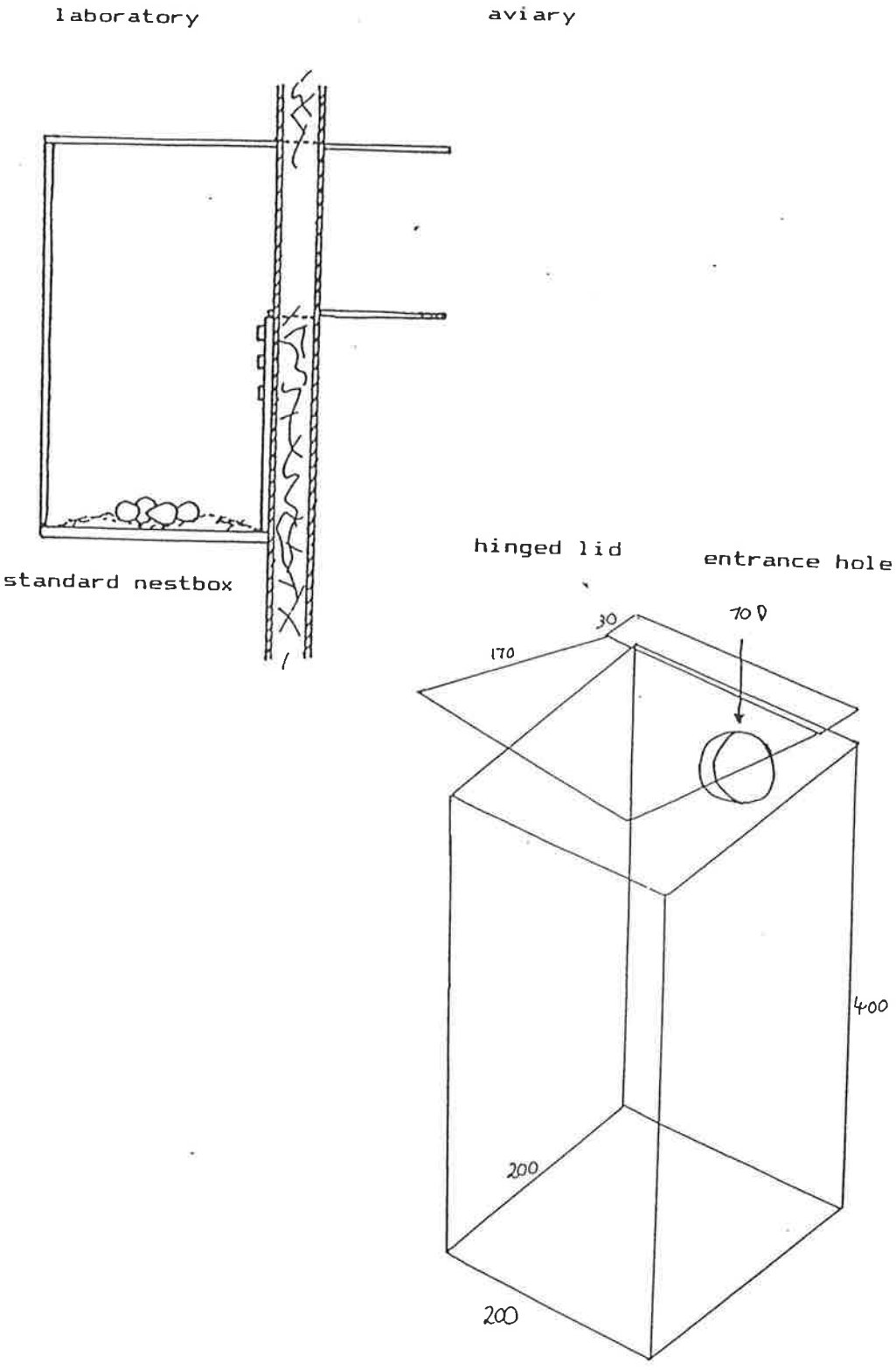


Appendix 1. Aviaries in the Animal yards of the Zoology Department. King quail and cockatiel were housed together in five aviaries 3m x 2m x 2m. Aviaries 3 & 4 were located adjacent a laboratory.



Appendix 2. Standard cockatiel nestboxes were 200mm x 200mm x 400mm. In aviaries 3 and 4 only, some nestboxes were hung inside the laboratory with only the nestbox entrances protruding into the aviary. Boxes contained a mixture of potting mix and sawdust for nesting material.