The Impact of Habitat Alteration on the Population Dynamics of a Declining Woodland Bird in the Mount Lofty Ranges

Photo by Peter Waanders 2016

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Abstract

Biotic invasions are among the main drivers of ecosystem change and contribute to species declines. In the southern hemisphere, perennial native understorey plants have been largely outcompeted by fast-growing annual crop grasses and herbs. This significant compositional change has altered patterns of seed production. Granivores such as the diamond firetail (*Stagonopleura guttata*) are likely to be affected by such alterations. This species has been declining nationally since large-scale land-clearance prior to 1980. Focussed, species-specific research is required to identify the threats and their interactions that contribute to ongoing declines. This thesis examined an isolated meta-population in the Mount Lofty Ranges (MLR), South Australia, subsisting in heavily degraded grassy woodland dominated by exotic annual grasses. The hypothesis that changes in grass seed phenology associated with invasion by exotic annual species has resulted in seasonal food shortages was tested.

An assessment of the seed resources available to ground-foragers in the southern MLR confirmed that introduced, annual species dominate the understorey. Total seed biomass was over seven times greater in spring (4.08 g m^{-2}) than in autumn, when biomass was just 0.53 g m^{-2}. High spring seed biomass was predominantly produced by annual grasses. The subsequent drop in biomass coincided with breaking autumn rains, implicating mass-germination as the cause. Variation in seed biomass was attributed to seasonal changes in the seed abundance of annual weedy grasses and forbs. Diet analyses found that *S. guttata* diets mirrored the abundance and diversity of seasonal resources. However, during winter, when grass seed biomass was scarce, *S. guttata* relied heavily on the seeds of the drooping sheoak (*Allocasuarina verticillata*).

A mark-resight study determined that *S. guttata* populations were affected by seasonal resource fluctuations. *Stagonopleura guttata* encounters were strongly correlated with seed abundance and *S. guttata* densities reflected seed biomasses. To further explore the reason for low numbers of *S. guttata* in autumn and winter, an in-field food supplementation experiment was conducted. The food-supplemented population had significantly higher survival than the non-supplemented population, indicating that food is limiting for *S. guttata*. Juveniles were less efficient foragers than adults, highlighting their vulnerability during times of seed scarcity. However, food supplementation appeared to increase the proportion of juveniles that survived their first winter. The transition of independent fledglings from

spring/summer breeding into young breeding adults is critical for recruitment and is likely to be hampered by winter food shortages.

Overall densities of *S. guttata* in the southern MLR were 0.023–0.062 birds/ha, lower than the minimum viable population estimate of 0.069 birds/ha. As such, this meta-population is not sustainable at current densities. To improve the persistence of *S. guttata*, it is essential that the grassy woodlands of the region are managed to create consistent, year-round food resources, particularly during winter. This requires the restoration of perennial native grasses in the understorey that seed more consistently and over longer time periods than annuals. In addition, rehabilitation of *A. verticillata*, a key resource, will improve food availability during times of scarcity.

Declaration

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Chapter 1. General Introduction

1.1 Biodiversity loss

The current anthropogenic exploitation of the earth's surface is unprecedented, with over three-quarters of ice-free land affected by human use (Intergovernmental Platform on Biodiversity and Ecosystem Services 2019). Continued global human population growth demands ever more resources, resulting in ongoing degradation of natural systems. Global grain production has doubled in the last century, greatly contributing to alleviating famine but at an enormous cost to the environment through loss of natural ecosystems, consumption of water resources and greenhouse gas emissions (Vitousek *et al.* 1997). Croplands now cover 12–14% of the earth's terrestrial surface (Olssen *et al.* 2019) and a further 10^9 ha of natural habitat is predicted to be cleared for agriculture by 2050 (Tilman *et al.* 2001). This large-scale clearance of vegetation for agriculture is considered to be the primary cause of habitat loss (Foley *et al.* 2005), resulting in a significant decline in biodiversity worldwide (Boakes *et al.* 2010). Species extinction rates now are at their highest since humans colonised the earth, with approximately 1200 species, 617 of which are vertebrates (Ceballos *et al.* 2015) known to be lost since 1500 due to modification and destruction of the natural environment (Stork 2010).

1.1.1 Habitat fragmentation and degradation

Habitat loss threatens biodiversity by decreasing the area that a species can occupy and fragmenting populations (Tilman *et al.* 2017). Both of these processes directly reduce total abundance and/or resource availability (e.g. Ford *et al.* 2001). Habitat fragmentation has been found to reduce biodiversity by up to 75% and impair ecosystem function by decreasing biomass and altering nutrient cycles (Haddad *et al.* 2015). More recently, Fahrig (2017) reviewed the evidence for ecological responses to habitat fragmentation, and found that most responses were non-significant. However, Fletcher *et al.* (2018) argue that Fahrig's results are biased, explaining that habitat loss and fragmentation are intrinsically linked. Fahrig *et al.* (2019) clarified that habitat fragmentation measures that are confounded with habitat loss generally show negative relationships to biodiversity. Indeed, the effects of fragmentation such as declining patch area and reduced connectivity have been shown to have lasting effects on biodiversity (Haddad *et al.* 2015), and elicit numerous degrading processes (Heinrichs *et al.* 2016). The effects are most severe in the smallest and most isolated fragments, due to higher edge to area ratio increasing exposure to adjacent human land uses and thus susceptibility to degradation (Fletcher *et al.* 2018). Degradation—the gradual deterioration of habitat quality—is linked with processes such as weed invasion (Driscoll 2017), predation (McCormick and Lonnstedt 2016), competition (Calizza *et al.* 2017), grazing pressure (van Doorn *et al.* 2015) and dispersal (Fonturbel *et al.* 2015). All of these processes interact, with one or more being significant for a species. Often, complex, non-additive interaction effects lead to species declines, rather than single factors (Didham *et al.* 2007). For example, invasive brown-headed cowbirds (*Molothrus ater*) heavily predated the nests of native neotropical migrants at the edges of fragmented forest in the USA, but only in landscapes with moderate to high modification (Donovan *et al.* 1997). Species that require large areas of habitat for survival, such as large-bodied or wide-ranging animals, are more likely to have a strong negative response to reductions in habitat size and fragmentation (Villard *et al.* 1999). Consequently, 80% of extant terrestrial bird and mammal species are threatened by habitat loss and fragmentation (Tilman *et al.* 2017).

1.1.2 Biotic invasions

Isolated habitat patches are susceptible to interactions with the surrounding modified environment. A common result of fragmentation is the invasion of exotic or pest species, becoming more frequent with increased edge to area ratio (Laurance 2002). Invasive species can directly affect populations through predation (e.g. Burbidge and Manly 2002), aggressive exclusion (Maron and Kennedy 2007) or competition for resources (e.g. Hobbs 2001). For example, the aggressive noisy miner (*Manorina melanocephala*) preferentially occupies edge habitat, resulting in significant reductions in abundance and diversity of small woodland bird species in heavily fragmented patches (Clarke and Oldland 2007; Maron and Kennedy 2007). Indirectly, invasive species can alter the composition and structure of key resources for native species (e.g. D'Amore *et al.* 2009). For example, invasive plants can out-compete native plants thereby limiting their abundance, distribution and productivity, negatively affecting the fitness and growth of dependent fauna (Montserrat *et al.* 2011). The effects of habitat loss, fragmentation and invasive species are all significant for native biota. However, their effects are more pronounced when these factors interact, for example where invasive species benefit from an increase in edge habitat (Sala *et al.* 2000).

1.2 Avifaunal declines

Moreso than for other vertebrate groups, there is good quantitative evidence of avifaunal declines and their causes (Ford 2011; Garnett *et al.* 2011). At the largest scale, the major reasons are undeniably habitat loss and degradation (Garnett *et al.* 2011; Robinson and Triall 1996). Globally, 141 species and 138 subspecies of birds have become extinct since 1500 (Szabo *et al.* 2012). A geographic concentration of bird extinctions has occurred in Australia, with 29 species lost since European settlement (Szabo *et al.* 2012) and 17% of extant species now threatened (Garnett *et al.* 2011). A high proportion of threatened birds occur in Australia’s southeast (Garnett *et al.* 2011; Woinarski and Braithwaite 1990). This region has been extensively cleared to make way for agriculture, with approximately 500,000 km^2 of woodland vegetation removed, representing one of the most significant vegetation changes in Australian history (Yates and Hobbs 1997). Consequently, temperate woodland birds are the most adversely affected group of avifauna in Australia (Garnett and Crowley 2000). The situation is not stabilising, with many woodland species continuing to decline (Attwood *et al.* 2009; Geyle *et al.* 2018), such as the brown treecreeper (*Climacterus picumnus*), hooded robin (*Melanodryas cucullata*) and restless flycatcher (*Myiagra inquieta*) (Ehmke *et al.* 2014).

1.2.1 Woodland birds

While habitat loss and fragmentation are the broadest causes of woodland bird declines, a range of interacting flow-on effects threaten different suites of avifauna (e.g. Antos and Bennett 2006; Ford *et al.* 2001; Paton *et al.* 2004; Watson *et al.* 2002). Species that are unwilling to move between fragments are subject to edge-effects. For example, small insectivores such as the red-capped robin (*Petroica goodenovii*) and scarlet robin (*Petroica boodang*) require interior habitat (away from the edge) because of aggressive competition from noisy miners at the edges (Catterall *et al.* 1991). Species that move between habitat patches to use different resources are at risk of different interacting processes (e.g. Lambeck 1995; Merigot and Paton 2018). Nectarivores such as the swift parrot (*Lathamus discolour*) and the critically endangered regent honeyeater (*Anthochaera phrygia*) rely on a series of habitats to provide sequential flowering resources across a year (Saunders *et al.* 2007). As such, the disproportionate loss of certain habitat types can create a resource gap (Ford *et al.* 2001). Similarly, the interaction between patterns of seed production and habitat degradation threatens many granivores. A reduction in available grass seeds, particularly from native perennial grasses, due to cattle grazing reduced the capacity of degraded lands to support specialist granivores in central Monte Desert, Argentina (Marone *et al.* 2017). In Australia, the replacement of native grasses by exotic species has altered the timing of seed resources, while overgrazing has reduced the density of mid-layer vegetation providing cover for foraging granivores (Cole and Lunt 2005; Yates and Hobbs 1997). These compounding factors were responsible for the disappearance of the peaceful dove (*Geopelia placida*), red-browed finch (*Neochmia temporalis*) and double-barred finch (*Stagonopleura bichenovii*) from a New-England area (Ford 1985). Similarly, a reduction in grass seed availability due to overabundant kangaroos has been linked to declines of small granivorous birds in areas where dingoes – a kangaroo population control – are functionally extinct (Rees *et al.* 2017).

More than half of declining woodland bird species forage on the ground (Robinson 1994; Reid 1999). These species have multiple, specific habitat requirements, including suitable ground-layer substrates and structural elements such as fallen timber to support foraging activities (Paton *et al.* 2004; Recher *et al.* 2002). For example, hooded robins (*Melanodryas cucullata*) forage in a leaf-litter substrate and favour open understoreys, but require horizontal branches within ~2–4 m of the ground from which to ground-pounce (Reid 1999). In addition, many ground substrates are particularly vulnerable to degradation (Antos and Bennett 2005). Inappropriate fire regimes can reduce leaf-litter and fallen timber (Gill *et al.* 1999) while overgrazing can alter the understorey and ground layer via processes such as trampling and compaction (Martin and Possingham 2005). Similarly, weed invasion can impede access to forage substrates and is suspected to affect the temporal continuity of resources for species such as the red-rumped parrot (*Psephotus haematonotus*) and diamond firetail (*Stagonopleura guttata*) (Paton *et al.* 2004). Previous studies (e.g. Antos and Bennett 2005; Antos *et al.* 2008) have highlighted the diversity of responses to different threats among ground-foraging species. Consequently, effective management of declining ground-foragers must consider the habitat requirements unique to each species, as well as the degrading processes impacting them.

1.2.2 The diamond firetail

Among the ground-foraging woodland birds declining throughout their range is the diamond firetail (*S. guttata*). *Stagonopleura guttata* are small (~17 g), granivorous Estrildid finches, endemic to the woodlands and open forests of temperate, semi-arid and arid southeastern Australia (Higgins *et al.* 2006). These finches forage almost exclusively on the ground where they take the seeds of grasses and herbaceous plants, either directly from the plant or from the soil surface. Foraging habitat consists of grasslands with scattered trees, grassy clearings in woodlands, or paddocks bordered by trees and bushes (Antos *et al.* 2008). The species is predominantly sedentary, with an average home range of 12 ha (Ankor 2005). Foraging flocks can range from five to 40 individuals. The larger flocks appear after the breeding season, which is typically August to January and again in autumn if conditions are suitable (Immelman 1982). Courtship displays commence in August, during which time pair-bonds are established (O'Gormon 1980). Pairs will nest in trees and shrubs with thick foliage or in clumps of mistletoe (Cooney and Watson 2005), generally within three metres of the ground. The large (250–300 mm by 130–200 mm), bottle-shaped nests are built from the stems of grasses and feature a narrow entrance tunnel (Immelman 1982). Clutches comprise four to six eggs, and both parents incubate eggs and nestlings (Higgins *et al.* 2006). Fledging takes place 24–25 days after hatching, and juveniles gain their adult plumage within 10–20 weeks (Forshaw *et al.* 2012). Individuals are known to live for at least five years (Higgins *et al.* 2006).

Stagonopleura guttata has been declining throughout Australia since at least the 1980s (Blakers *et al.* 1984; Barrett *et al.* 2003; Garnett and Crowley 2000). It mainly occurs in open, grassy woodlands in southern Queensland, eastern New South Wales, south of the Great Dividing Range in Victoria and in the southeast, the Mount Lofty Ranges (MLR), Eyre Peninsula and Southern Yorke Peninsula in South Australia (SA) (Figure 1.1). The SA populations exist in fragmented patches of remnant grassy woodland, and are isolated from larger populations in the eastern states by a stretch of unsuitable habitat. The species is listed as 'Vulnerable' in SA under the *National Parks and Wildlife Act, 1972* (SA legislation). The decline of *S. guttata* is broadly representative of other ground-foraging woodland birds across temperate Australia, all sharing similarities in their ecological niches and declining trajectories (Reid 1999). Like other declining birds, *S. guttata* was once common across a large range, but is now at risk of local extinctions across the wider landscape (Reid 1999).

Figure 1-1 The broad distribution of *Stagonopleura guttata* in Australia. The species exists in fragmented populations within this range. Map produced by BirdLife International (2019)

Habitat clearance is widely accepted as having played a major role in the decline of *S. guttata* (e.g. Ford *et al.* 2001; Reid 1999). As such, reinstating habitat and addressing further degradation of remaining habitat are key to reversing this trend. However, good conservation planning requires knowledge of the specific population limitations and threatening processes affecting individual species (Ford *et al.* 2001; Paton *et al.* 2004; Yates and Hobbs 1997). At a regional scale, several processes that interact with, or flow from, habitat loss, have been proposed as contributors to *S. guttata* declines. Dieback of eucalypt woodlands was implicated in New South Wales (Ford and Bell 1981). Cats have been proposed as a threat in the southern MLR (Read 1994). High nest predation, likely by avian predators, was found in the northern MLR (McGuire and Kleindorfer 2007). The replacement of native grasses with exotic grasses, altering seed resources, is a commonly reported threat (Crowley and Garnett 1999; Forshaw *et al.* 2012; Garnett and Crowley 2000), thought to contribute to declines near Armidale (Ford 1985), Canberra (Er *et al.* 1998), Victoria (Higgins *et al.* 2006) and the MLR (Paton *et al.* 2004). Exotic grasses not only alter seeding patterns compared with natives (Paton *et al.* 2004), but may lack important micronutrients (e.g. Yeoh and Watson 1981). Zanollo *et al.* (2013) found that higher quality female *S. guttata* (determined by spot number; Crowhurst *et al.* 2012; Zanollo *et al.* 2012) laid larger eggs containing more yolk carotenoid, thus suboptimal nutrition could result in reduced maternal investment in offspring. A study on *S. guttata* in central New South Wales dismissed seed resources as an issue because estimates of seed biomass did not correlate with estimates of finch abundance (Schopfer 1989). However, populations have continued to decline across the range of *S. guttata* since 1989, and Ford *et al.* (2001) suggested that altered food supplies are likely to be a significant threat to finch species. Shortages of native seed naturally occur seasonally for tropical and northern temperate annual granivorous birds (Crowley and Garnett 1999; Tidemann 1993). These species have adapted to cope with such shortages using a variety of strategies including diet switching (e.g. Dostine and Franklin 2002), mobility (e.g. Tidemann 1996) and habitat shifts (e.g. Dostine *et al.* 2001). However, in temperate zones, if seed shortages are a result of exotic grass invasion and thus a relatively recent phenomenon, granivores may not have had the opportunity to adapt. Thus, food may be a limiting factor where the effects of altered food resources and habitat loss interact, such as for the fragmented populations in the MLR.

1.2.3 The Mount Lofty Ranges

The MLR is located to the east of the Adelaide plains, extending northwards towards the Flinders Ranges and south to include the Fleurieu Peninsula. Eastwards, the ranges stretch into dry, open pastures towards the Murray River (Department for Environment and Heritage 2010; Wilson and Bignall 2009). The combination of relatively high rainfall (approximately 800–1000 mm annually; Bureau of Meteorology 2019), steep hilly topography and high peaks makes this region biogeographically unique within SA, with distinct biota (Department for Environment and Heritage 2010). A range of vegetation types, from sclerophyll forests, dry heathy woodlands and grassy woodlands to swamps and wetlands, support diverse flora and fauna. Over 450 bird species have been recorded in the MLR, and 75% of the state's avifauna is found here (Wilson and Bignall 2009). The eucalypt woodlands lie on the western periphery of Australia's south-eastern woodland distribution and are separated from similar vegetation by semi-arid mallee and drier woodlands (Paton *et al.* 1994). Consequently, the region is a 'biological island', with isolated populations on the outermost reaches of their continental range; prone to regional extinctions. The MLR has experienced extinctions before other areas (such as eastern Australia), having already lost 10 avian species, with another 30–40 in decline (Paton *et al.* 1999; Szabo *et al.* 2011).

Prior to European settlement and clearance for agriculture, extensive areas of eucalypt forests and woodlands existed in the MLR (Laut *et al.* 1977; Paton *et al.* 1999; Specht 1972). Sclerophyllous vegetation communities dominated the nutrient-deficient soils of the higher rainfall areas, whilst drier open heathy woodlands were common in the northern parts of the ranges and on the Fleurieu Peninsula (Department for Environment and Heritage 2010). Open forest blanketed the MLR spine, dominated by *Eucalyptus baxteri*, *Eucalyptus obliqua*, *Eucalyptus goniocalyx* and *Eucalyptus dalrympleana*, with a shrubby understorey (Paton *et al.* 1999). At lower elevations and on heavy soils, the open forest gave way to grassy woodlands of *Eucalyptus leucoxylon* and *Eucalyptus viminalis*. *Eucalyptus microcarpa* and *Eucalyptus odorata* grassy woodlands occurred at even lower elevations, with *Eucalyptus porosa* grassy woodlands on drier soils (Paton *et al.* 1999; Specht 1972). Mid-storey and understorey vegetation was often dominated by *Acacia pycnantha*, *Acacia paradoxa*, *Bursaria spinosa* and *Hibbertia riparia*. *Rytidosperma* spp, *Austrostipa* spp and *Themeda triandra* were prominent grasses (Paton *et al.* 1999). The woodlands were interspersed with native grasslands and shrublands, although their distributions were not as extensive as the grassy woodlands.

Like all other agricultural regions in SA, the MLR has been subject to dramatic landscape changes since European settlement. The region was one of the first places in Australia to undergo extensive vegetation clearance, beginning in the mid-19th century (Paton *et al.* 2004; Yates and Hobbs 1997). The northern Ranges, beyond Gawler, have suffered particularly severe changes, with only 2% of the native vegetation remaining. Less than 5% of the original vegetation remains on the Fleurieu Peninsula, while only 7% of the pre-European woodlands are intact in the MLR as a whole (Department for Environment and Heritage 2010; Paton *et al.* 2004; Robinson and Triall 1996). The landscape today comprises small, isolated remnants embedded in a matrix of urban and agricultural land-types (Paton *et al.* 2004). Much of this remaining vegetation has been modified to some degree by anthropogenic influences, with very few entirely intact areas (Department for Environment and Heritage 2010). Of the vegetation types that were dominant in pre-European times, it was the grassy ecosystems—grassy woodlands and grasslands—that were the most extensively cleared or modified due to their relatively fertile soils and open vegetation. Ninety-nine per cent of grasslands have been cleared to date in the region (Benson and Redpath 1997; Lindenmayer *et al.* 2010).

1.2.4 Diamond firetails in the MLR

The heavily cleared and highly modified grassy woodlands and grasslands of the MLR continue to support the region's extant *S. guttata*. This isolated meta-population has contracted from its pre-European range, remaining in fragmented populations in the northern and eastern parts (Figure 1.2), though once present across the central spine (Paton *et al.* 1994). Significant changes in the composition of grass communities have occurred across its current distribution, with the introduction of weed species and the subsequent reduction in native understorey species diversity (Ankor 2005; Davies 1999; Ford *et al.* 2001). Invasive species are predominantly annuals from the northern hemisphere (Davies 1999), well suited to the temperate MLR (Crossman *et al.* 2011; Davies 1997). With no insects or diseases to impede their growth, these weedy species have overwhelmingly outcompeted native species, 90% of which were perennial grasses (Davies 1999). The significant differences in seeding and growth patterns between annuals and perennials have altered the understorey habitat. Native perennial grasses grow during winter and/or summer, and are known to seed predominantly in spring or in autumn (Gibbs 2001; Jessop *et al.* 2006). In contrast, annual grasses produce large amounts of seed within a short timeframe during spring (Bazzaz *et al.* 1987). As such, the seasonal availability of seed resources has changed substantially due to exotic invasions (e.g. Ford *et al.* 2001; Paton *et al.* 2004).

Changes in seed availability for *S. guttata* have been identified by two short-term studies (Ankor 2005; Houdet 2003). Ankor (2005) found that *S. guttata* in the Monarto region of the MLR relied heavily on seeds from exotic annuals, but concluded that these were not a reliable food source year-round as most annuals exhibit one short seed drop after flowering in spring. Houdet (2003) found that several widespread exotic grass species occurring in the MLR experience high germination success with high rainfall, which would directly reduce topsoil seed availability after late autumn rains. Ankor (2005) demonstrated this *in situ*, recording high numbers of shoots of the invasive oat grass, *Avena* sp., appearing in response to late autumn rains. Their seed availability subsequently decreased to near zero (Ankor 2005). Thus, abundant annual grasses may provide copious seed in spring, but this seed is likely to diminish rapidly with mass-germination triggered by the first heavy rains of the year.

These patterns raise important questions about the year-round availability of food for MLR *S. guttata*. Both studies spanned less than a year and were geographically small-scale, thus their broader applicability is limited. Given the magnitude of change within this system since European colonisation, the potential effect of this change on a fundamental requirement (food), and multiple studies from elsewhere that flag food availability as an issue for *S. guttata*, it is likely the species is experiencing food shortages. Furthermore, food shortages would manifest after mass-germination in autumn, when there is additional pressure on resources due to the new recruits from spring and summer breeding. Consequently, the survival of juveniles through winter comes into question. To adequately inform land management to support this species, further investigation is required into their year-round food availability, the species that provide this food consistently, and the impacts of altered food resources on *S. guttata*.

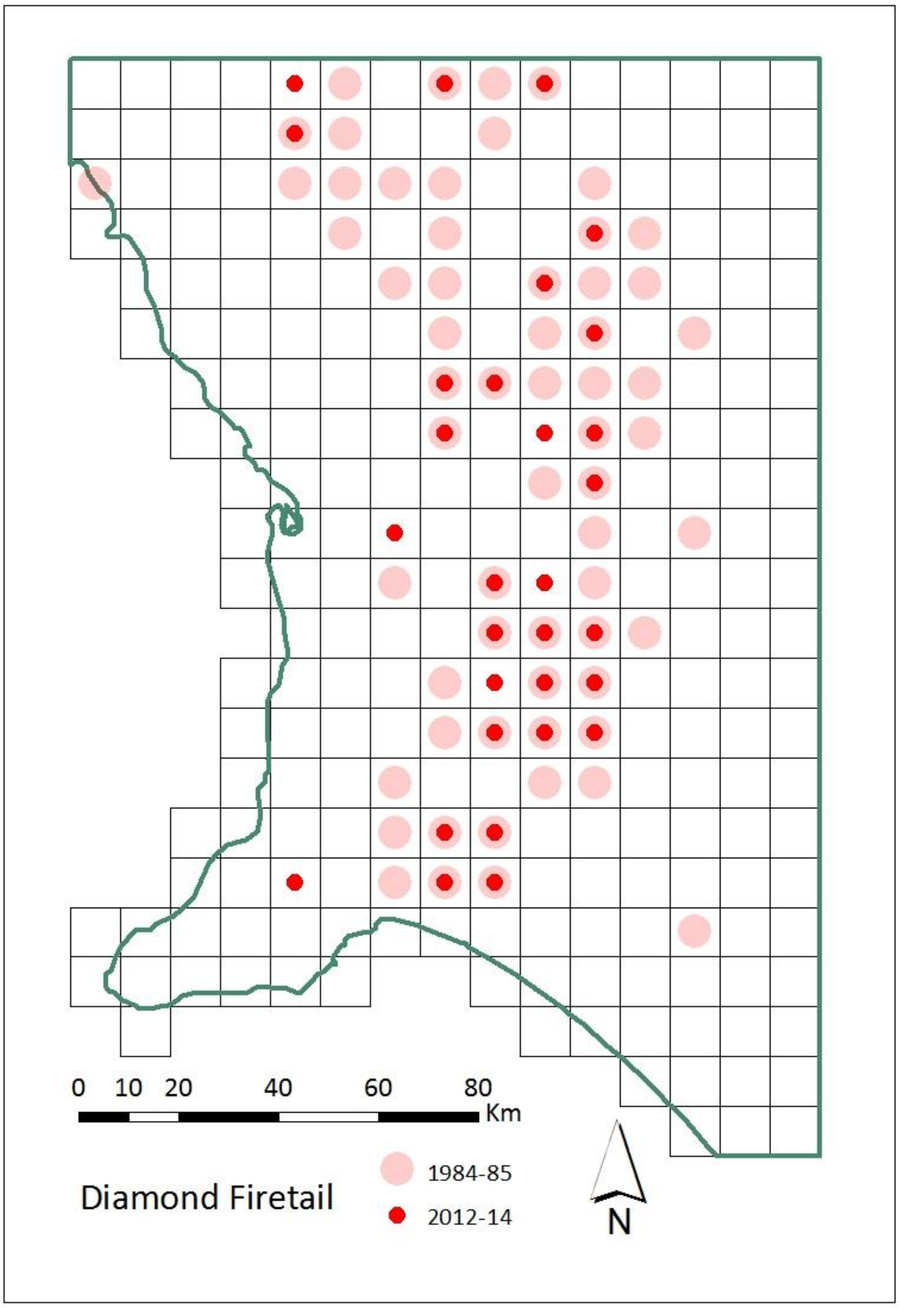

Figure 1-2 Grid cells within which *Stagonopleura guttata* were recorded in 1984–85 c.f. 2012–2014 in the southern MLR, taken from ‘A third bird atlas of the Adelaide Region’ (DC Paton 2017 unpub.).

1.3 Aims and outline

This thesis aims to investigate the importance of food availability as a contributing factor to the ongoing decline of *S. guttata* in the southern MLR, to inform habitat restoration and assist in reversing declines. More broadly, it provides a case study for the impact of compositional changes to grassy woodlands and grasslands on granivores. Specifically, this thesis tests the hypothesis that the invasion of weedy grasses has changed seeding patterns in the understorey such that *S. guttata* experiences seasonal food shortages, by addressing:

- seasonal seed resource composition changes and the effect on total seed abundance
- key plant taxa in the diet of *S. guttata* and their correlation with seasonal seed resource shifts
- *S. guttata* density and seasonal density patterns relative to seed resources
- the survival of *S. guttata* supplemented with seed versus *S. guttata* subject to seed shortages
- the impact of seed supplementation on juvenile survival

In Chapter 2, the seed resources available to ground-foraging granivores in the southern MLR are examined. Seed abundance, seed biomass, and seeding species composition were measured seasonally within *S. guttata* habitat. This determined how changes to the composition of understorey plant communities affects seed availability.

The diet of *S. guttata* in the southern MLR examined using crop analysis and observational studies is described in Chapter 3. Seasonal diet diversity and the selection of different food types are compared with available resources to determine whether *S. guttata* diets are mirroring local resource patterns.

Chapter 4 discusses the density of *S. guttata* in the southern MLR and seasonal changes in density. A qualitative comparison of *S. guttata* density patterns and seed resources was undertaken to determine how seed availability impacted *S. guttata* abundance.

Chapter 5 describes an *in situ* seed supplementation experiment that tested the impact of additional seed resources on *S. guttata* survival. Supplemented populations are compared with non-supplemented populations. In addition, the proportion of daily caloric requirements that *S. guttata* obtained from supplemented seed was measured monthly to examine temporal changes to their level of dependence on this seed.

Finally, Chapter 6 provides a summary and synthesis of the findings of Chapters 2–5, recommendations for the management of *S. guttata*, areas of future research to improve the management of the species, and discusses the broader application of results.

1.3.1 Study sites

This study examined *S. guttata* populations of the southern MLR (running south from approximately Keyneton, east of Gawler), as this is where the larger proportion of its present-day MLR distribution is located (Figure 1.2). Following preliminary assessments of thirty sites across the region (G Hodder 2014 unpub.), six distinct sub-regions were chosen from within the finch's current range (Figure 1.3). The sub-regions were near-equidistant and aligned roughly north-south along the length of the southern MLR. All sub-regions consisted of grassy woodlands and grasslands within an agricultural matrix on the eastern scarp of the ranges. From north to south, the sub-regions were located at: Karinya, Springton, Rockleigh, Monarto, Hartley and Milang, all of which were between 12 and 24 km apart (Figure 1.3). Distances between sub-regions were expected to preclude frequent movement of *S. guttata* between them, as <10% of banded individuals have been re-captured greater than 10 km from their capture site (Higgins *et al.* 2006). Within each sub-region, three distinct sample sites (each approximately 80–180 ha and separated from each other by 1-8 km) were selected, totalling 18 sites. All sites consisted of mid to low open woodlands of, to varying extents, *Eucalyptus fasciculosa*, *E. porosa*, *E. odorata*, *Callitris gracilis* and *A. verticillata* interspersed with open patches of grassland. Sparse mid-storeys of *A. pycnantha*, *A. paradoxa*, *B. spinosa*, *Melaleuca lanceolata*, *Melaleuca acuminata*, *Melaleuca uncinata*, *Dodonea viscosa*, *Eremophila longifolia* or *Senna artemisioides* ssp, were occasionally present, though generally limited. The understoreys at all sites were heavily degraded and dominated by similar species of weedy grasses and forbs, with the exception being Rockleigh, which had areas dominated by a near-monoculture of *Ehrharta calycina*. Native grasses were present to a lesser degree, interspersed with the weedy species. All sites have been historically grazed by livestock, and the Karinya sites were rotationally grazed during the study. The steep slopes with flanking gullies at the Springton sites have been largely cleared of overstorey and mid-storey vegetation, but a strip of woodland consisting primarily of eucalypts and tall shrubs persisted along the gullies and on open, rocky outcrops. Patches of remnant and revegetated habitat are present at all three Monarto sites. The large revegetated patches had open overstoreys of mature mixed non-native eucalypts, planted in the 1970s for amelioration purposes (Paton *et al.* 2004), but a very limited mid-storey.

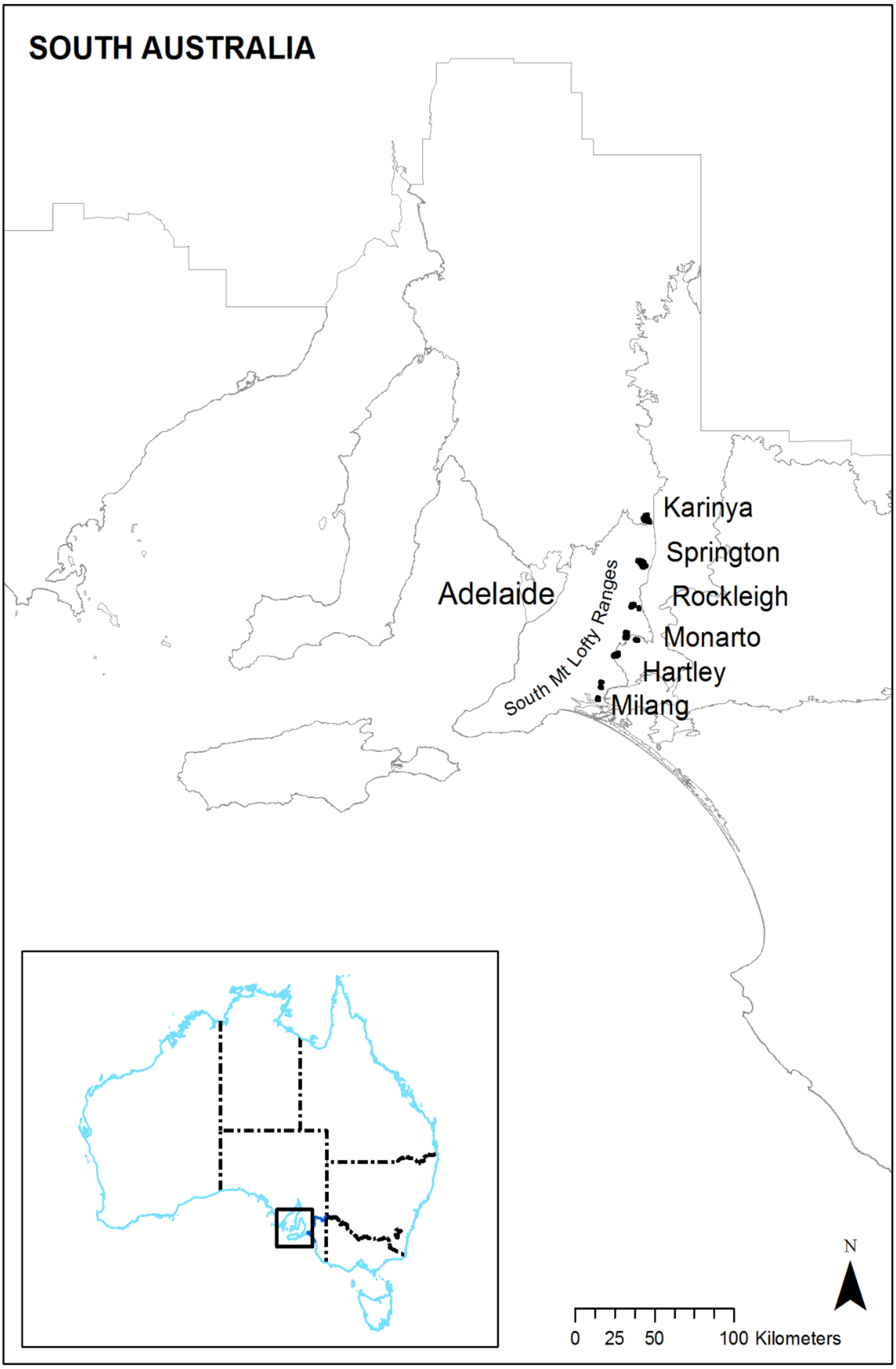

Figure 1-3 The six sub-regions: Karinya, Springton, Rockleigh, Monarto, Hartley and Milang, each containing three sampling sites (black shapes clustered within sub-regions).

Statement of authorship

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Name of Principal Author	Grace Hodder		
Contribution to the paper	Conceptualised and designed the experiment, collected and analysed data, interpreted the results and wrote the manuscript.		
Percentage contribution	85%		
Signature		Date	16/12/2019

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Chapter 2. Seasonal seed resource availability for granivorous birds in the southern Mount Lofty Ranges

Photo by Helga Kieskamp 2016

2.1 Introduction

Introduced species increasingly compromise the interactions between native species, as biotic invasions become more pervasive (Sala *et al.* 2000). Such interactions play a fundamental role in the structuring of ecosystems and thus can affect other ecological processes (Tylianakis *et al.* 2008). Invasive plants for example, can impact local resources for animal populations by changing the composition and structure of plant communities (Montserrat *et al.* 2011). Such changes have been found to alter food availability for birds in ecosystems around the world (e.g. Blendinger and Ojeda 2001; Thompson *et al.* 1991). For example, the intensification of grazing has changed the composition of grassland species in African Savannas (O'Connor and Pickett 1992) and in northern Australia (Crowley and Garnett 2001b), resulting in reduced seed availability for granivores. Structurally diverse and species-rich grasslands have been replaced by dense, uniform swards in Britain with similar effects (Vickery *et al.* 2001). Changes to resource availability can seriously affect wildlife populations and result in local (Paton *et al.* 2004), regional (Ford *et al.* 2001) and global declines or even extinctions (Ford 2011; Gurevitch and Padilla 2004; Wilcove *et al.* 1998).

The Mount Lofty Ranges (MLR) in South Australia has undergone extensive changes since European settlement, with over 90% of the region's native vegetation cleared for agriculture (Bickford and Gell 2005; Paton 2010). These changes have resulted in the fragmentation and degradation of remaining patches of native vegetation, facilitating the introduction and spread of a suite of exotic species (Szabo *et al.* 2011). The grassy ecosystems of the region are today dominated by invasive grasses from the northern hemisphere that have displaced indigenous grasses (Davies 1999), 90% of which are perennials (Davies 1997). Exotic annuals can produce copious seed during a short period in spring, but their seeds are known to mass germinate in response to the first heavy rains after summer (Monks *et al.* 2009; Torssell and McKeon 1976). Studies in Northern Australia have shown that very few grass-seeds remain after mass germination events (Crowley and Garnett 1999; Dostine *et al.* 2001; Mott and Andrew 1985). Thus, a switch to an annual-dominated system has the potential to result in significant seasonal variation in food availability (Ankor 2005; Carpenter 2012; Houdet 2003; Paton *et al.* 2004).

As a consequence of extensive landscape modifications, a majority of extant woodland birds in the MLR are declining in range (Paton *et al.* 1994; DC Paton 2017 unpub.). At least 40 species are predicted to go extinct based on the area of habitat remaining (Ford and Howe

1980; Szabo *et al.* 2011). Population declines are closely associated with foraging guild (Ford 2011). Ground-foraging birds, being susceptible to disturbances in the ground layer, are at risk of the effects of invasive understorey plants (Antos *et al.* 2008). Alterations to seed resources are particularly threatening for species that rely wholly on seeds for subsistence, like the declining diamond firetail, *Stagonopleura guttata* (Antos and Bennett 2006). The MLR *S. guttata* populations are small and fragmented, persisting in heavily cleared and degraded habitat dominated by invasive annual grasses (Paton *et al.* 1994). Despite the cessation of land clearance in the 1980s, populations continue to decline in range and abundance (Paton 2010). Short-term studies have concluded that food shortages may be a major contributor to these declines (Ankor 2005; Houdet 2003; Read 1994). However, the seed resources of the southern MLR have not yet been quantitatively measured at a landscape-scale, nor has this been undertaken elsewhere in temperate Australian grassy woodlands.

This study aims to quantify the availability of seed resources for granivorous birds in the southern MLR by measuring resources in areas where *S. guttata* were observed foraging. Seeding species will be individually identified and measured to track seasonal changes in plant community composition. Specifically, this study examines: i) the seasonal availability of seed biomass for granivorous birds in the MLR; ii) if weedy annual species dominate these seed resources and provide abundant seed year-round; and iii) how seasonal changes in the composition of understorey seed species influence total seed availability. The findings will inform conservation management for the recovery and future protection of *S. guttata*.

2.2 Methods

2.2.1 Study area and sampling sites

This study was conducted in the MLR; a temperate, biodiversity hotspot in South Australia supporting a system of heathy and grassy woodlands and forests. Populations of MLR *S. guttata* have largely contracted to the open, grassy woodlands in the eastern parts of the southern MLR. As such, sampling was undertaken across six sub-regions in the southern MLR over a two-year period (late spring 2014 to late winter 2016). The sub-regions (Milang, Hartley, Monarto, Rockleigh, Springton and Karinya) lie longitudinally along the eastern scarp of the southern MLR, approximately 12–24 km apart. Each sub-region was divided into three sampling sites (n = 18), comprising small patches of remnant or revegetated open eucalypt woodland with stands of *Allocasuarina verticillata, Callitris gracilis* and predominantly grassy understoreys dominated by weedy annual species. Sampling sites were set in an agricultural matrix within 8 km of one another, and each supported small populations of *S. guttata* (see Figure 1.3 in the *General Introduction*).

2.2.2 Sampling points

Seed resource availability and composition was measured during the latter half of summer, autumn, winter and spring at all 18 sites in the first year of study, which ran from late spring 2014 to late winter 2015 (Table 2.1). To determine the relationship between foraging areas selected by *S. guttata* and the broader seed resource availability, seed sampling was undertaken at forage points (sites where *S. guttata* were observed foraging) and compared to non-forage points (randomly generated locations in suitable habitat). Ten non-forage and up to ten forage points were sampled at each site in each season during the first year of study. Non-forage points were sampled on the same day as forage points, either after the forage points had been located and marked, or during periods when *S. guttata* could not be found. The locations of points varied between seasons and years, depending on where birds were observed foraging.

In the second year, sampling could not be undertaken in late spring 2015 due to unforeseen circumstances, but seed resources were sampled from late summer to late winter in 2016. Up to 20 forage points were sampled in each sub-region. Only forage points were sampled in the second year, as results from the first year indicated that *S. guttata* foraged in areas that were representative of the broader resource availability (see Section 2.3.1.2).

Table 2.1 The number of forage (F) and non-forage (NF) points sampled for seeds at each sub-region per season across two years in the southern MLR. Shaded squares denote unsampled seasons and sub-regions.

Sub-region (3 sites each)	Study Year 1								Study Year 2								Total
	2014		2015								2016						
	Spring		Summer		Autumn		Winter		Spring		Summer		Autumn		Winter		
	F	NF	F	NF	F	NF	F	NF	F	NF	F	NF	F	NF	F	NF	
Karinya	30	30	30	30	30	30	30	30	0	0	17	0	10	0	7	0	**274**
Springton	24	30	20	30	20	30	20	30	0	0	19	0	19	0	20	0	**262**
Rockleigh	10	30	10	30	30	30	10	30	0	0	14	0	13	0	20	0	**217**
Monarto	10	30	30	30	20	30	0	30	0	0	15	0	19	0	20	0	**234**
Hartley	2	30	22	30	10	30	10	30	0	0	0	0	12	0	0	0	**176**
Milang	6	30	0	30	0	30	2	30	0	0	5	0	10	0	12	0	**155**
Total	**82**	**180**	**112**	**180**	**110**	**180**	**72**	**180**	**0**	**0**	**70**	**0**	**83**	**0**	**79**	**0**	**1318**

2.2.2.1. Forage points

Forage points were obtained by following *S. guttata* groups or individuals for 6–10 hours per day (an average of 7.78 hrs ± 1.28 SD). Observations were initiated at sunrise and undertaken by the primary author. Individuals were located by identifying calls and making visual observations with binoculars. Once located, *S. guttata* were followed at a distance of >8 m, to avoid disrupting their activity. The time and locations (± 20 cm) at which birds removed seeds from the ground or plants were recorded. Foraging locations were marked with a flag once the focal birds left the area, and a location reading was taken using a Global Position System (Garmin GPS 72) at each foraging point that was considered independent from the last. Foraging points were deemed independent when either: a) observations of seed removal were ≥ 15 minutes apart, b) observations of seed removal were ≥ 15 metres apart, or c) there was a break in foraging to fly to a perch (e.g. for vigilance or preening). This is based on the principle that a foraging *S. guttata* can move freely to any other area within its home range of 12 ha (Ankor 2005) within 15 minutes (G Hodder 2015 pers. obs.), or following a break in foraging after which a new, precise site is chosen (Swihart and Slade 1985). Where a group of foraging points were dependent the most exactly located or most used point was flagged. Once foraging points were flagged, *S. guttata* were located again where possible and observed until the next independent foraging point was obtained. Within each site, groups/individuals were followed for one day per season. A total of 608 foraging points were located and data were collected from each—376 in the first year of study, and 232 in the second year (Table 2.1).

2.2.2.2. Non-forage points

To obtain non-forage points, fifty locations were randomly generated within each site for each season using ArcGIS 10.3.1. Within each site, ten of the generated points that fell within suitable foraging habitat (grassy understorey), but where *S. guttata* had not been observed foraging, were sampled per season. Where locations had logistical constraints (e.g. coordinates fell over a tree, dense bush or in inaccessible habitat) the nearest random location was chosen instead. A total of 710 non-forage points were collected in the first year of study (Table 2.1).

2.2.3 Seed resource availability

2.2.3.1. Seed species abundances and composition

Seed abundance and composition were determined by collecting seeds at forage (n = 608) and non-forage (n = 710) points. All seeding species of grasses, forbs, small understorey shrubs and sheoaks (both in fallen and open cones on the tree) were sampled, as they are known or likely food sources for *S. guttata* (Ankor 2005; Read 1987, 1994; Schopfer 1989). The available seed resources were determined by measuring the standing crop seeds (all seeds held on plants) within a 50 x 50 cm quadrat centred over the forage/non-forage point, and soil surface seeds (all seeds found on the soil surface) using a 25 x 25 cm quadrat centred over each point. A smaller quadrat size was chosen for the soil surface sample to minimise the amount of material requiring transportation and storage prior to processing in the laboratory.

The abundance of seeding species in the standing crop was measured by collecting all seeds (of all development stages) held on focal plants (e.g. in grass seed-heads or open sheoak cones) within each quadrat. All seeds collected from within quadrats were placed in paper bags (separated by species) in the field for later processing in the laboratory. In cases where *S. guttata* foraged in sheoaks, quadrats were placed in the canopy of the tree and all standing cones intersecting the plane of the quadrat were removed and bagged. In the laboratory, all collected seeds were extracted from seed-heads, fruits, pods or cones and identified under an Olympus VMZ 1x – 4x Stereo Microscope with the aid of plant and seed guides (Jessop *et al.* 2006; State Herbarium of South Australia 2007). The numbers of seeds present for each species was then counted.

Topsoil seeds were collected after standing crop seeds were removed. This was done by using a flat spade to remove the top 1 cm of soil and any litter or fallen plant material within the quadrat and placing it into paper bags. Topsoil samples were sifted through a 2 mm sieve to remove leaf litter and other large material, and then sifted through a 0.43 mm sieve to remove any fine material and seeds too small to be eaten by *S. guttata* (Read 1987; Schopfer 1989). Sieve sizes were based on previous studies of seed sizes in *S. guttata* diet by Read (1987) and Schopfer (1989). The remaining material was sifted over a corrugated tray, and all seeds were extracted using a magnifying glass and tweezers. Collected seeds were then identified and counted. Where seeds could not be identified from reference guides, they were planted in soil and watered regularly until they grew large enough for identification.

2.2.3.2. Seed biomass

The total seed biomass of each seeding plant species was calculated for each quadrat by determining the average seed mass of each species and multiplying it by the number of seeds within the quadrat. Average seed mass (g) of each species was calculated by weighing a sample of 100 dried seeds. Seeds were weighed using a Mettler AE 200 Analytical Balance, which has a readability and reproducibility of 0.1 mg.

2.2.4 Statistical analyses of patterns

Patterns in seed resource availability were analysed using generalised linear models. The seasonal availability of seeds was examined using the total seed biomass of all seeding species. Compositional changes to seed species communities were examined using the seed abundances of individual species. Each of these response variables were treated with two sets of analyses: one of first-year data only, and one for the entire two-year data set. Analyses of the first-year data examined differences in seed resources between forage and non-forage quadrats across all four seasons and sub-regions. Analysis of the two-year data set examined differences in seed resources between seasons, sub-regions and years. As spring sampling was only conducted in the first year, spring was removed from the two-year analysis to create a balanced study design. The standing crop seeds and the soil surface seeds were examined separately within each analysis. All analyses were done in R 3.5.1 (R Core Team 2016).

Despite equal search effort per site, there was missing foraging data at some sites within some seasons. As *S. guttata* were scarce, it was not possible to locate foraging individuals on every sampling day. The southern-most sites had fewer *S. guttata* and therefore the highest incidences of missing data (Table 2.1). In a factorial design, unequal sample sizes can lead to confounded row, column and interaction effects. To balance the design, levels of the sub-region and season factors that contained missing data were removed. As such, Milang was removed from models assessing patterns of seed biomass across the two years. Milang, Hartley and Monarto were removed from models assessing differences between forage and non-forage points, and models assessing seed species composition. However, to ensure patterns emerging from these analyses were consistent across the removed sub-regions, additional models were run with subsets of the data to enable their inclusion (i.e. to include Milang in the models, the summer and autumn sampling periods were removed). In addition, the three-way interactions in the models of seed biomass could not be fitted.

2.2.4.1. Seed biomass

To assess temporal patterns of overall seed biomass, the two measures (standing crop and soil surface) were first scaled out to a metre-squared measure and then summed to obtain total biomass per metre-square. For this initial exploration, data were pooled across study sites, sub-regions and years. The average seed biomass per m^2 was then calculated in each season for different plant forms (forb, grass, sedge, sheoak or shrub), plant origin (introduced or native) and growth cycle (perennial or annual). The average seed biomass per season per year was also calculated.

The standing crop and soil surface seed biomass variables were analysed separately using Tweedie compound Poisson generalised linear mixed models fit by the Laplace approximation (Zhang 2013). This model was used because the biomasses are continuous variables with a point mass of exact zero values, and as such the compound poisson was appropriate for the variance in biomass. The seed biomass response variables were modelled against combinations of the following factors: year, sub-region (Hartley, Monarto, Rockleigh, Springton and Karinya), season and forage versus non-forage quadrats. Site was included as a random factor to account for the nested design and the non-independence between sites, as *S. guttata* were capable of moving between sites within a sub-region (Manly *et al.* 2004). Model fits were checked by plotting raw deviances against fitted values and did not indicate any deviations from a linear form, showing relatively constant variances across the fitted range (Appendix A).

The global model contained the two-way interactions of the variables: sub-region, season, year and forage/non-forage plots. Each two-way interaction was dropped in turn from the model and compared with the global model. Likelihood ratio tests (LRTs) were used to assess differences in the response variable among the levels of each two-way interaction term (α=0.05). There were differences among the levels for all two-way interactions tested, therefore model-testing did not go further. Models were fit using package ‘cplm’ (Zhang 2013).

To determine how the response differed among the levels of each factor, post-hoc analyses were undertaken for the global models. Contrast matrices were constructed to compare pairs of factors in turn and used to generate simultaneous tests for general linear hypotheses. This produced mean estimates of seed biomass for each level of the factors being compared. Simultaneous 95% confidence interval estimates of the model parameter estimates were also generated. Post-hoc analyses were performed using the multcomp package (Hothorn *et al.* 2008).

2.2.4.2. Seed species composition

Multivariate generalised linear models were used to investigate spatial and temporal variation in the composition and abundances of seeding species. Standing crop and the soil surface seed composition were modelled separately against combinations of the following factors: year, sub-region, season, and forage versus non-forage quadrats with the mvabund package (Wang *et al.* 2012). The mvabund package cannot account for random effects, so variation among sites within sub-regions was not accounted for. As sites had similar understorey habitats, the analyses should not have missed a significant amount of between-site variation.

Patterns of seed species abundances were investigated with response matrices comprising abundance counts of the number of seeds per species (108 species in the standing crops, 95 species on the soil). Patterns in the presence/absence of individual species were investigated separately. The explanatory variables in the global models comprised all factors (sub-region, season, forage/non-forage and year) and their interactions. Models were initially fitted with a Poisson distribution, which identified overdispersion in the data. Therefore, a negative binomial distribution was subsequently fitted and used for interpretation of the data. Model assumptions were checked by graphing the Dunn-Smyth residuals versus the linear predictor values (Wang *et al.* 2012; Appendix B).

Likelihood ratio tests were used to test the effects of explanatory variables and their interactions. The global models for the one-year and two-year analyses were compared with subsets of these global models. P-values for these comparisons were obtained via the PIT-trap method that bootstraps Probability Integral Transform (PIT) residuals, by resampling under the null hypothesis, giving reliable Type I error rates (Warton *et al.* 2017). As there were clear differences in the multivariate response among all tested interaction terms, model-testing did not go further, and no interaction terms were dropped from the models. Sequential test statistics and p-values for each interaction term in each of the global models were then obtained with 999 bootstrap iterations. Univariate test statistics for each seed species and their individual p-values (adjusted for multiple testing), calculated using a step-down resampling algorithm (Westfall and Young 1989), were obtained with the same method. This determined which species differed among the levels of the explanatory variables. The mvabund package was used for all tests (Wang *et al.* 2012). Due to the intensive computational power required to generate such complex models, the Phoenix HPC supercomputer at the University of Adelaide was used to generate the results.

Model estimates of mean abundance (or mean probability of presence) for individual seed species that differed among the levels of the explanatory variables, and their deviances, were extracted from an ANOVA output using contrast matrices. Model estimated means were scaled (multiplied by 16 for soil surface seed measurements, and by 4 for standing crop seed measurements), to display seed abundance estimates per m^2. These analyses were generated with the multcomp (Hothorn *et al.* 2008) and lsmeans R packages (Lenth 2016).

2.3 Results

A total of 1,318 points were sampled (*n* = 608 forage; *n* = 710 non-forage) across the entire study period. In the first year, 924 forage and non-forage points containing 80,129 seeds were sampled. Across the two-year period, 608 forage points containing 115,360 seeds of 108 species were sampled. Results are presented as means ± standard errors unless otherwise stated.

2.3.1 Seed biomass

2.3.1.1. Combined soil surface and standing crop biomass

Average seed biomass per m^2 was lowest in autumn (0.54 ± 0.13 g m^{-2}). Spring was the most productive season with an average biomass of 4.08 ± 0.67 g m^{-2}, followed by summer (1.30 ± 0.45 g m^{-2}). Seed biomass in winter varied between years, with 1.44 ± 0.32 g m^{-2} in the first year and 0.42 ± 0.12 g m^{-2} in the second year.

Grass seeds made up the largest component of seed biomass in all seasons (0.99 ± 0.14 g m^{-2}; Figure 2.1 A). Seeds from sedges and sheoaks were scarce across all seasons ($<0.01 \pm <0.01$ g m^{-2} and 0.03 ± 0.01 g m^{-2} respectively). The seed biomass in the understorey was dominated by introduced plants in all seasons (spring: 2.97 ± 0.52 g m^{-2}; summer: 0.71 ± 0.15 g m^{-2}, autumn: 0.53 ± 0.20 g m^{-2}; winter: 0.98 ± 0.16 g m^{-2}) particularly during spring (Figure 2.1B). Native plants contributed substantially to seed biomass in summer (0.62 ± 0.28 g m^{-2}), almost equalling the seed biomass of non-native plants. In all other seasons, native plants had much lower seed biomass (autumn: 0.12 ± 0.03 g m^{-2}; winter: 0.11 ± 0.03 g $m^{-2;}$ spring: 0.44 ± 0.13 g m^{-2}). Annual plants dominated the seed biomass in spring and winter (2.86 ± 0.53 g m^{-2} and 0.93 ± 0.16 g m^{-2} respectively), while in summer and autumn seeds from perennial plants were more prominent (0.93 ± 0.30 g m^{-2} and 0.49 ± 0.20 g m^{-2} respectively Figure 2.1 B). A representation of the seasonal proportions of different resource types is shown in Appendix C.

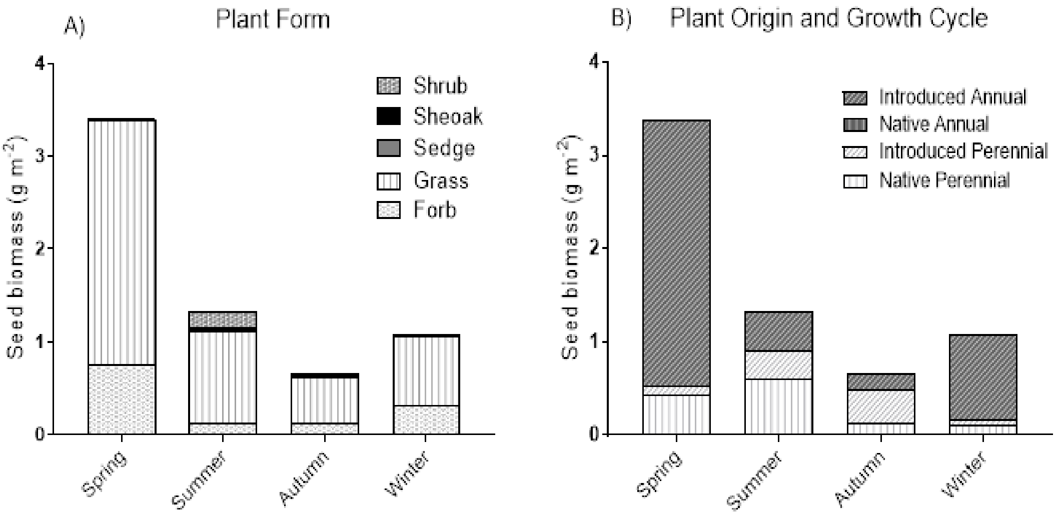

Figure 2-1 The average total seed biomass (g m^{-2}) of (A) all seeds of grasses, sedges, forbs, small shrubs and sheoaks and (B) plants with annual or perennial growth cycles and the relative amounts from introduced or native plants, found in the standing crop and on the soil surface at *Stagonopleura guttata* foraging points.

2.3.1.2. Biomass of seeds in the first year

Seed biomass in the first year differed between seasons depending on the sub-region and on whether seeds were sampled from forage or non-forage quadrats. This pattern was found for the soil surface and standing crop seeds ($P < 0.001$; Table 2.2). These differences were due to the interaction between season, sub-region and forage versus non-forage quadrats (Table 2.2). However, there was a strong overall pattern of seasonality across combined sub-regions (Figure 2.2, top).

Post-hoc analysis for the soil surface and standing crop seed models revealed that seed biomass measured in the first year was generally at its lowest in autumn (Figure 2.2, top). When averaged over forage and non-forage quadrats soil surface seed biomass was lower in autumn compared with spring and summer at Karinya ($P < 0.001$) and Springton ($P < 0.001$; Figure 2.2, top left). However, seed biomass at the soil surface was higher in autumn compared with spring and winter at Rockleigh ($P < 0.001$). Standing crop seed biomass was lower in autumn compared with spring at all sub-regions ($P < 0.001$), lower in autumn compared with winter at Karinya ($P < 0.001$), and lower in autumn compared with summer at Rockleigh ($P < 0.001$).

There was a stronger seasonal pattern in seed biomass than there was between forage and non-forage quadrats. In most seasons seed biomass did not differ substantially between these two quadrat types (Figure 2.2, bottom). However, in winter, both the soil surface and standing crop seed biomass were higher in forage quadrats than non-forage quadrats ($P = 0.03$ and $P < 0.001$ respectively; Figure 2.2, bottom). Standing crop seed biomass was also higher in forage quadrats in summer ($P = 0.04$; Figure 2.2, bottom right). When averaged across seasons, there was a higher standing crop seed biomass in forage than non-forage quadrats at Rockleigh and Springton (all $P < 0.001$), and a higher soil surface seed biomass in forage quadrats at Springton ($P = 0.01$). There was no substantive difference in seed biomass between forage and non-forage quadrats at Karinya (all $P > 0.05$; Table 2.2).

Table 2.2 Model testing using likelihood ratio test statistics for the effects of Season, Year, Forage vs. Non-forage quadrats and their interactions on the seed biomass found a) in the standing crop and b) on the soil surface in 353 quadrats at nine sites in the southern MLR during 2014–2015.

	logLik	K	χ^2	Pr> χ^2
Seeds in inflorescences				
Subreg*Seas*F/NF	-35.45	26		
Subreg*Seas*F/NF – Subreg:Seas:F/NF	-61.97	20	53.04	<0.0001
Seeds on soil surface				
Subreg*Seas*F/NF	293.38	26		
Subreg*Seas*F/NF – Subreg:Seas:F/NF	281.90	20	22.95	0.0008

Explanatory variables are: Subreg = Sub-region, each with 3 sites, Seas = 'Season' or period when seed sampling occurred, and F/NF = quadrats at which *S. guttata* were observed foraging (F) and quadrats placed elsewhere throughout study sites (NF). 'Site' was included in each model as a random variable. The three-way interaction *and* its full expansion is denoted by '*' in the global model, which was tested against this model without the three-way interaction. This is shown using ':' which denotes the interaction *only* between two/three factors. logLik = the log likelihood of the model, K = the number of estimated parameters, χ^2 = the chi-square test statistic, Pr> χ^2= the probability of observing a sample statistic as extreme as χ^2, assuming the null hypothesis is true. Best fit models are shown in bold face.

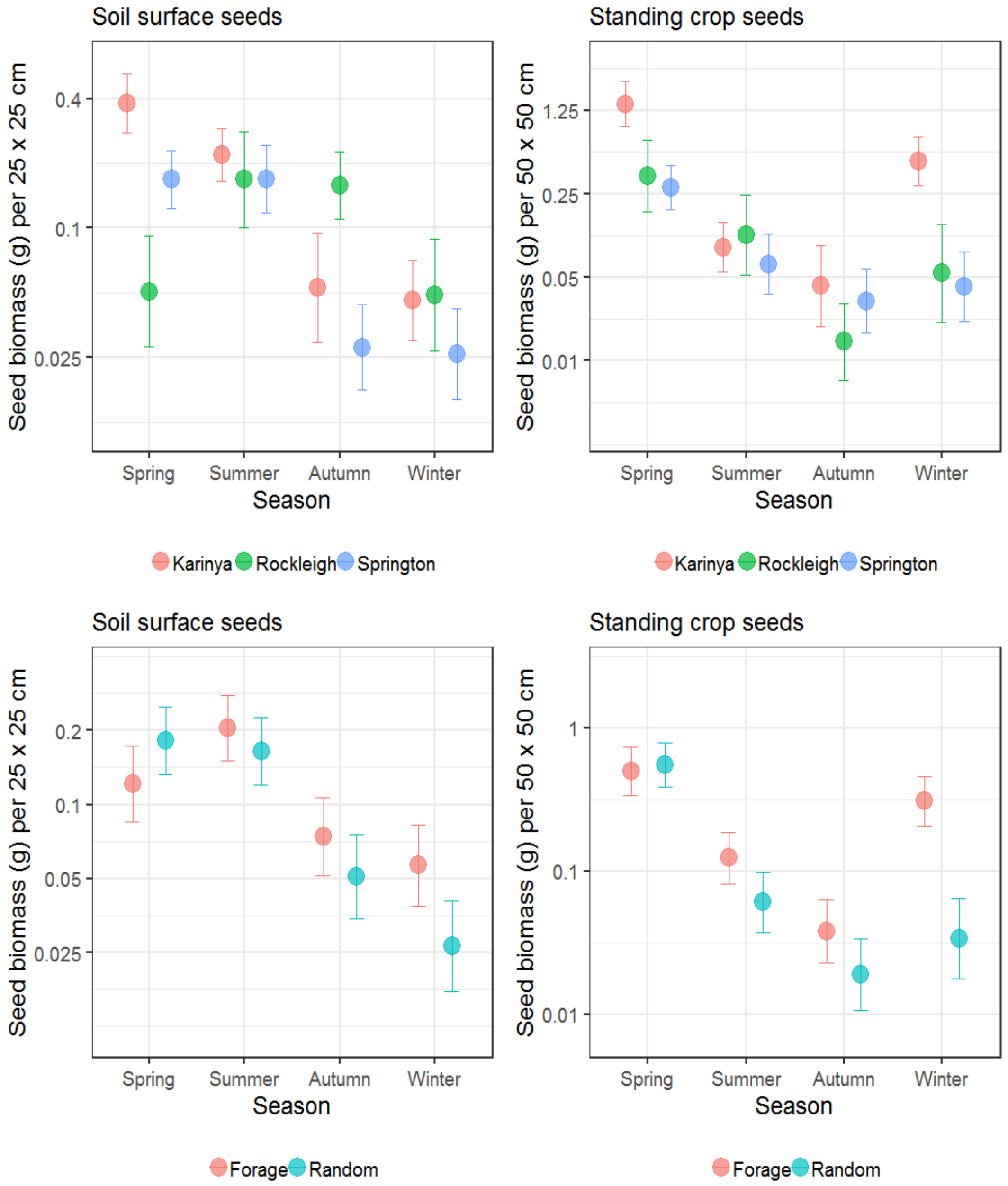

Figure 2-2 Modelled seed biomass (g) on the soil surface (left) and in the standing crop (right) measured in quadrats (n = 353) where *S. guttata* foraged and quadrats in non-forage habitat throughout three sub regions in the southern MLR during 2014–2015. Error bars denote 95% confidence intervals, which are plotted as logarithms and have not been back-transformed. Scale of y-axis=logarithmic.

2.3.1.3. Biomass of seeds across two years

The total seed biomass sampled from quadrats where *S. guttata* were observed foraging varied across seasons, depending on the year and sub-region.This was found for seeds on the soil surface and for seeds in the standing crop (all $P < 0.05$; Table 2.3). Similar to the seed biomass patterns across the first year, there was a strong overall pattern of seasonality across combined sub-regions and years (Figure 2.3). Post-hoc analysis of the best models (Table 2.3) revealed that soil surface seed biomass was generally lower in autumn and winter than summer across sub-regions and years (Figure 2.3). The exception was Hartley, where soil surface seed biomass increased in winter relative to autumn ($P = 0.005$). Standing crop seed biomass was lower in autumn compared with summer at Hartley, Rockleigh and Springton ($P < 0.01$), and lower in autumn compared with winter at Hartley, Monarto, Rockleigh, and Springton ($P < 0.01$ for all locations). Overall, seed biomass was lower in autumn compared with summer in both 2015 and 2016 when averaged across sub-regions ($P < 0.001$; Figure 2.3; Table 2.3).

Table 2.3 Model testing using likelihood ratio test statistics for the effects of Season, Year, Sub-region and their interactions on the total seed biomass found (a) in the standing crop and (b) on the soil surface in 509 quadrats where *S. guttata* were observed foraging at 15 sites in the southern MLR during 2015–2016.

Candidate model	logLik	K	χ^2	Pr> χ^2
Seeds in inflorescences				
Subreg*Seas*Yr – Subreg:Seas:Yr	107.38	24		
Subreg *Seas*Yr – Subreg:Seas:Yr – Subreg:Seas	97.91	16	18.92	0.015
Subreg *Seas*Yr – Subreg:Seas:Yr – Subreg:Yr	95.80	20	23.13	0.0001
Subreg *Seas*Yr – Subreg:Seas:Yr – Seas:Yr	89.97	22	34.8	<0.0001
Seeds on soil surface				
Subreg *Seas*Yr – Subreg:Seas:Yr	226.11	24		
Subreg *Seas*Yr – Subreg:Seas:Yr – Subreg:Seas	210.50	16	31.21	0.0001
Subreg *Seas*Yr – Subreg:Seas:Yr – Subreg:Yr	200.61	20	50.99	<0.0001
Subreg *Seas*Yr – Subreg:Seas:Yr – Seas:Yr	218.42	22	15.37	0.0005

Explanatory variables are: Subreg = Sub-region, each with 3 sites, Seas = 'Season' or period when seed sampling occurred, and Yr = 2015 or 2016. 'Site' was included in each model as a random variable. The three-way interaction *and* its full expansion is denoted by '*' in the global model, which was tested against this model without the three-way interaction. This is shown using ':' which denotes the interaction *only* between two/three factors. logLik = the log likelihood of the model, K = the number of estimated parameters, χ^2 = the chi-square test statistic, Pr> χ^2= the probability of observing a sample statistic as extreme as χ^2, assuming the null hypothesis is true. Best fit models are shown in bold face.

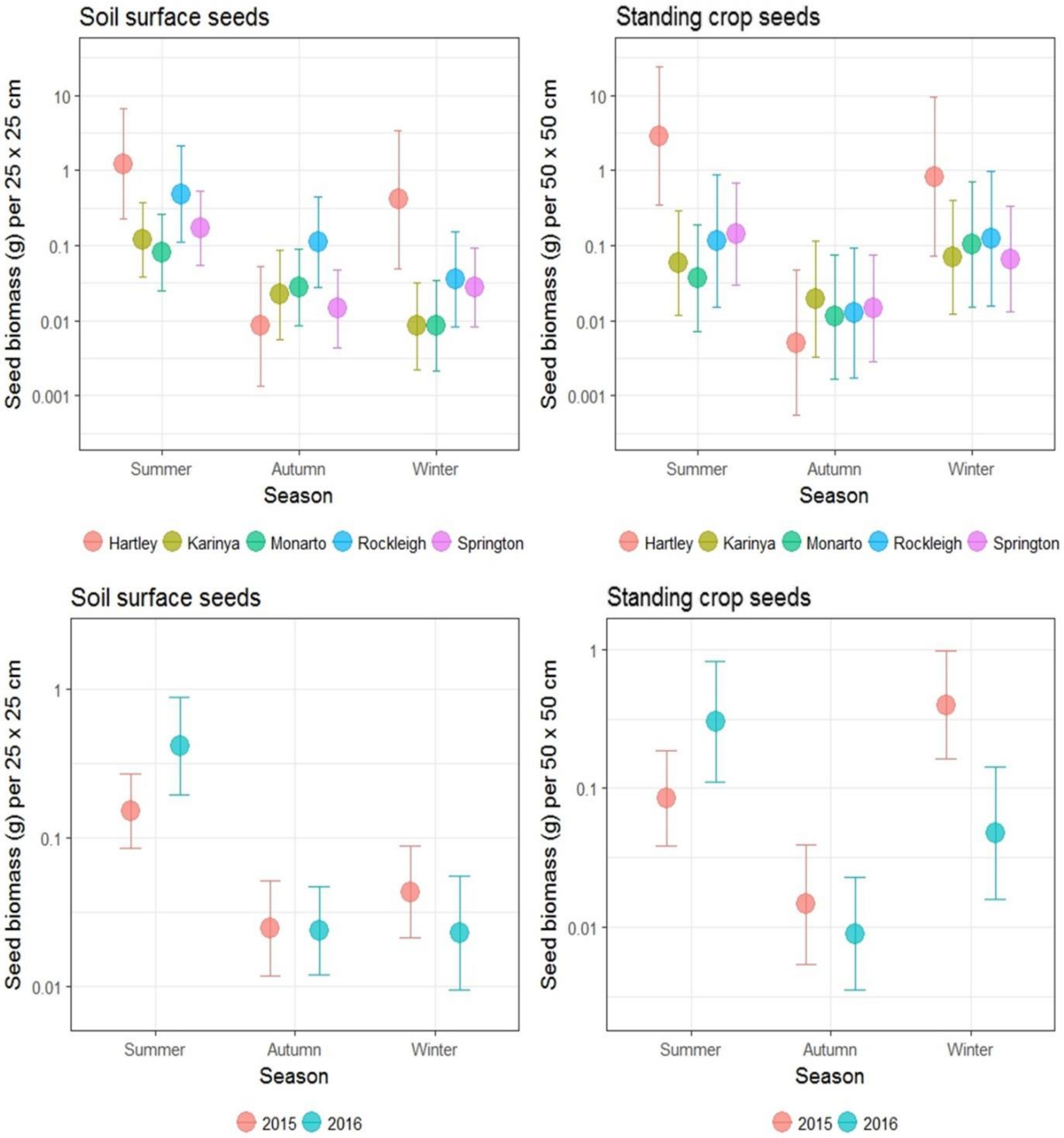

Figure 2-3 Modelled seed biomass (g) on the soil surface (left) and in the standing crop (right) of all seeding species of grasses, forbs, small shrubs and sheoaks found in quadrats (n = 465) where *S. guttata* foraged at 5 subregions in the southern MLR during 2015–2016. Error bars denote 95% confidence intervals, which are plotted as logarithmics and have not been back-transformed. Scale of y-axis=logarithmic.

2.3.2 Seed species composition

2.3.2.1. Individual species abundances across the first year

The composition of seed species in the first year differed between seasons depending on the sub-region and on whether seeds were sampled from forage or non-forage quadrats (Table 2.4). This was true for the composition of seed species on the soil surface ($P = 0.001$) and in the standing crop ($P = 0.006$). The predictors sub-region and season explained a greater amount of variation in the data than the forage versus non-forage predictor, as indicated by their higher deviances (where higher deviance indicates a stronger prediction of the response variable) (Burnham and Anderson 2002; Table 2.4).

In addition to the overall patterns of seed composition exhibited across the first year, many individual species showed significant responses to the predictors of season and sub-region, alone (Appendix D). The seed abundances of 24 species sampled from the soil surface changed across seasons and 23 species differed among sub-regions ($P < 0.05$). The seed abundances of 36 species in the standing crop changed across seasons, while 26 species changed with sub-region ($P < 0.05$). Very few of the species differed in association with the interaction of the variables of sub-region by season, sub-region by forage/non-forage and forage/non-forage by season (Appendix D). Therefore, seasonality of seed did not vary between sub-regions or quadrat types in general.

Variation in soil surface seed resources was predominantly attributed to seasonal changes in seed abundances of annual weedy grasses (> 34%) and forbs (> 33%), together accounting for over 67% of the variation in seed resources (Figure 2.4). A majority of annual, weedy species displayed similar seasonal trends, with peaks in soil surface seed abundances in spring or summer that decreased into autumn and were lowest in winter (Appendix E). Species demonstrating this trend included grasses such as *Avena* sp., *Briza maxima* and *Brachypodium distachyon*, and forbs such as *Romulea rosea*, *Erodium* sp. and *Hypochaeris glabra* ($P < 0.05$). The only four (of > 40 recorded) perennial species whose seed abundances changed substantially between seasons were native grasses and shrubs: *Aristida behriana*, *Rytidosperma caespitosum*, *Vittidinia* sp. and *Senecio* sp. These native species had high seed abundances in summer that dropped during autumn ($P < 0.05$; Appendix E). Twenty out of the 24 species (83.3%) whose soil surface seed abundances changed between seasons were weedy annual grasses or forbs, while the remaining four were native perennial grasses or forbs (Appendix D).

Table 2.4 Model testing using likelihood ratio test statistics for the effect of Season, Sub-region, Forage vs. Non-forage quadrats and their interactions on individual species seed abundances found a) in the standing crop and b) on the soil surface in 435 quadrats at nine sites in the southern MLR during 2014–2015.

Candidate model	Residual DF	DF diff.	Deviance	P-value
Seeds in inflorescences				
Null	433			
Subreg	431	2	755.5	0.001
Season	428	3	1591.2	0.001
F/NF	427	1	173.2	0.001
Subreg:Season	421	6	239.7	0.008
Subreg:F/NF	419	2	95.6	0.014
Season:F/NF	416	3	147.2	0.002
Subreg:Season:F/NF	410	6	85.7	0.006
Seeds on soil surface				
Null	433			
Subreg	431	2	1219.2	0.001
Season	428	3	2274.8	0.001
F/NF	427	1	191.6	0.001
Subreg:Season	421	6	572.4	0.002
Subreg:F/NF	419	2	176.6	0.001
Season:F/NF	416	3	270.8	0.001
Subreg:Season:F/NF	410	6	201.6	0.001

Explanatory variables are: Subreg = sub-region, each with 3 sites, Season = period when seed sampling occurred, and F/NF = quadrats at which *S. guttata* were observed foraging (F) and quadrats placed elsewhere throughout study sites (NF). ‘:’ separates factors and denotes interactions in candidate model set. Residual DF = Residual Degrees of Freedom; DF diff. = DFm^1 – DFm^2; Deviance = the log-likelihood ratio test statistic; P-value = the probability of observing a sample statistic as extreme, assuming the null hypothesis is true. Best fit models are in bold face.

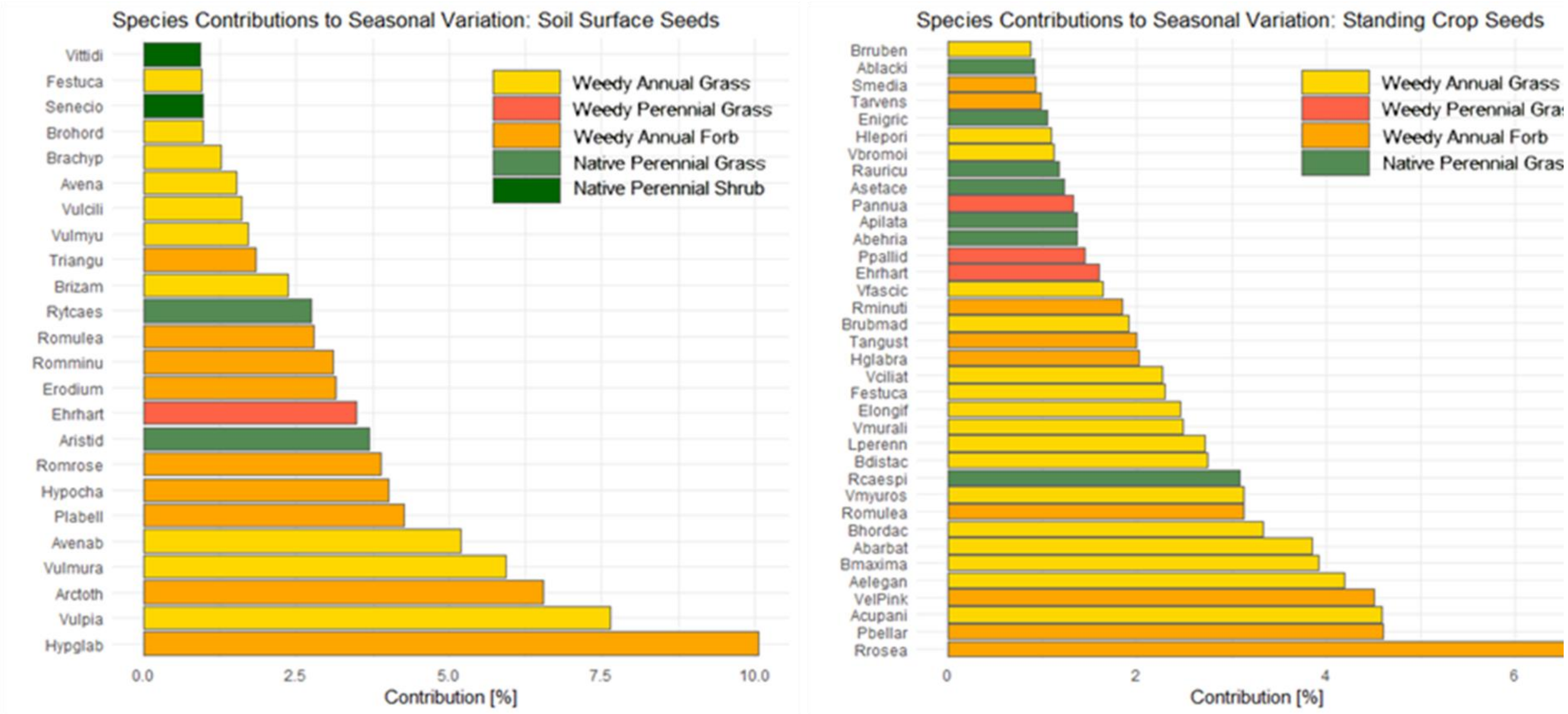

Figure 2-4 The percentage each understorey species (y-axes) contributed to the total seasonal variation in soil surface seed abundance (left) and standing crop seed abundance (right) sampled from nine study sites within three sub-regions across four seasons in the eastern MLR between 2014–2015.

Variation in standing crop seed resources was predominantly attributed to seasonal changes in seed abundances of annual weedy grasses (> 43%) and forbs (> 25%), together accounting for over 68% of the variation in seed resources (Figure 2.4). Annual grass and forb seeds in the standing crop displayed consistent seasonal patterns which differed from those on the soil surface (Appendix F). Annual grass and forb seed abundances were generally very high in spring and dropped to at or near zero in summer and autumn. Some weedy annual grasses produced small amounts of seed in winter while others remained at zero (Appendix E). Grass species with these trends included *Aira cupaniana*, *B. maxima* and *Vulpia myuros* ($P = 0.001$), and forb species *R. rosea*, *Plantago bellardii* and *H. glabra* ($P = 0.001$). Some native perennial grasses, including *Rytidosperma auriculatum*, *Rytidosperma caespitosum* and *Austrostipa pilata* also peaked in seed abundance during spring ($P < 0.005$). However, other perennial species had different seasonal trends. Seed abundance of the native grass *Enneapogon nigricans* peaked during autumn ($P = 0.01$), the introduced grass *Poa annua* seeds peaked in winter ($P = 0.003$), and the native grass *A. behriana* seeds peaked during spring but persisted in the standing crop into summer ($P = 0.003$). Twenty-seven out of the 36 species (75%) whose standing crop seed abundances changed with season were weedy annual grasses or forbs, eight were native perennial grasses and one was an introduced perennial grass (Appendix E).

2.3.2.2. Compositional differences between forage and non-forage quadrats

Only four species had significantly different seed abundances between forage and non-forage quadrats (Appendix E). There were more standing crop seeds from *P. annua* found in forage than non-forage quadrats ($P = 0.04$). Fewer standing crop seeds of *Gahnia deusta* were found in forage than non-forage quadrats ($P = 0.04$). On the soil surface, more *Ehrharta longiflora* seeds were found in forage quadrats than non-forage quadrats ($P = 0.008$), while more *A. behriana* seeds were found in non-forage than forage quadrats ($P = 0.002$). There were five species whose soil surface seed abundances differed between forage and non-forage quadrats dependent on season (Appendix E).

2.3.2.3. Presence or absence of seeding species

Similar to the seed abundance models, the presence or absence of seeding species varied with season and was dependent on sub-region and forage or non-forage quadrats (Appendix G). Most variation in the composition of species presence-absence was attributed to season and sub-region, rather than to forage versus non-forage quadrats. Almost all species whose abundances were affected by sub-region or season were also present or absent depending on sub-region or season. A more comprehensive explanation of the presence-absence analyses can be found in Appendix G.

2.3.2.4. Individual species abundances across two-years

The composition of seed species across two years differed between seasons depending on the sub-region and year (Table 2.5). This was true for the composition of seed species on the soil surface ($P = 0.001$) and in the standing crop ($P = 0.004$). As with the first-year models, most of the variation in the data was explained by sub-region and season across two years. The amount of variation explained by year was comparatively low, and the general patterns of seed species composition and abundances between seasons and sub-regions exhibited across the first year were also shown across the second year. Within individual species, seasonal trends of seed abundance were generally consistent between years (Appendix D).

As with the first-year dataset, most of the variation in seed abundances across two years was attributed to seasonal changes in the seed abundance of weedy, annual grasses and forbs. Most of these species exhibited higher seed abundances in summer compared with autumn and winter ($P < 0.05$). A smaller percentage of the variation in seed abundance across two years was attributed to seasonal changes in perennial grass seeds, such as *A. behriana*, *R. caespitosum*, and *E. nigricans*. These grasses were mostly native and had varying seasonal patterns of seed abundance. Some species (e.g. *A. behriana*, *E. nigricans* and *R. caespitosum*) had more seeds in summer compared with autumn and winter ($P < 0.01$), while others (e.g. *P. annua* and *E. calycina*) had more seeds in winter or autumn ($P < 0.01$; Appendix D).

Table 2.5 Model testing using likelihood ratio test statistics for the effects of Season, Year, Sub-region and their interactions on individual species seed abundances found a) in the standing crop and b) on the soil surface in 359 quadrats at nine sites in the southern MLR during 2015–2016.

Candidate model	Residual DF	DF diff.	Deviance	P-value
Seeds in inflorescences				
Null	305			
Subreg	303	2	428.95	0.001
Season	301	2	389.76	0.001
Year	300	1	234.34	0.001
Subreg:Season	296	4	278.34	0.007
Subreg:Year	294	2	85.52	0.020
Season:Year	292	2	44.78	0.002
Subreg:Season:Year	288	4	14.21	0.004
Seeds on soil surface				
Null	304			
Subreg	302	2	813.86	0.001
Season	300	2	904.45	0.001
Year	299	1	433.97	0.001
Subreg:Season	295	4	299.07	0.029
Subreg:Year	293	2	185.01	0.001
Season:Year	291	2	155.68	0.001
Subreg:Season:Year	287	4	41.35	0.001

Explanatory variables in candidate models are: Subreg = sub-region, each with 3 sites, Season = period when seed sampling occurred, and Year = 2015 or 2016. ':' separates factors and denotes interactions in candidate model set. Residual DF = Residual Degrees of Freedom; DF diff. = DFm^1 – DFm^2; Deviance = the log-likelihood ratio test statistic; P-value = the probability of observing a sample statistic as extreme, assuming the null hypothesis is true. Best fit models are in bold face.

2.4 Discussion

The total seed biomass of grasses, forbs, small shrubs and sheoaks across the southern MLR was over seven times greater in spring than autumn, when the lowest biomass of all seasons was found. High seed biomass in spring was predominately attributed to introduced annual grass seeds. The significant drop in soil seed biomass from late summer to late autumn coincided with autumn breaking rains. As such, low seed biomass in late autumn is likely a result of the germination of the majority of seeds that were present on the soil surface in late summer. This considerable decline in seed resources during autumn may have been exacerbated by ongoing seed consumption by granivores at a time when seed production was low. Most of the variation in seed resources was attributed to seasonal changes in seed abundances of annual weedy grasses and forbs, which dominated the understorey. Perennial seed biomass was scarce in all seasons, though made up the largest portion of seed biomass in late autumn. These findings indicate that the seasonal fluctuations in seed abundances are predominantly caused by annual weedy grasses and forbs. This study supports suggestions that mass-germination of seeds could lead to food scarcity for ground-foraging granivorous birds in the MLR (Ankor 2005; Carpenter 2012; Houdet 2003; Paton *et al.* 2004).

2.4.1 The role of weedy species in seed resource depletion

Seeds from weedy, annual grasses far outnumbered the seeds of any other plant form in the understorey in all sub-regions. This supports findings that invasive weedy grasses have largely outcompeted their native counterparts (Crossman *et al.* 2011; Ford *et al.* 2001; Kriticos *et al.* 2010; Paton *et al.* 2004). Over 80% of seeds counted were from introduced species, while less than 20% were from native species. Approximately 75% of invasive species were annuals, while over 99% of native species were perennials. Similarly, Davies (1997) found that most invasive weed species of temperate native grassy woodlands were annuals and 90% of indigenous grasses were perennials. Prior to European settlement and the invasion of annual weedy species, low woodland vegetation in the southern MLR had an open grassy and herbaceous understorey of native perennial grasses such as *Austrostipa* spp and *Rytidosperma* spp (Geoscience Australia 2017).

Over 70% of seed biomass in late autumn was produced by perennial plants such as *E. nigricans*, *A. behriana*, *Setaria constricta* and *Panicum effusum,* despite their small representation in the understorey. Drooping sheoaks (*A. verticillata*) also produced seeds in open cones during autumn, though their overall contribution to the total seed biomass was small; and reflected their restricted abundance. The only exotic perennials producing seeds during autumn were *Ehrharta calycina* and *Pentaschistis pallida*, the latter of which has seeds smaller than those preferred by *S. guttata* (Read 1987; Schopfer 1989). In contrast, annual plants mass-seeded in spring and summer producing abundant seed resources, but their contribution to the total seed biomass in late autumn was < 4% (< 5% of their spring contribution). This significant decline in seed biomass in autumn coincided with the first heavy rains of the year (Bureau of Meteorology 2019), following which annual grasses in temperate climates are known to mass-germinate (Houdet 2003; Mott 1972; Torsell and McKeon 1976). Similar patterns have been found in tropical systems in northern Australia with annual seeds mass-germinating at the start of the wet season leaving very few seeds available to granivores (Crowley and Garnett 1999; Dostine *et al.* 2001; Mott and Andrew 1985). Thus, the findings of this study are in contrast to Read's (1994) suggestion that weedy species could produce abundant year-round seed resources in areas of the MLR, and rather supports theories by Ankor (2005), Carpenter (2012) and Paton *et al.* (2004) that invasive annuals produce less year-round seed resources for granivores. A system dominated by native perennial grasses is likely to produce more seed during late autumn than one dominated by annuals as, unlike annuals, perennials do not mass-seed in one season (Smith *et al.* 1999). In addition, a mix of summer-growing and winter-growing perennial grasses, with different seeding times (Gibbs 2001; Jessop *et al.* 2006), are likely to yield more consistent, year-round seed.

2.4.2 The effect of seed resource depletion on granivores

Seed biomass in the MLR peaked in spring (4.07 g m^{-2}) and reached an overall low in autumn (0.53 g m^{-2}). A similar study on sympatric finch species in North Carolina, with comparable seasonal patterns to a Mediterranean climate, found finch abundance was strongly correlated with a decline in seed biomass to 0.25 g m^{-2} at the end of winter, suggesting the decline was caused by scarce winter food supply (Pulliam and Enders 1971). In contrast, the seed resources of finches in central NSW which peaked in autumn (1.9 g m^{-2}) and were lowest in winter (0.33 g m^{-2}) were not found to correlate with finch abundance (Schopfer 1989). However, the NSW study estimated seeds in seed heads rather than counting individual seeds, and seed biomass was low year-round compared with North Carolina and the MLR. In addition, the *S. guttata* in NSW fed predominantly on native grasses (Schopfer 1989), whereas *S. guttata* and red-browed finches (*Neochmia temporalis*) in the MLR are known to have diets comprised predominantly of weedy species (Read 1994). This suggests that native seeds were more abundant in central NSW in 1989, and the area is likely to have had more intact native grassland compared with present-day MLR (Bradshaw 2012). Abundant native perennials may have provided important seed resources in central NSW during critical times, such as when young fledge in summer and autumn (Schopfer 1989). Granivores in the MLR do not have access to abundant native perennial seeds, and may be required to move elsewhere in search of seeds, or may be experiencing high mortality during critical times as a result. Chapter 3 investigates whether there is a correlation between finch density and seed biomass in the MLR.

The reduction in seed biomass experienced by MLR granivores between late spring and late autumn was approximately seven-fold. Such abrupt depletion of food resources have been detrimental to other granivorous bird populations (Crowley and Garnett 1999; Garnett and Crowley 1995a; Garnett and Crowley 1995b). For example, golden-shouldered parrots in tropical northern Australia were forced to spend most of their days foraging after soaking rains caused mass-germination of their otherwise abundant annual grass seed resources (Garnett and Crowley 1995a, 1995b). Similarly, Crowley and Garnett (1999) described complete depletion of the seed-bank across an entire region in northern Australia following heavy rains, which severely affected Gouldian finches that are entirely dependent on grass seeds for food (Tidemann 1993). Given annual grasses have replaced native perennial grasses and forbs across much of the temperate agricultural zone in Australia (Davies 1997; Prober *et al.* 2004; Prober and Thiele 2005), their mass-germination could be a considerable cause of food scarcity for granivores. There is evidence of this in Victorian *S. guttata* populations, which declined in the 1950s when native summer-seeding grasses were replaced by exotic spring-seeders (Higgins *et al.* 2006). A similar pattern was found for a population near Canberra (Er *et al.* 1998). Many other granivorous birds such as the peaceful dove (*Geopelia placida*), double-barred finch (*Taeniopygia bichenovii*) and red-rumped parrot (*Psephotus haematonotus*) that are already affected by habitat fragmentation (Barrett *et al.* 1994; Watson *et al.* 2002) may also be limited by late autumn and winter food shortages. The mass-germination of dominant annual grasses as a cause of food scarcity for granivores in other Australian temperate systems, therefore, requires further research.

Although the low seed biomasses recorded for the MLR in late autumn are comparable to shortages of seeds recorded elsewhere (Pulliam and Enders 1971), even these low numbers may not adequately reflect the limited amount of seeds on offer. Despite there being up to 19 different species sampled within quadrats, not all of them may be available to *S. guttata*.

Some seed species may be difficult to extract from their sheaths or from the plant itself, such as *Plantago* spp and *Hydroctyle* spp which are encased in thick, tough exteriors, while others such as *Trifolium* spp may contain toxins that *S. guttata* would avoid (Dong *et al.* 2008). In addition, the soil surface samples may have included seeds that were underneath the surface and therefore not visible to foraging birds. If this is the case, seed biomasses measured here would be an overestimate of seed availability for *S. guttata*, and their food sources may be even more limited than demonstrated. The seed species that *S. guttata* are able to exploit are explored further in the proceeding chapter on diet.

In addition to a decline in seed resources during autumn and winter, the ability of *S. guttata* to access seeds may be inhibited by shorter day lengths. This decreases available foraging hours for birds to meet their energy requirement, while colder night time temperatures may increase caloric and fat requirements (Chaplin 1974). Willson and Harmeson (1973) hypothesised that during the onset of winter, once seed fall finishes and there is no renewal of resources, the effects of seed removal by seed-eaters and colder temperatures may reduce the number of seeds suitable for consumption. Therefore, energy intake during winter must pose a critical problem for granivores. Birds may compensate by selecting seeds with higher calories, as observed in cardinals in Illinois (Willson and Harmeson 1973). Whether *S. guttata* uses this strategy is currently unknown and an area for future research. Furthermore, competition from other granivores such as ants, rodents and other ground foraging birds (e.g. parrots and pigeons) that are all foraging for seed during times of food shortage, may have a considerable impact on already scarce resources (Davidson *et al.* 1980). Thus, the compounding effects of mass-germination of annual seeds, increased competition, shorter foraging hours and higher caloric requirements during winter may cause a resource pinch-point.

2.4.3 Differences between foraged and surrounding habitat

The seasonal patterns of seed production measured in the environment were generally consistent with the patterns observed in the quadrats where *S. guttata* foraged. However, in late winter soil and standing crop seed biomass was higher in forage quadrats than non-forage quadrats. As there were some grass species that began seeding in late winter, this difference may reflect *S. guttata* seeking out patches where plants held seeds in the standing crop. These species may have also provided isolated patches of soil surface seeds that were sparse in the general environment. There were also differences in late summer when standing crop seed biomass was higher in forage quadrats than non-forage quadrats. Seeds were very abundant on the soil surface in late summer while standing crop seeds were scarce as this is when most exotic annuals drop their seeds (Garnier 1992; Groves 1986). However, *S. guttata* still foraged on the standing crop during summer, suggesting they sought out plants still holding seeds. This may be because fresh seeds also provide a source of moisture. Selection for seeds with higher moisture content has been found in other granivores (e.g. Frank 1988; Murray and Dickman 1994). Overall, the patterns of seed production experienced by foraging *S. guttata* reflected the broader seed resources in the environment, except when seeds were sparse or patchily distributed.

2.4.4 Caveats and limitations

While this study has documented a significant depletion of food resources for granivores in the southern MLR, there remain some limitations to this research. Seed abundance and weight (mass) were used as measures of seed availability. To determine mass, the entire seed, including glumes and “wings”, was weighed, although large protective structures around forb seeds (such as *Medicago* spp) were removed. However, the seeds of *Allocasuarina* species vary in fertilisation rate and kernel fill (Clout 1989), as do those of grasses. *Stagonopleura guttata* de-husk seeds with their mandibles prior to digesting the kernel (Read 1987). Thus, while extracting the kernels from each of the >80,000 seeds sampled was not feasible given time constraints, the biomass calculations presented here are likely to be over-estimates of the amount of food (kernels) actually available to granivores. In addition, variations in kernel mass to seed mass ratios between species may have skewed biomass comparisons between seed types. However, given the large differences in seed biomass between seasons, and the scarcity of sheoak biomass contributing to these totals, this issue should not affect broad conclusions regarding total biomasses. Nor are the conclusions regarding seasonal seed species composition affected, as these analyses were calculated using seed abundance (number) rather than biomass.

As the locations of habitat patches within which *S. guttata* foraged could not be pre-determined, seed resources in these quadrats could only be measured after *S. guttata* had removed some seed from them. Therefore, forage quadrats may have contained a higher biomass or different composition than was measured after the birds had fed. However, any such difference should be minimal as there were few differences in seed biomass and composition between forage and non-forage quadrats, and *S. guttata* foraged over an area much larger than the quadrats during a single foraging bout. In addition, as the late spring season could not be sampled in the second year of study, comparisons of spring seed resources across the two years was not possible. However, as there was greater variation in seed biomass between seasons than there was within seasons across years, and similar seasonal trends occurred in both years, it is likely that spring resources were similarly abundant in the second year of the study. Lastly, as *S. guttata* were scarce in the environment and difficult to locate, it was not possible to obtain foraging data for all six sub-regions in all four seasons. While the results presented here are from three to five sub-regions only, the same analyses were also applied to the remaining sub-regions with fewer seasons. The seasonal trends in seed biomass and species composition were consistent across the broader spatial scale. These results should, therefore, be broadly applicable to the full extent of the southern MLR.

Comparisons between forage and non-forage quadrats determined whether the broader patterns of seed resources available in the environment were also applicable to patches in which *S. guttata* foraged. The scale at which these resources were measured was too large to capture any selection between seed species within a foraging patch. However, in many instances *S. guttata* were observed taking seeds from open cones in *A. verticillata* trees, clearly selecting these seeds for the duration of a foraging bout. Therefore, the following chapter investigates the relative importance of certain food species, particularly *A. verticillata,* for *S. guttata,* to better understand how the reduction of seeds in late autumn affects their diet.

2.4.5 Summary

This study has identified significant seasonal variability in the availability of seeds for granivores in the southern MLR. A rapid reduction of seeds in autumn appears to be driven by breaking rains that cause the mass-germination of weedy annual grass species. This relative food scarcity is likely to be affecting foraging opportunities for *S. guttata,* a species experiencing an ongoing decline (Paton *et al.* 1994; DC Paton 2017 unpub.). Given the dominance of invasive annual grasses across much of temperate agricultural Australia, this study also raises concerns that similar seasonal reductions in seed availability are occurring elsewhere across these productive zones, where many species are already at risk due to heavy habitat fragmentation (Prober and Thiele 2005). Future research should investigate late autumn and winter seed availability for other granivores elsewhere across this zone. Overall, this research has identified a resource pinch-point that is a consequence of the displacement of perennial native grasses by introduced annual grasses. These findings have implications for the survival of granivorous MLR birds, particularly as winter approaches.

Statement of authorship

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Name of Principal Author	Grace Hodder		
Contribution to the paper	Conceptualised and designed the experiment, collected and analysed data, interpreted the results and wrote the manuscript.		
Percentage contribution	85%		
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Signature		Date	16/12/2019

Chapter 3. Composition and diversity of the diet of diamond firetails (*Stagonopleura guttata*) reflects seasonal resource availability

Photo by Peter Waanders 2016

3.1 Introduction

Food availability is often cited as the most important factor affecting animal abundances (White 1978; White 2008), particularly mobile endotherms such as birds (Law 1994). Seasonal and unpredictable fluctuations in food resources can have significant effects on wild avian populations (Ford *et al.* 1993; Franklin *et al.* 1989; Leck 1972; Recher 1999). When key resources are periodically unavailable, fundamental population processes such as breeding success, rate and length of breeding attempts, number of eggs and juveniles, level of parental care, dispersal and body condition, can be negatively impacted (Kitaysky *et al.* 1999; Martínez-Abraín *et al.* 2012; Newton 1980; Strong and Sherry 2000; Yom-Tov 1974; Zanette *et al.* 2000). Therefore, declines in food resources can have serious consequences, particularly where a population is already vulnerable to other pressures such as habitat fragmentation and isolation (Rockwell *et al.* 2012). Food shortages have led to declines in bird species (Ford 2011; Watson 2011) and even species extinctions. For example, the passenger pigeon is thought to have gone extinct due to annual and geographic variations of seed production caused by habitat alteration (Bucher 1992).

Food abundance is influenced by the combination of species producing food, and in many systems, this changes seasonally (Dostine and Franklin 2002; Feinsinger and Swarm 1982; Vickery *et al.* 2001). Many avian species have adapted to natural fluctuations in food availability by migrating to follow seasonal resources (Levey and Stiles 1992; Studds and Marra 2011), switching to alternate food sources (Garnett and Crowley 1994; Todd *et al.* 2003) or halting reproduction until food is more abundant (Leck 1972; Martin 1987). However, when a system is altered by land clearance and habitat degradation, natural cycles of food production can be disrupted and cause more extreme environmental fluctuations (DiTomaso 2000; Skórka *et al.* 2010), against which bird populations can be poorly adapted (Benton *et al.* 2002; Wilson *et al.* 1999). For example, some Australian honeyeaters are food-limited due to fluctuations in nectar resources caused by seasonal compositional changes (McFarland 1986) which is compounded by land clearance limiting alternative resources in surrounding habitat (Collins *et al.* 1984; Paton 1980).

Fluctuations in resource composition and abundance can also affect dietary diversity (Feinsinger and Swarm 1982; Levey 1988). The original optimal foraging theory predicts that when resources are abundant, optimal foragers focus on favoured prey, resulting in a narrower diet breadth (MacArthur and Pianka 1966). More recently, the opposite has been found for birds whose diets track local resources, with wider diet breadths reflecting times of relative abundance (Renton 2001; Sánchez and Blendinger 2014; Schluter 1982). As such, granivores are particularly sensitive to resource fluctuations, as their diets often mirror the proportions of available resources (Camín *et al.* 2015; Renton 2001; Sánchez and Blendinger 2014). This has been observed in horned larks (*Eremophila alpestris*), whose diets change seasonally according to the proportions of available seeds and insects, with low diet diversity in association with low resource diversity (Rotenberry 1980).

Food resources for diamond firetails, *Stagonopleura guttata*, have changed significantly since European settlement in the Mount Lofty Ranges (MLR). Many native food species have become less abundant or lost from the region altogether (Read 1994), and invasive annual grasses now dominate much of the understorey (Chapter 2). Due to mass-seeding of annuals in spring, their seeds are abundant on the soil surface through summer, but they mass germinate following the first heavy rains of the year (usually in autumn) (Chapter 2). This leaves few seeds of annual or perennial grasses available for foraging birds in winter. In times of food scarcity, *S. guttata* may exhibit a switch to another food type. Ankor (2005) found the seeds of a native perennial grass, *Setaria constricta*, and drooping sheoak *Allocasuarina verticillata* dominated the diet of *S. guttata* in August, inferring these were critical foods during times when annual grass seeds were scarce. In contrast, Read (1994) found the diet of *S. guttata* to be dominated by seeds from introduced annual grasses in summer and autumn and suggested annuals may support higher local populations than native vegetation due to their prolific seeding. Thus, the impact of such large seasonal changes in food species composition and abundance on *S. guttata* remain unclear.

To determine whether S. *guttata* are experiencing periodic food shortages in the MLR or are affected by seasonal compositional changes to these resources, a better understanding of their seasonal diets is required. If *S. guttata* forage generally from the range of available food resources, they are likely to be experiencing the same seasonal fluctuations as these resources. In contrast, *S. guttata* may select for certain seed types regardless of their availability. Specifically, this study aims to determine: i) the key plant taxa comprising the seasonal diets of *S. guttata*; ii) if the diet of *S. guttata* tracks the seasonal composition and abundances of available resources; and iii) if the diversity of plant species that *S. guttata* are harvesting reflects the diversity of available resources within seasons. The findings will determine the susceptibility of *S. guttata* to seasonal compositional changes and shortages of food species.

3.2 Methods

3.2.1 Study area and sampling sites

This study was conducted across the range of *S. guttata* in the southern MLR over a two-year period, from late winter 2014 to late winter 2016. Sampling was conducted across six sub-regions (Milang, Hartley, Monarto, Rockleigh, Springton and Karinya) which supported small populations of *S. guttata*. These sub-regions lie along a longitudinal gradient on the eastern scarp of the southern MLR, approximately 12–24 km apart. Sampling occurred at three sites within each sub-region (*n* = 18 sampling sites). Sites comprised small patches of remnant or revegetated open eucalypt woodland with stands of *A. verticillata* and *Callitris gracilis* and predominantly weedy understoreys. The sites were located < 8 km from one another and set in an agricultural matrix (see Figure 1.2 in the *General Introduction* for site details).

3.2.2 Sampling methodology

The diets of *S. guttata* were sampled from winter 2014 to winter 2015 in the first year and spring 2015 to winter 2016 in the second year of the study. To allow a comprehensive assessment of the composition of *S. guttata* diets, their foraging behaviour was observed to identify the plant species that they were feeding on *in situ*. In addition, seeds were sampled from the crops of captured *S. guttata* to determine what species they were feeding on. A crop is a sac-like extension of the oesophagus allowing birds to eat quickly and store their seeds before being digested in the stomach (Figure 3.1). Foraging observations were undertaken in October–November, February–March, May–June and August–September. In the second year, unforeseen circumstances prevented fieldwork from occurring during October–November. Crop sampling was undertaken seasonally in both years.

Figure 3-1 The crop of a *S. guttata* individual captured in a mist-net in the southern MLR

3.2.2.1. Observations on foraging birds

Stagonopleura guttata individuals were observed for 6–12 hours continuously per day, and their behaviour recorded. At each site, one day of tracking was undertaken per season. Individuals were located by listening for their calls and making visual observations with binoculars. The plant species birds foraged on were conclusively identified when the bird could be seen taking the seed directly off the standing crop (seeds held on plants), from a cone or occasionally when the seed could be identified as it was consumed. A total of 680 observations of foraging *S. guttata* individuals were recorded (summer $n = 135$; autumn $n = 129$; winter $n = 248$; spring $n = 167$). Food species were able to be identified during 95 of these observations (summer $n = 31$; autumn $n = 3$; winter $n = 27$; spring $n = 24$). There were no seasonal biases in foraging observations, as birds were observed foraging on standing crops year-round when seeds were prevalent. However, if some species were only consumed once their seeds had fallen from the plant they may have been missed during foraging observations.

3.2.2.2. Crop sampling

To account for seeds that may have been missed during foraging observations, crop sampling was conducted. To sample *S. guttata* crops, birds were trapped by erecting 6–12 mist-nets at each site during each season. Unsuitable weather conditions during winter and the risk of disturbing breeding birds in spring prevented equal seasonal trapping efforts (number of trapping days: summer n = 15, autumn $n = 28$, winter $n = 7$, spring $n = 4$). Mist nets were placed in areas where *S. guttata* were known to be active. Nets were erected prior to dawn and monitored every 20–30 minutes until dusk, or earlier if weather conditions became unsuitable (e.g. too windy, rainy or hot). The positioning of mist nets around water sources enabled higher catch rates of *S. guttata* during summer and autumn when they visited water points frequently ($n = 79$, $n = 237$), compared to winter and spring ($n = 38$, $n = 36$ respectively).

Once an *S. guttata* was caught, its crop was examined. The thin, transparent wall of crops allowed their contents to be viewed from the outside by blowing apart the feather covering (Figure 3.1). Crops containing seeds were photographed and their dimensions (length, width and height) were measured to the nearest mm using a ruler. Empty crops were also recorded. Where a crop was full and bulging (at least 1 cm x 1 cm in dimension), attempts were made to extract seeds (as explained below). A total of 115 photographs of crops were taken (summer *n* = 21, autumn *n* = 89, winter *n* = 5, spring *n* = 0). In total, crop dimensions of 291 trapped *S. guttata* were measured.

Seeds were extracted from crops using the Tube Insertion Method (TIM), a non-destructive method of crop sampling developed for zebra finches (*Taeniopygia guttata*) (Zann and Straw (1983) and modified for use on firetail finches, *Stagonopleura* spp (Read 1987, 1994). The TIM involves the insertion of a soft, flexible plastic tube into the bird's throat, to collect seeds from the crop. Tubing (3.5 mm in diameter) was guided into the crop by pushing on the membranous crop wall from the outside, and seeds were gently pushed into the tubing and extracted. The section of tubing containing the seed(s) was then placed in a sealed envelope. The TIM method provides minimal disturbance to birds and has no direct effects on mortality (Read 1987; Zann and Straw 1983). Seeds were successfully extracted from *S. guttata* crops using the TIM during ~ 40% of attempts in this study. Eighty seeds in total were obtained from 24 *S. guttata* individuals during the study period. Between one and eight seeds were extracted from each successfully sampled crop.

3.2.2.3. Identification of food species

Initially, seeds from crop samples were identified by comparing their dimensions, colour, shape and other distinctive characteristics with those of seeds collected from field sites. However, only a small percentage of samples could be identified in this manner as the seeds were de-husked and sometimes fragmented. Thus, identification of plant fragments using a standardised DNA sequence (DNA barcoding) was used to identify the seed fragments. This method has been successfully implemented in many diet studies (e.g. Deagle *et al.* 2007; Hofreiter *et al.* 2017; Valentini *et al.* 2009;). Samples were prepared for DNA analysis by separating the seeds in each crop sample based on their size, shape and colour. Larger seeds were placed in individual test tubes while smaller fragments were grouped in samples of two or three to maximise the amount of genetic material available in each test tube. This resulted in a total of 66 samples (summer *n* = 13; autumn *n* = 29; winter *n* = 3; spring *n* = 21). Samples were sent to the Australian Genome Research Facility (AGRF) for DNA extraction and quantification using Polymerase Chain Reaction (PCR) and Sanger sequencing.

Genomic DNA was extracted from silica dried seed material using the Machery-Nagel NucleoSpin Plant II Extraction Kit, mini tubes and PL2 lysis buffer (Macherey-Nagel 2014). To increase the concentration of genomic DNA, samples were purified and eluted once in

30 µL of Buffer PE. DNA was then quantified using a Quantifluor ds DNA System (Geneworks). Standard AGRF protocols were used to amplify the primary barcoding loci *trn*L (chloroplast DNA) and ITS2 (nuclear ribosomal DNA) for each sample (124 PCRs; see Appendix H for primer sequences). PCR reactions were run on a Veriti Thermal Cycler (Applied Biosystematics; Appendix H). Unpurified PCR products (PD+) were sent to the AGRF sequencing team for purification and high throughput Sanger sequencing using Applied Biosystematics 3730 and 3730 *xl* capillary sequencers (McGrath 2015). AGRF uses Big Dye Terminator Chemistry version 3.1 (Applied Biosystems) under standardised cycling PCR conditions. Sequence data were provided as a Basic Local Alignment Search Tool (BLAST) file (Altschul *et al.* 1990). Consensus sequences were produced using De Novo Assembly in Geneious version 10.0 (https://www.geneious.com). The assembled contigs were queried using BLAST to match regions of similarity within sequences from the nucleotide collection (nr/nt; DNA) databases held at the National Centre for Biotechnology Information. Species matches were sorted by grade, a measure of genetic similarity between the sample DNA and the database match. The top five matches with the highest grades for each *trn*L and ITS2 sequence alignments were selected. Any species that were known not to occur in the MLR were removed. The remaining species are presented in Appendix I with their relative grade values. The validity of identifications made from DNA barcoding was confirmed by comparing top BLAST matches with samples identified using morphometrics alone. All initial morphometric identifications were confirmed by DNA barcoding identification.

3.2.2.4. Crop photograph analysis

Seeds captured in crop photographs were categorised according to shape, size and colour. The seeds that were successfully identified from crop samples and de-husked seeds from known species in the field were used to determine the species present in the photos based on their morphometric characteristics. However, some species had similar morphometric characteristics and species identifications were not always possible. Thus, to determine the most likely occurring species, they were grouped according to their morphometric characteristics (groups were: *Aristida* spp/*Austrostipa* spp; *Arctotheca* spp/*Galenia* spp/*Stellaria media*; *Panicum* spp/*Briza* spp; *Ehrharta* spp; *Avena* spp; *Poa* spp/*Eragrostis* spp and *Rytidosperma* spp).

3.2.2.5. Resource selection and availability

Resource selection was explored by comparing the seeds consumed by *S. guttata* (resource use) with available seed resources (resource availability). Consumed seeds comprised of the seeds identified during foraging observations and in crop samples. Available seeds comprised of species sampled on the soil surface and in the standing crop. Samples of available resources were taken during the foraging observation sampling periods (described above). Plots were sampled within study sites at locations where *S. guttata* were observed foraging. Between 10 and 30 independent foraging points were sampled in each site during each season, dependent on *S. guttata* foraging at sites on field days. Seeds were sampled from the soil surface and from the standing crop within each point and identified and counted in the laboratory. See Chapter 2 for a detailed account of this methodology.

3.2.3 Statistical analyses

3.2.3.1. Seasonal diet and resource composition

The composition of *S. guttata* diets across four seasons was assessed by combining species consumed during foraging observations with species identified in *S. guttata* crops. Seasons were assigned based on the month in which observations and samples were collected: spring (September–November), summer (December–February), autumn (March–May) and winter (June–August). Species that were identifiable in crops were assigned weightings according to their proportion of total crop contents, determined from photographs or crop samples (1 seed or ≤ 25% of crop = 0.25, 2–4 seeds or 26–49% of crop = 0.5, ≥ 5 seeds or ≥ 50% of total crop = 1). Species that were identified during foraging observations were given a weighting of 1 for each independent observation during which it was consumed. Food species were displayed as a proportion of the total number of independent observations and the total number of combined crop weightings per season (Figure 3.2).

3.2.3.2. Seed intake during times of seed scarcity

To determine whether *S. guttata* individuals harvested fewer seeds during times of low seed availability, the proportion of crops with and without seeds was compared between periods of low (May–September) and relatively abundant (October–April) seed availability (Chapter 2). Fisher's exact tests were performed to compare crop proportions between periods (due to small sample sizes) in GraphPad Prism version 7.0 (La Jolla California USA). The Monarto study area was excluded from analysis as individuals had access to artificially supplemented seed and were not representative of natural seed consumption (see Chapter 5).

Therefore, the dimensions from 235 crops were analysed (May–September *n* = 7 crops, October–April *n* = 228 crops). Due to small sample sizes, data were pooled across years, sites and sub-regions.

To compare seed consumption with seed availability, the monthly seed biomass of each species sampled in foraging plots was calculated by multiplying seed abundances by the average seed mass of that species. Seed masses were obtained by calculating the average mass of 100 seeds of each species using a Mettler AE 200 Analytical Balance. The total seed biomass and average seed mass within foraging plots was then calculated and pooled across sites, sub-regions and years (see Chapter 2).

3.2.3.3. Selection ratios of seed types

As *S. guttata* eat a wide variety of grass species rather than focusing on one or two (Read 1994; Schopfer 1989) the proportion of seed resources in their diet was compared with available resources at a broad plant functional grouping level. Seed species were categorised by origin and plant form (native grass, native forb, weed grass, weed forb, sedge or sheoak). In addition, seeds were grouped into six size categories: very small (≤ 0.00015 g), small (0.00016–0.0003 g), medium (0.00031–0.00069 g), large (0.0007–0.0013 g), very large (0.0015–0.004 g), and extra-large (≥ 0.0041 g) according to their average seed mass. The number of seeds of each species (*n* = 122) sampled in forage plots (*n* = 553) informed resource availability, while the number of seeds of each species (*n* = 17) sampled in crops (*n* = 24) and foraging observations (*n* = 95) informed resource use. Forage plots were used as they were a more immediate representation of the seeds available to foraging *S. guttata* than were non-forage plots. Any prior selection of foraging habitat was not reflected at the plot level as there were only minor differences in species abundance and composition between the two plot types (see Section 2.3.1.2 in Chapter 2). For resource availability, the sum of the number of seeds in each category were calculated within each sub-region and season. Then, the median of the sub-region totals was calculated for each season. Medians were used rather than sum totals to account for the large amount of variation between sub-regions and seasons. The median values for resource availability were: sheoak *n* = 184, native grass *n* = 3,768.5, native forb *n* = 1,209, weed grass *n* = 11,476, weed forb *n* = 10,410, and very small *n* = 132, small *n* = 516, medium *n* = 389, large *n* = 81, very large *n* = 152.75 and extra-large *n* = 50.5. Sample sizes for resource use were: sheoak *n* = 22, native grass *n* = 41, native forb *n* = 9, weed grass *n* = 43, weed forb *n* = 9, and very small *n* = 8, small *n* = 28, medium *n* = 23, large *n* = 37, very large *n* = 13 and extra-large *n* = 15. There were no records of *S. guttata* feeding on seeds from any sedge species.

Diet proportions were calculated as the number of foraging observations during which *S. guttata* ate that seed type or size and the number of sampled crops in which that seed type or size was found, divided by the total number of crops sampled and independent foraging observations. For the purpose of analyses, available resources were assigned to the season in which they were sampled to reflect the categories in which resource use samples were placed (described above). The relationship between seed size and seed type was also assessed by plotting the total number of seeds from each plant form category within each seed size category across the 24-month study.

To assess whether *S. guttata* selected for certain seed types or sizes, selection ratios (wi = used/available) were calculated using the Manly selectivity measure (Manly *et al.* 2004). This statistic compared the proportions of used and available resources under the Design I framework, where individuals are not identified and resources are measured at the population level. Computation of selection ratios was performed using the wides I function from the adehabitatHS package in R version 3.3.1 (R Core Team 2016). The wides I function tests resource selection with the Khi2 of Pearson and log-likelihood Khi2 (Calenge 2006). To examine the selection ratios of important resources further, the seasonal proportions of the total number of seeds sampled were plotted against the seasonal proportions of the diet of *S. guttata* for the plant type categories of native grass, weedy grass and sheoak. These three categories were chosen due to their significant selection ratios (see section 3.3—Results).

3.2.3.4. Diversity of diet and available resources

To assess the diversity of the seasonal diet of *S. guttata*, two diversity indices were calculated: the Shannon-Weaver Index (SW) and Gini–Simpson Diversity Index (GS). The SW index is a measure of the number of individuals and species, where high values represent many species with few individuals, while the GS index is a measure of the proportion of species relative to total number of species, giving greater weighting to dominant species. Seed species sampled from crops (n = 95) and those identified during foraging observations (n = 95) were combined for these calculations, and sub-regions and years were pooled. In order to capture the full diversity of seeds sampled, the number of seeds of each species extracted from crops was used. Data from crop photographs could not be included as the number of different species present in photographs was difficult to distinguish. Graphs were produced using ggplot2 (Wickham 2009). Diversity indices were calculated using the diversity function from the vegan package (Oksanen *et al.* 2016) in R version 3.3.1 (R Core Team 2016).

The diversity of available seeding species was measured under the Maximum Entropy theory of ecology using species richness and abundances. Entropy is defined as the amount of uncertainty calculated from the frequency distribution of a community (Jost 2006; Marcon *et al.* 2014). Analyses were performed using the entropart package (Marcon and Hérault 2015). Seed species counts in forage plots were pooled across study sites and years for each sub-region. Sub-regions were weighted according to the number of plots sampled. Standing crop and soil surface data were analysed separately. Each season was partitioned into its alpha and beta components, with an estimation-bias correction, using the DivPart function. Alpha diversity is defined as the diversity within local assemblages, i.e. the diversity of individuals within a sub-region, while beta diversity is the diversity between local assemblages, i.e. the diversity of the sub-regions. These measures were plotted as the Gamma diversity: the diversity of the season itself, encompassing both alpha and beta diversities (Marcon and Herault 2015). Graphs of sub-region entropies were produced using ggplot2 (Wickham 2009).

3.3 Results

3.3.1 Seasonal diet composition

Stagonopleura guttata fed on a wide range of species during this study (Appendix E). Their diet consisted predominantly of grass seeds, along with some forb and sheoak seeds. Native and non-native perennial grasses were key foods year-round (together comprising 37% of their summer diet, up to 67% in autumn, 28% in winter and 56% in spring). Introduced annual grasses were important during spring (14%) and summer (22%) (Figure 3.2). Seeds from introduced and weedy forbs made up a small percentage of diets in summer (5.3%), autumn (9.2%) and winter (1.8%), while some native shrubs and forbs were important during spring (29%). Seeds from sheoaks formed a large part of diets during winter (46%; Figure 3.2) when seed biomass was lowest (Figure 3.3a). An account of the foraging observations separated by site and year is presented in Appendix J and the crop sample species separated by site and year can be found in Appendix K.

During summer 2015 and 2016, *S. guttata* ate a variety of grass and forb seeds, with small amounts of sheoak seeds (Figure 3.2). Native wallaby grasses (*Rytidosperma* spp) and spear-grasses (*Austrostipa* spp) were common food species. Non-native grasses such as *Avena* spp and *Ehrharta* spp were almost equally as common. Their summer diet included small weedy forbs such as *Galenia* spp and *Dysphania pumilio*. During autumn 2015, *S. guttata* predominantly ate the seeds of a perennial, introduced grass *Ehrharta calycina* (up to ~50%; Figure 3.2). A mix of other grass and forb seeds (such as *Poa* sp. and *Arctotheca* sp.) also featured in their autumn diet, being almost as prominent as native perennial grasses (such as *Aristida* spp and *Enneapogon nigricans*). The seeds of sheoak *Allocasuarina verticillata* comprised a small part of the autumn diet (6.2%). In winter 2014, 2015 and 2016, the seeds from *A. verticillata* were a key resource, comprising almost half of the winter intake (46%; Figure 3.2). The intake of sheoak seeds was supplemented with seeds from native grasses (including *Austrostipa* spp and *A. behriana*) and native forbs (e.g. *Dysphania pumilio*). Seeds from weedy annual grasses such as *Avena sp.* and *Briza maxima* made up a small component of the winter diet (10.5%). These weedy grass seeds were likely to have been old, un-germinated seeds from the previous summer based on their natural seeding times. During spring 2014 and 2015, *S. guttata* predominantly ate seeds from native, perennial grasses such as *Rytidosperma* spp, *Austrostipa* spp and *A. behriana* (48%; Figure 3.2). Native forb *D. pumilio* comprised a moderate percentage of the spring diet (26%). Weedy grasses, such as *Avena* spp and *Ehrharta calycina*, made up a smaller component (22%).

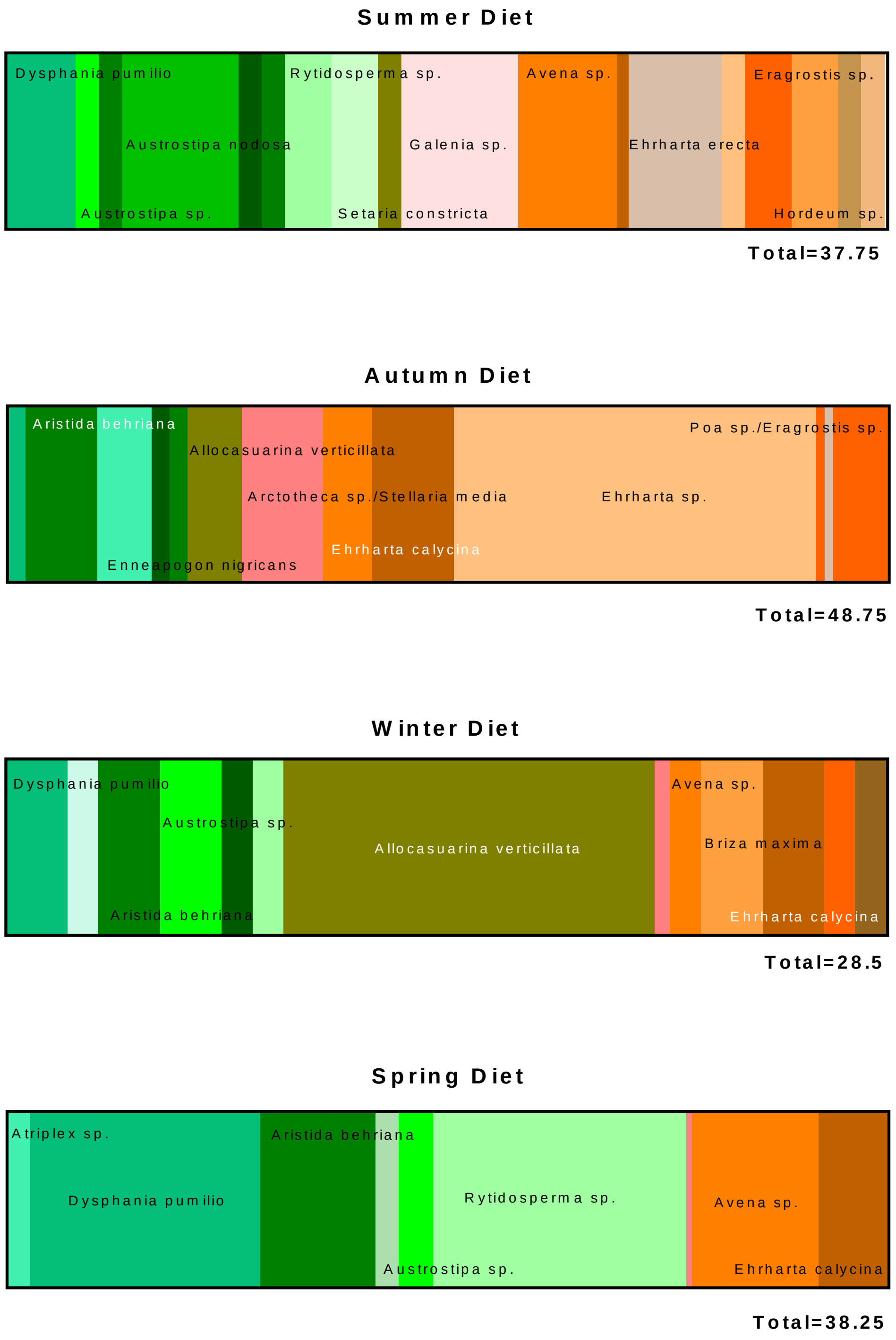

Figure 3-2 Seasonal profiles of the proportion of food species in *S. guttata* diets collected in summer (2015 & 2016); autumn (2015); winter (2014, 2015 & 2016) and spring (2014 & 2015). Species are colour-coded by plant origin (native = greens, non-native = reds/oranges). From left to right, species are ordered by plant form: native forbs, native grasses, native sheoaks, weedy forbs, weedy grasses and weedy sheoaks. Sample sizes (weightings) are displayed underneath each profile and prominent species are labelled.

3.3.2 Seed intake during times of scarcity

The average seed biomass in foraging plots was highest during spring and summer, peaking in October, with an abundance of seeds in standing crops and on the soil surface (total 2.23 g plot^{-1} Figure 3.3a). Seed biomass on the soil surface remained high throughout summer but began to decrease steadily from March onwards. From May through to September, total seed biomass was low, the lowest period being August when the average seed biomass per plot was 0.2 grams.

During May–September, seven *S. guttata* crops were sampled as birds were scarce and hence capture rates were low. In contrast, a total of 228 crops were sampled from *S. guttata* during October–April, when birds were more abundant at study sites. The majority of birds sampled during October–April had seeds in their crops (Figure 3.3b), while most birds sampled during May–September had empty crops. Fisher's exact test showed no significant difference in the proportions of empty crops compared to crops containing seeds between these two time periods ($P = 0.1$; Figure 3.3b).

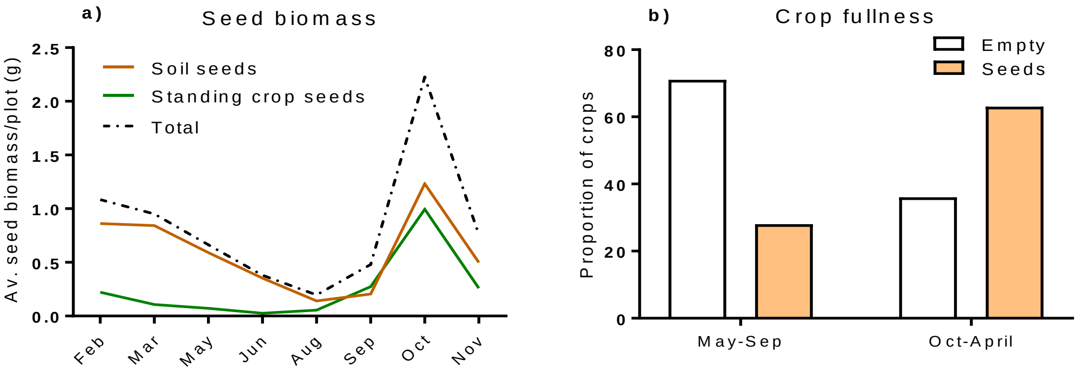

Figure 3-3 (a) Average seed biomass of seeding species on the soil and in standing crops and total per quadrat where *S. guttata* foraged. (b) The proportion of *S. guttata* crops containing seeds versus empty crops for the months May–September c.f. October–April.

3.3.3 Selection ratios of seed types

Stagonopleura guttata selected certain seed types in greater proportions relative to their availability (Figure 3.4a: $P < 0.001$, $\chi^2 = 174.1$, df = 4). Native grasses were selected in higher proportions relative to their availability ($P < 0.001$). Sheoak seeds from *A. verticillata* and *Casuarina glauca* were also selected for in higher proportions relative to their availability ($P < 0.001$). Weedy forbs, on the other hand, were eaten in lower proportions relative to their availability ($P < 0.001$). There were no differences between used and available proportions of native forbs ($P > 0.05$). The availability of seeds from native forbs, however, was low. Introduced and weedy grasses were relatively abundant and eaten in proportion to their availability ($P > 0.05$). Sedges were generally low in availability and were not recorded as a food species, so were excluded from analyses.

Seed size influenced *S. guttata* food selection ($P < 0.001$, $\chi^2 = 52.9$, df = 5; Figure 3.4b). Extra large seeds (average seed size ≥ 0.0041 g) were most strongly selected for (wi = 4.7), followed by very large seeds (average seed size 0.0015–0.004 g, wi = 3.8) and large seeds (average seed size 0.0007–0.0013 g, wi = 1.8), Very small, small and medium seeds (≤ 0.00069 g) were selected against (Figure 3.4b).

Weedy grasses dominated the understorey and were the most common seed type in almost all size categories (Appendix L). Weedy grass seeds were predominantly large, very large or extra large. Native grass seeds were predominantly medium or very large. Sheoak seeds were either large or very large. Most weedy forbs were large, while native forbs dominated the very small category.

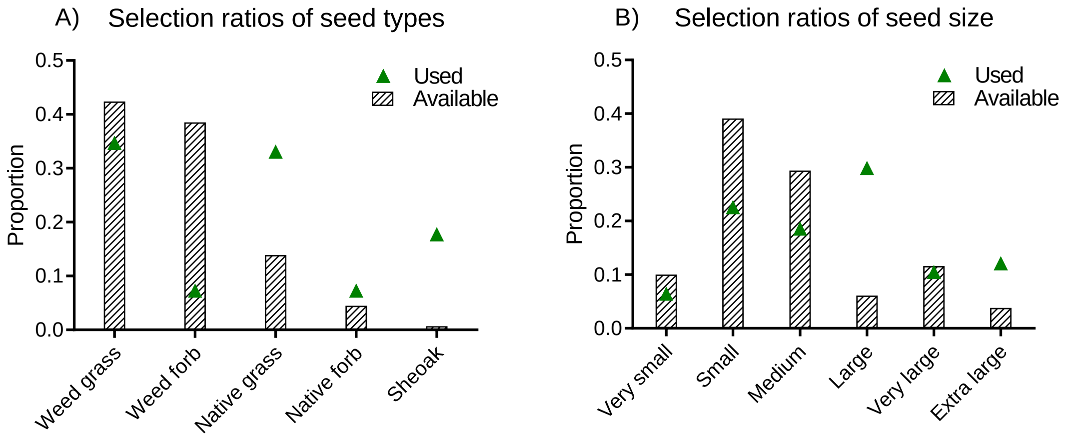

Figure 3-4 Selection ratios of seeds consumed by *S. guttata* (used) compared to available resources across 24 months in 2014–2016 for (a) plant types and (b) seed sizes.

Stagonopleura guttata consumed native and weedy grasses as well as sheoak seeds in their overall diet. Native grasses made up a large proportion of the available resources (0.45) during summer and *S. guttata* ate their seeds in similar proportions (0.35; Figure 3.5a). During autumn, the availability of native grasses dropped (0.07), as did their prevalence in *S. guttata* diets (0.05; Figure 3.5a). The availability of native grasses remained relatively low throughout winter (0.12) and spring (0.08), though *S. guttata* ate their seeds in larger proportions relative to their availability during these seasons (0.22, 0.59 respectively; Figure 3.5a). Weed grasses made up the largest proportion of available seeds in all seasons other than summer (summer = 0.34; autumn = 0.76; winter = 0.67; spring = 0.69) when native grasses were available in higher proportions (Figure 3.5b). The relative intake of weedy grasses versus native grasses by *S. guttata* complemented one another seasonally, with weedy grasses consumed in larger proportions where native grasses were consumed in smaller proportions (i.e. in autumn) (Figure 3.5b). However, weedy grass seeds were consumed in smaller proportions relative to their availability in all seasons except for summer (summer = 0.78; autumn = 0.65; winter = 0.11; spring = 0.31; Figure 3.5b). Notably, the consumption of weedy grass seeds dropped in winter, while the consumption of native grass seeds increased (Figure 3.5b). Sheoak seeds were in very low abundances year-round, relative to grass seeds (summer = 0.02; autumn = 0.01; winter = 0.03; spring = 0.0006). However, *S. guttata* relied on sheoak seeds during winter, when native grass seed availability was low, consuming these seeds in much greater proportions relative to their low availability (0.52; Figure 3.5c).

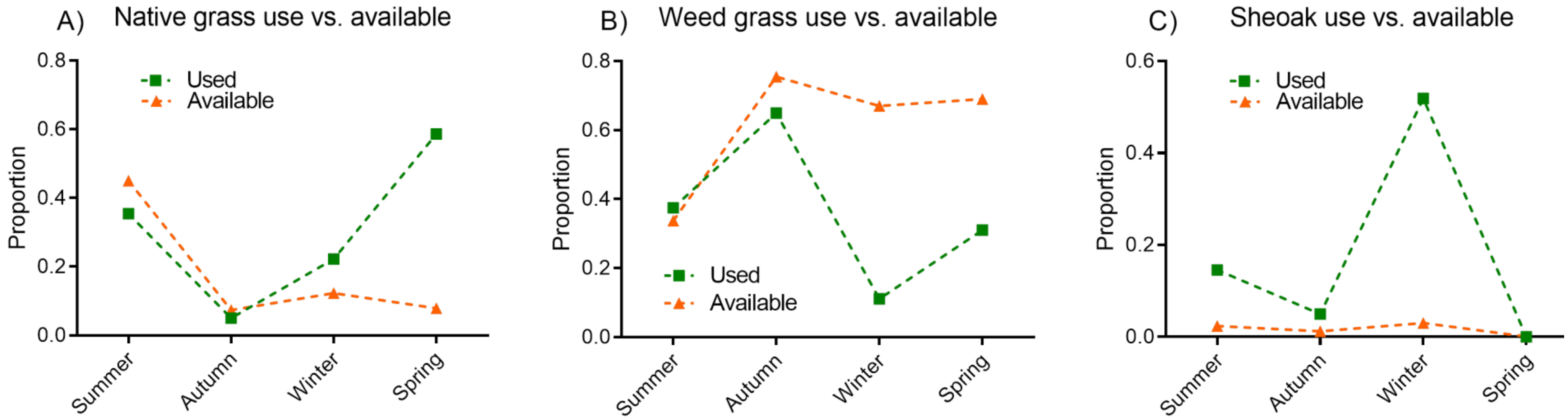

Figure 3-5 Proportion of all seeds sampled from foraging plots over 24 months in 2014–2016 at sites in the eastern MLR that came from (a) native grasses, (b) weedy grasses and (c) sheoaks (Available) c.f. proportion of occasions *S. guttata* were observed foraging on these plant types and the proportion of *S. guttata* crops in which these plant types were found (Used), in each season. Dashed lines represent trend lines between seasons.

3.3.4 Diversity of diet and available resources

The diversity of *S. guttata* diet was highest in summer (species richness = 18, SW index = 2.57, GS index = 0.90; Figure 3.6). Diets were also diverse during autumn (species richness = 15, SW = 2.36, GS = 0.87; Figure 3.6), though less so compared to summer. Diet diversity was lower in spring (richness = 10, GS = 0.86) compared to summer or autumn. Spring was the season of lowest diversity according to the SW index (2.08), though low sample sizes could account for this. According to the GS index (0.81), winter was the season of lowest diet diversity, although a greater range of species were eaten during winter compared with spring (richness = 13, SW = 2.13; Figure 3.6).

The standing crop and soil seedbanks were very species rich, with many different seeding species available in most seasons, and few species that were super-abundant above others (Figure 3.7). Gamma diversity, which accounts for the diversity of seeding species within and among sub-regions, was highest during late summer for soil surface seeds (richness = 61.0, SW = 25.93, GS = 19.23) and standing crop seeds (richness = 23.45, SW = 16.5, GS = 16.5; Figure 3.7). The standing crop seedbank was also relatively diverse during late spring (richness = 50.0, SW = 17.77, GS = 9.98), with late autumn being the third most diverse period (richness = 31.0, SW = 11.18, GS = 7.37) and late winter being the period of lowest diversity (richness = 27.0, SW = 5.69, GS = 3.98). The diversity of soil surface seeds was similar for late spring (richness = 44.0, SW = 13.57, GS = 8.60), late autumn (richness = 39.0, SW = 12.54, GS = 7.92) and late winter (richness = 41.0, SW = 14.23, GS = 9.65), but far less diverse than late summer.

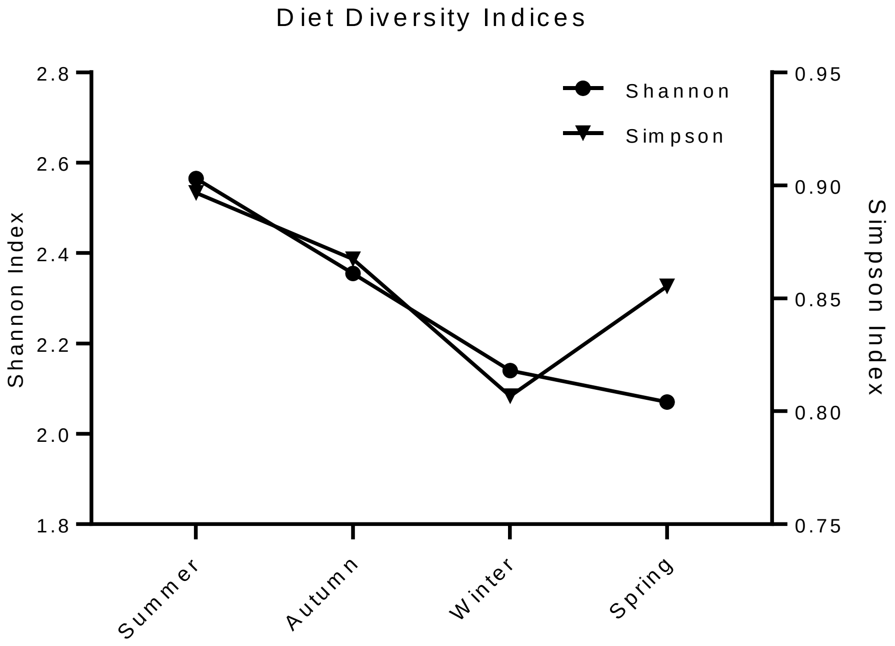

Figure 3-6 Diversity indices (Gini–Simpson and Shannon–Weaver) of *S. guttata* food species. Food species was the sum of seeds extracted from crops and species identified during foraging observations combined. Diversity increases with increasing index values (y-axes).

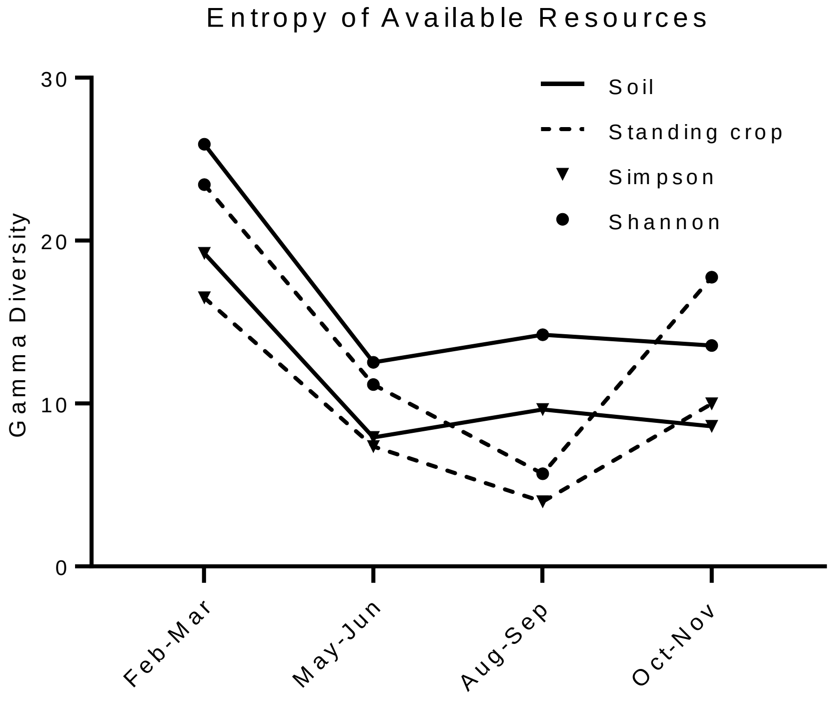

Figure 3-7 Entropy of local area assemblages and individuals within local assemblages comprising soil surface seeds and standing crop seeds for Shannon's diversity and Simpson's diversity indices. Diversity increases with increasing index values (y-axis).

3.4 Discussion

This study examined the seed species comprising the diet of *S. guttata* in the southern MLR to assess how seasonal fluctuations in food resources affect *S. guttata*. The proportions of different seed types, abundance and diversity of seasonal diets were compared with local, seasonal seed assemblages. *Stagonopleura guttata* ate a wide variety of grass, forb and sheoak seeds, with grass seeds being the most commonly consumed food in all seasons. Grass seeds (both native and weedy) were also the most dominant food item consumed by *S. guttata* in other studies (Ankor 2005; Read 1994; Schopfer 1989). Plant types with the largest seeds were selected for; these were mostly grasses and sheoaks. Native grasses were preferentially selected, particularly in times of abundance, while weedy grasses were less likely to be selected. However, the relative proportions in which these two plant types were consumed was seasonally complementary. The diversity of *S. guttata* diets followed the diversity of available resources. During winter, when overall seed biomass was low, *S. guttata* crops were predominantly empty. Similarly, the diversity of *S. guttata* diet was low, and diets shifted to rely on alternative seed sources. These findings determine that *S. guttata* are affected by winter seed scarcity in the MLR.

3.4.1 Seed abundance in diets and the environment

Winter is a period of food scarcity for MLR *S. guttata*, when grass seeds are low in abundance (Chapter 2) and dead, thatchy introduced grasses smother areas of open ground, preventing access to the ground-layer (Carpenter 2012). The crops of *S. guttata* were mostly empty during times of seed scarcity. In contrast, when seed was abundant, most crops were full or near-full. Despite this clear pattern, the comparison of crop-fullness between scarce and abundant times was not statistically significant. Few crops were examined during scarce periods as *S. guttata* capture rates were low, likely reflecting reduced numbers in the environment. As such, the small sample size may have prevented a statistically significant difference being detected. Ankor (2005) also found that the number of seeds in *S. guttata* crops decreased during June–August, coinciding with the reduction of introduced annual grass seeds to nearly zero after late autumn rains caused mass-germination. Mass-germination was associated with a severe depletion of seed resources at all six sub-regions in the southern MLR (Chapter 2). The high winter proportion of weedy grass seed availability displayed in the present study is due to a perennial introduced grass, rather than the presence of annual grass seeds which mass germinate in autumn. Total seed biomass from May onwards, however, is low. Despite a small sample size, the correlation between low seed availability and empty crops suggests that *S. guttata* are going hungry as a result of food shortages.

3.4.2 Diversity of diets and available resources

The diversity of *S. guttata* diet broadly mirrored the diversity of local seed assemblages, being lowest during spring and winter, and highest during summer. The range of seed species consumed in spring was low but these species were consumed in similar proportions to each other, thus increasing Simpson diversity. While the range of species consumed in winter was greater than spring, *A. verticillata* dominated their diet with other species being eaten less, thus decreasing Simpson diversity. Similarly, the diversity of local seedbanks was lowest in late autumn and late winter and highest during summer. Therefore, low diet diversity during winter reflected the restricted seed availability in the environment, indicating that low food availability limits the variety of food consumed. In contrast, Read (1994) found spring and summer to be the periods of greatest diet diversity for MLR *S. guttata*, though sample sizes were not sufficient for statistical seasonal analysis. Read suggested that spring and summer were periods of food stress, consistent with the predictions of optimal foraging theory that foragers should focus on their most favoured prey when resources are abundant, resulting in a narrower diet breadth (MacArthur and Pianka 1966). However, the diets of granivores as a group have been shown to contradict optimal foraging theory and instead fluctuate in response to the natural availability of seeds (Sánchez and Blendinger 2014). Granivorous lilac-crowned parrots (*Amazona finschi*) for example, exhibit diets that are closely related to temporal variations in food resource availability and are narrower when availability is low (Renton 2001). When an animal with an otherwise diverse diet is forced to adopt a narrow diet breadth, their ability to obtain sufficient food becomes dependent on the yield of fewer species and is, therefore, more precarious. This highlights winter as a period when MLR *S. guttata* are at risk of food shortages.

3.4.3 Selection of seed types

The preference by *S. guttata* for seeds from native grasses and sheoaks, despite their relative scarcity, can be explained by their large size and thus their ability to provide more energy per unit of foraging effort (Brown *et al.* 1975; Hulme and Benkman 2002). However, though they were large and abundant, *S. guttata* only consumed a small portion of weedy forb species such as *Galenia* spp, *Arctotheca* spp and *Stellaria media* on occasion. The majority of abundant weedy forbs, including *Plantago* spp, *Romulea* spp, *Trifolium* spp, *Petrorhagia* *dubia*, *Emex australis*, *Erodium* spp, *Hypochaeris* spp, and *Medicago* spp, were not consumed, nor were they recorded as food species in other studies (Ankor 2005; Read 1994; Schopfer 1989). These species may contain toxins or be difficult for *S. guttata* to extract or de-husk, requiring specialisation. *Plantago bellardii* for example, has small seeds that are deeply encased in a tough exterior and may be difficult for short, stout bills to extract (G Hodder 2016 pers. obs.). *Medicago polymorpha* and *Trifolium subterraneum* are prone to mycotoxin contamination due to *Fusarium* infection (Tan *et al.* 2011a; 2011b). Similarly, *Trifolium repens* has been found to hyperaccumulate arsenic (Dong *et al.* 2008), while high mercury levels have been recorded in *Plantago* spp (Crowder 1991), and *Romulea rosea* is known to cause intoxication in sheep (Finnie *et al.* 2011). In order to limit overconsumption of these indigestible compounds, granivores and herbivores have adopted a strategy of maximising dietary diversity (Palminteri *et al.* 2016; Wiggins *et al.* 2006). Thus, *S. guttata* may have to either completely avoid many of the weedy herbaceous species that are common in the southern MLR, or consume them in small quantities, which places pressure on other food resources. This may explain the fact that native forb seeds, which were generally very small, were consumed in proportion to their availability. Overall, *S. guttata* eat a wide variety of seed types with selectivity driven by seed size rather than species. Their diet fits the description of an obligatory generalist – a species that feeds on a range of available food resources within some constraint, e.g. plants that do not have toxic chemicals (Shipley *et al.* 2009).

The consumption of *A. verticillata* seeds increased by over four-fold in winter. This increase was correlated with the low total seed biomass and drop in grass seed availability observed during winter (Chapter 2), requiring *S. guttata* to compensate with an alternative food source. Ankor (2005) found a similar response in the Monarto population of *S. guttata*, with 40% of their diet consisting of *A. verticillata* seeds in August, an increase from May–June consumption. This switch in diet was thought to reflect the change in grass seed availability from 600–1400 seeds m^{-2} in May to near-zero (<30 seeds m^{-2}) in August. Ankor (2005) suggested *A. verticillata* was a poorer-quality alternative food source, as their seeds were smaller than most grass seeds. However, *A. verticillata* seeds are high in protein (43–44%), lipid (37–38%) and nitrogen (3.24–3.88%) content (Crowley and Garnett 2001a) in comparison to even the highest protein grass seeds, which are native perennials such as *Rytidosperma* spp (25%) and *Aristida* spp (22.5%) (Yeoh and Watson 1981). As a granivorous diet is prone to protein deficiency and often lacking in essential amino acids

(Allen and Hume 1997), *A. verticillata* seeds may provide desirable nutritional qualities. This may also explain the clear selectivity for native grass seeds. However, *A. verticillata* have declined in abundance and range since European settlement (Bickford and Gell 2005), with a reduction of 78% (Area of Occupancy) in *A. verticillata*-associated woodlands (Rogers 2011). Remaining populations of *A. verticillata* have low recruitment due to grazing from over-abundant herbivores such as kangaroos and rabbits (Cooke 1988), leaving few stands of old trees that are prone to damage, have high levels of dieback and are less productive than they once were (DC Paton 2017 pers. obs.). Despite their low numbers, *A. verticillata* provides a critical food source during times of food scarcity and their contracting populations must be addressed and managed as a conservation priority for *S. guttata*.

3.4.4 Caveats and limitations

The abundance and diversity of *S. guttata* diet in the MLR are reflective of seasonal patterns of seed availability, with *S. guttata* experiencing a reduction in seed availability and diversity during winter. However, *S. guttata* are scarce in the MLR and trapping success was lowest during winter. Consequently, trapping success and crop sampling were skewed towards summer and autumn. Though 342 *S. guttata* were trapped, less than a quarter had crops that were near-full and able to be sampled, leading to small sample sizes for crop contents. As a result, heterogeneity between individuals could not be assessed. To minimise bird handling time, up to three attempts were made to extract seeds from near-full crops, resulting in 1–8 seeds successfully removed from each crop. As *S. guttata* crops can contain up to 54 seeds (Read 1987), the proportion of different seed types within crops cannot be accurately estimated from crop samples alone. While the morphometric identification of species in crop photographs, cross-referenced with DNA barcoding, was used to sample the proportions of seed types in crops, identifications could only be made to genus or a group of species. In addition, identifying the species selected by birds in the field was difficult as it required a direct line of sight to the seed or standing crop. Due to these difficulties, future studies on seasonal *S. guttata* diets should explore other methods of dietary analysis, such as collecting and analysing faeces from trapped birds or nests using Next Generation Sequencing. Regardless, the combined data from crop samples, crop photos and foraging observations collected across 24 months have provided a valuable insight into *S. guttata* diets in the MLR, allowing seasonal comparisons and the identification of key food resources where previously little was known.

3.4.5 Summary

The invasion of annual grasses into the MLR region has caused large seasonal fluctuations in understorey composition and therefore total seed abundances (Bickford and Gell 2005; Paton *et al.* 2004). These fluctuations are reflected in the diets of local *S. guttata*. After annual grass seeds mass-germinate in autumn and total seed biomass drops, *S. guttata* demonstrate a narrower diet with the loss of a profitable food source. During winter, *S. guttata* diet consists predominantly of native grass seeds and the seeds of *A. verticillata*, highlighting these as critical food resources. Despite prevailing in very low proportions in the environment relative to weedy annuals, the seeds of *A. verticillata* and many perennial native grasses provide more consistent year-round seed (Chapter 2). Given this, broad understorey restoration towards an increase in the proportion of native perennial grasses would benefit *S. guttata*, as well as other local granivorous bird species. In addition, restoring the declining populations of *A. verticillata* would not only provide additional useful structure for birds, but increase the availability of an important food source at a time prone to shortages. Overall, this study has contributed to the list of known food species for MLR *S. guttata*, demonstrated that changes in the diet are consistent with food shortages in winter, and identified critical winter food species.

Statement of authorship

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Name of Principal Author	Grace Hodder		
Contribution to the paper	Conceptualised and designed the experiment, collected and analysed data, interpreted the results and wrote the manuscript.		
Percentage contribution	85%		
Signature		Date	16/12/2019

Name of Co-Author	Assoc. prof. David Paton		
Contribution to the paper	Assisted in study conceptualisation and design, and commented on draft manuscript.		
Signature		Date	16/12/2019

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Contribution to the paper	Assisted in study conceptualisation and design, and commented on draft manuscript.		
Signature		Date	16/12/2019

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Contribution to the paper	Assisted in data analysis.		
Signature		Date	16/12/2019

Chapter 4. Temporal densities of a vulnerable, granivorous finch follow fluctuating seed resources

Photo by Helga Kieskamp 2016

4.1 Introduction

In our anthropocentric world, humans are continually encroaching upon the natural environment and throwing ecosystems off-balance (Foley *et al.* 2005; Vitousek *et al.* 1997). Consequently, the complex interactions between plants and animals which are fundamental to their survival (Christian 2001; Traveset and Riera 2005) have been greatly impacted (e.g. Kearns *et al.* 1998; Magrach *et al.* 2014; Martinson and Fagan 2014). Plant populations are impacted when processes such as pollination, seed predation and herbivory are altered. Similarly, animals are intrinsically linked to plants that provide them with fundamental resources such as shelter, nesting material and food. For example, the intensification of grassland management and the subsequent loss of cereal stubbles in western Britain have reduced the amount of food available in winter, contributing towards granivorous bird declines (Buckingham *et al.* 2011). Therefore, when a plant resource is altered by disruptions such as invasive species or overabundant herbivores, the survival and health of animals reliant upon the plant can suffer (Maron and Lill 2005; Martin and Possingham 2005; Wilcove *et al.* 1998).

Native vegetation has been greatly modified since European settlement in Australia (Bradshaw 2012). As such, plant resource composition (e.g. Yu *et al.* 2011), structure (e.g. Prior *et al.* 2011) and species (e.g. Whalley *et al.* 2011) have changed, with flow-on effects for the animals that rely on them. In southern and eastern Australia, where once-wooded landscapes have experienced one of the most significant changes to vegetation in Australian history (Yates and Hobbs 1997), many plant-animal interactions have been drastically affected. For example, the clearance of large eucalypts has reduced the abundance of hollows for hollow-nesting species such as the purple-crowned lorikeet (*Glossipsitta porphyrocephala*) and western pygmy possum (*Cercartetus concinnus*) (Gibbons *et al.* 2000) contributing to their decline. Scattered eucalypts in open grassland are good nectar providers as they have less competition from neighbouring trees and flower more regularly as a result (H Merigot 2019 pers. comm.). These trees complement other habitats with their nectar production, together providing year-round resources for species that move between patches such as the brown-headed honeyeater (*Melithreptus brevirostris*) (Merigot and Paton 2018). As such, the removal of these trees can create a resource gap, while similar alterations to plant resources have caused population declines among many species (Ford *et al.* 2001).

While habitat destruction is the broadest reason for the national decline of a southeast Australian Estrildid finch, the diamond firetail (*Stagonopleura guttata*) (Ford *et al.* 2001; Longmore 1978;), the more specific ecological processes affecting ongoing declines have not been explicitly tested at a landscape-scale. The significance of different threats to this species may vary between regions, with several contributors proposed, including: the dieback of eucalypt woodlands (Ford and Bell 1981), historical trapping for aviculture (Higgins *et al.* 2006; Lord 1956) and high nest predation (McGuire and Kleindorfer 2007). A commonly reported threat is changes in the abundance of food resources due to compositional changes to plant communities (e.g. Er *et al.* 1998; Ford *et al.* 1985; Forshaw *et al.* 2012). For *S. guttata* that reside in the Mount Lofty Ranges (MLR), South Australia, severe habitat loss and fragmentation have resulted in drastic changes to foraging habitat (Paton *et al.* 2004; Paton 2010). Exotic grasses, 75% of which are annuals, have invaded the understorey and largely replaced perennial native grasses and shrubs (Chapter 2). This compositional shift to an annual-dominated system has changed the timing and abundance of seasonal seed production, resulting in relative seed scarcity during late autumn and winter that affects *S. guttata* foraging habitat (Chapter 2).

As obligate granivores with diets comprised of 90–100% seeds (Schopfer 1989; Chapter 3), *S. guttata* do not have the ability to utilise alternate food resources when seeds are scarce (Dostine and Franklin 2002; Franklin *et al.* 2005; Swihart *et al.* 2003). As such, they are particularly vulnerable to changes in food availability. In the MLR, the diet of *S. guttata* follows seasonal shifts in resource abundance and diversity. Low food availability during late autumn and winter resulted in low diet diversity and high incidence of empty crops (Chapter 3), suggesting the population experiences seasonal food scarcity. If *S. guttata* populations are affected by seed fluctuations, they either move further afield in search of food or perish during times of scarcity. As such, *S. guttata* density would be expected to decrease during late autumn and winter. This study assesses the densities of *S. guttata* in the southern MLR using mark-recapture techniques. Specifically, this study examined: i) the density of *S. guttata* populations in the southern MLR, ii) whether these densities changed seasonally, and iii) whether *S. guttata* densities follow seasonal seed resource fluctuations.

4.2 Methods

4.2.1 Study area and sampling sites

This study was conducted across the range of *S. guttata* in the southern MLR over two years, between 2014 and 2016. Preliminary assessments in 2014 examined *S. guttata* across 30 sites in the region. Based on that data, five sub-regions were selected for this study (Milang, Hartley, Rockleigh, Springton and Karinya). Each sub-region contained three sampling sites (see Figure 1.2 in Chapter 1) located approximately 1–4 km apart. Sites consisted of patches of remnant, open eucalypt woodland with disturbed, predominantly weedy understoreys. Adjacent sub-regions were between 25 and 31 km apart. It was assumed there was no movement between sub-regions based on recapture distances of <10 km in 99.5% of banded birds (Higgins *et al.* 2006).

4.2.2 Sampling methodology

4.2.2.1. Tagging of individuals

To investigate the density and demographics of *S. guttata* populations, individuals were captured and tagged with a unique combination of coloured leg bands. Individuals were captured by erecting 6–12 mist-nets at each site. Mist-nets were erected at dawn throughout an approximate 20 ha area of suitable habitat and monitored regularly until late-afternoon unless weather conditions became unsuitable (too hot, too windy or raining). When a *S. guttata* was caught, a metal band with a unique code provided by the Australian Bird and Bat Banding Scheme to identify where and when the bird was banded was placed on its left leg. In addition, a unique combination of plastic colour-bands were attached to its legs, one on the left and two on the right leg (Figure 4.1). This allowed for the bird to be identified without recapture. The age category of each bird (juvenile, immature, sub-adult or adult, identified by examining plumage and beak colouration; Forshaw *et al.* 2012), site and capture date were recorded. Re-captures of tagged *S. guttata* were also recorded.

Trapping *S. guttata* was difficult due to their low densities, with some sub-regions proving more successful than others. Thus, after the first few trapping attempts at each sub-region, the three sub-regions with the highest numbers of tagged *S. guttata* (Hartley, Rockleigh and Springton; see Figure 1.2 in Chapter 1) were chosen as focus areas to maximise trapping effort. Trapping continued at these three sub-regions annually, with 3–7 trapping days per year throughout the monitoring period. In total, ten trapping days were conducted at Rockleigh between February and April in 2014, 2015 and 2016. At Springton, 15 trapping days were conducted in May, August and November 2014, and then in April of 2015 and 2016. At Hartley, nine trapping days were conducted in April 2015 and February 2016.

Figure 4-1 An adult *S. guttata* captured at Rockleigh and banded with a unique metal identifying band on its left leg together with a unique combination of plastic colour-bands on both legs.

4.2.2.2. Camera monitoring

Motion sensor cameras were used to obtain resightings of colour-tagged *S. guttata*. A combination of Reconyx HC500 HyperFire Infrared Trail Cameras and Moultrie M-990i Infrared Digital Game Cameras monitored *S. guttata* between February 2015 and December 2016. At each study site (n = 15), a resource station consisting of an automated water trough and small water tank (in cases where the landowner did not maintain the trough) surrounded by pig-wire fencing (to exclude large herbivores) was installed. A motion sensor camera was attached to the water tank and positioned so that its field of view horizontally captured birds visiting the attached trough (Figure 4.2). Cameras were set to record bursts of three images in quick succession once motion triggered, with no delay between bursts. The Passive Infrared detector sensitivity was set to high and vegetation was removed from the immediate 2 x 2 m area surrounding each camera to reduce false triggers. Cameras were fitted with rechargeable NiMH Panasonic Eneloop batteries and 16 or 32 GB SD cards and checked approximately every 4–8 weeks, when batteries and cards were replaced. Approximately 2–4 weeks of continuous footage were collected at every 4–8 week period, with occasional camera malfunctions occurring when adequate footage was not recorded for certain periods (24 occasions from 242 camera checks).

Figure 4-2 A resource station at (left) with provisioned water is surrounded by a pig-wire fence. Another resource station (right) that was maintained by the landowners. Motion sensor cameras attached to the tanks aim down the length of the water troughs.

4.2.2.3. Seed resource measurements

In conjunction with the mark-resight study, seed availability fluctuations were measured to enable a comparison with *S. guttata* population fluctuations. Naturally occurring seed resources were measured seasonally in late spring (October–November), late summer (February–March), late autumn (May–June) and late winter (August–September) across two years in all five sub-regions. In the second year of the study, late spring was not sampled due to extenuating circumstances. Up to ten locations where *S. guttata* were observed foraging and ten non-forage points located elsewhere throughout suitable habitat were sampled at each site during the first year of study. During the second year, between ten and twenty forage points were sampled from each sub-region.

Forage points were located by following flocks of *S. guttata* on foot for 6–12 hours per day and observing their behaviour with binoculars. When birds were observed foraging, the exact locations at which they removed seeds from the ground or a plant were noted. Once the flock had moved on forage points were marked with flagging tape. Flocks were re-located by listening for calls where possible and followed for as long as possible. When flocks were lost, systematic searches of known foraging hotspots were undertaken within sites until *S. guttata* were reencountered. Forage points were sampled on the same day as marking occurred. Non-forage points were randomly generated, within each site using a Random Number Generator in ArcGIS version 10.3.1. Once on site, ten of the 50 generated points that fell within viable *S. guttata* foraging habitat (i.e. an understorey comprised of grasses, small shrubs or forbs), but where *S. guttata* had not been observed foraging, were selected and sampled. Surveys were undertaken on one day per site seasonally, in conjunction with seed sampling (see Chapter 2).

Forage and non-forage points were sampled using a quadrat centred over each point. All seeds held on plants (e.g. in grass seed-heads, on forbs or in open sheoak cones), hereafter 'the standing crop' within the 50 x 50 cm quadrat were collected. Where possible, seeds were identified to species level and placed into separate paper bags. In cases where *S. guttata* individuals foraged in sheoak trees, the quadrat was placed within the canopy of the tree and all standing cones intersecting the plane of the quadrat were removed and bagged for subsequent analysis. Additionally, topsoil (~1 cm deep) from a 25 x 25 cm quadrat centred over the point was removed using a flat spade, along with litter and fallen plant material, and placed in a paper bag. Sampled seeds were identified and counted in the laboratory (see Chapter 2: section 2.2.3.1 for detailed methodology).

4.2.3 Camera image processing

Camera images were examined and those that did not contain *S. guttata* were discarded. The remaining images were grouped into series of the same bird or bird group. Series comprised images where the same individual(s) were present in subsequent images taken less than two minutes apart. For each series of images, the number of *S. guttata* encountered and their age class (juvenile, immature/sub-adult, and adult) were recorded. Where possible, *S. guttata* were identified based on their colour tags, however, some birds were partially identified if only one leg could be viewed, or colour-tags were obscured in images. In addition, sub-region, site, image number and the time of the first image in the series were recorded.

4.2.4 Statistical analyses of patterns

4.2.4.1. Patterns of S. guttata and seed resource fluctuations

Temporal patterns of *S. guttata* were explored using the mean number of encounters per day from each camera per month for all three sub-regions. GraphPad Prism version 7 for Windows (La Jolla California USA) was used for calculations and graphing. Daily encounters may have comprised multiple visits from the same individual, as observations did not discriminate between colour-tagged and untagged individuals. To assess the relationship between monthly *S. guttata* encounters and natural seed availability, the abundance of all seeds measured in quadrats was averaged for each season at each sub-region. Then, mean seed abundance per quadrat of all sub-regions per season was calculated with standard errors (n = number of sub-regions). Occasional in-field camera malfunctions resulted in some periods in each year that had few camera recording days, limiting the ability for comparisons between years. Data from 2015 and 2016 were pooled so a more robust representation of seasonal variation, and a longer-term average of monthly and seasonal differences could be produced. Seasonal variations in seed abundance between years were examined using Two-way ANOVA with the exception of spring, as no seed sampling was conducted for this season in 2016.

In addition to *S. guttata* camera encounters, the number of encounters during observational foraging surveys were calculated for every day spent tracking flocks across the first year of study. Observational encounters constituted the number of encounters with either an individual or flock of *S. guttata* that occurred at least five minutes apart. Five minutes was long enough for a flock to leave the field of view or escape the tracker, and hence were considered separate encounters. The frequency of *S. guttata* sightings, rather than the size of foraging flocks, were of interest for seasonal comparisons, therefore the number of birds in each flock was not included in this analysis. The average number of encounters per season was calculated with standard errors for all sub-regions. Data were tested for normality using D’Agostino-Pearson tests. Unpaired parametric *t*-tests were applied to compare seasonal differences in observational encounter rates.

4.2.4.2. Population density modelling

Population densities of *S. guttata* were calculated for the three focal sub-regions (Hartley, Rockleigh and Springton) using spatially-explicit mark-resight (SEMR) models in the secr package (Efford 2018; Efford and Hunter 2017) in R 3.5.1 (R Core Team 2016). Spatially-explicit mark-resight models use resighting and recapture data of tagged individuals at an array of detectors to estimate an activity centre for each animal and thereby estimate population density (Efford 2018). To maximise the number of re-sightings of tagged birds some assumptions were made about the identity of partially colour tagged *S. guttata*. As there were no records of *S. guttata* moving between sub-regions, it was assumed all re-sighted, partially tagged birds were originally caught in the sub-region they were re-sighted in. All left-leg colour bands were green at Springton and yellow at Hartley. Thus, the identity of partially tagged re-sightings containing only right-leg colour-combinations could be safely assumed for these sub-regions. Where the identity of a partially colour-tagged individual was recorded with a level of uncertainty, camera images were reviewed. If uncertainty remained about the bird's identity but the assumed colour-combination was possible for the sub-region within which it was recorded, it was presumed correct. If the colour-combination was not possible, the re-sighting was recorded as a partial identification. Despite this, models could not be fitted to the data from Hartley in 2015 and Springton in 2016 due to sparse re-sightings of colour-tagged birds. Densities were modelled separately for 2015 and 2016 at Rockleigh. To facilitate model computation, months when cameras operated for few days (<50% of total possible camera days) were removed. The periods modelled were Hartley: February–August 2016; Rockleigh: June–December 2015 and March–September 2016; and Springton: April 2015–March 2016.

Response variables for each SEMR included capture histories, detector layout files and counts of unmarked and partially-identified individuals. Capture histories were collated from mist-netting (capture) records of colour-banded birds and all full-identity resightings at cameras and consisted of occasions (days) and detectors (cameras or mist-nets) at which each colour-tagged bird was recorded. Detector layout files contained information about the capture area within each site (a centroid location for each set of mist-nets placed within an ~12 ha area), the exact camera locations, occasions during which mist-nets (marking occasions) and cameras (sighting occasions) were operated, and the period of time cameras were operational.

Three null models were run, each assuming a constant density of animals but with a different rate of detection with increasing distance from detectors (half-normal, exponential and hazard-rate detection curves). The half-normal detection curve was the best fit according to Akaike's Information Criterion corrected for small sample size (AICc) and was used in all further models (Appendix M). An initial estimate of sigma (an index of animal movement) was calculated using the RPSV (Root Pooled Spatial Variance) function (Efford 2018). Another series of four to five null models, each with increasingly large buffers (the distance from the detectors over which density estimates are made) were run until the buffer size at which sigma stabilised and density estimates showed little change between subsequent models was obtained (Appendix N). The buffers (radiuses) for each sub-region were 1917 m for Springton, 3501 m for Hartley, and for Rockleigh 3393 m (2015) and 1450 m (2016).

A candidate set of models was derived using combinations of season, month, rainfall and temperature variables as well as a transience variable *B* and a marking-resighting variable *ts*. Month was included to assess temporal patterns of *S. guttata* densities at a finer scale than season. The season and month variables were converted to ordinal factors. The effects of weather on *S. guttata* densities were assessed by including, daily rainfall (mm) and maximum daily temperature (^{o}C) data collected from the Bureau of Meteorology weather stations closest to each sub-region (within 10 km for rainfall and 20 km for temperature) (Bureau of Meteorology 2019). There was a lot of variation in daily rainfall and the distribution was right-skewed, so it was converted to a logarithmic scale to facilitate computation. Similarly, temperature was scaled by converting to its z-score. The transience parameter (*B*) is a measure of the likelihood that an individual will be resighted at the next occasion, based on whether it was resighted at the previous occasion, allowing for non-resident individuals that may be moving through the study area and only sighted or captured infrequently. The resighting variable *ts* allows estimates derived from the marking process to differ from estimates derived from the resighting process. Predictors (season, month, rainfall, temperature, *B* and *ts*) were allowed to vary with detection probability (g0) or with both detection probability and sigma (the index of animal movement). Models contained no more than two predictors, as the numbers of re-sightings of tagged birds at sub-regions was too sparse during some time periods to fit more complex models. Interactions between predictors could not be explored, and certain predictor combinations caused computational issues for some datasets, preventing the establishment of a common candidate set of models among sub-regions. Once the candidate models were established, they were run using the appropriate buffer (described above). The model of best fit was determined based on AICc and once identified it was re-run with the starting values specified from its initial fit and 2000 iterations. This increased the precision of the model estimates and dealt with any over-dispersion.

Seasonal density estimates of *S. guttata* were derived from SEMR models for late summer (January–March), late autumn (April–June), late winter (July–September) and late spring (October–December) (Appendix O). However, due to a smaller sample size for Rockleigh in 2016, late summer comprised March and April while late autumn comprised May and

June. At Springton late spring comprised November 2015–January 2016, while late winter comprised July–October 2015. Marking occasions did not occur at the start of every season, so in these cases models were run using only sighting occasions. The number of marked birds in the populations within seasons was unknown because seasons did not immediately follow marking occasions, therefore capture histories contained information about resighted animals only. The predictors season and month were not included in these models as the data only spanned one season and few months. In addition, the marking-resighting parameter (*ts*) was not appropriate because marking occasions were not included in the models. The *B* parameter was included in the Hartley model as it was significant in the best overall model (Table 4.1). Only null models were run for the remaining datasets in order to just obtain density estimates (Appendix O). The same buffer sizes derived from the complete dataset were used for seasonal subset models. Seasonal density estimates, along with 95% confidence intervals, were extracted from the models and graphed using ggplot2 (Wickham 2009).

The SEMR models assumed that the population was closed, meaning no births, deaths, immigrations or emigrations occurred during the period of monitoring (Efford 2018), which is highly unlikely for a two-year study of wild animals. Though random movement of individuals in and out of study areas has not been found to bias estimators from closed population models (Kendall 1999; Van Katwyk 2014), it does decrease precision because estimates of detection probabilities are less reliable in a population that is actually open (e.g. Rahel *et al.* 2013; Sollmann *et al.* 2013). Lower detection probabilities increase density estimates and lead to positive bias (Kissling and Garton 2006). The inclusion of a transience parameter *B* relaxes the assumption of closure somewhat. To assess the validity of this, one to two months of resighting data within which births, deaths, immigrations or emigrations were relatively unlikely was extracted and modelled separately. The time period directly following a trapping event between February–April was chosen, as it is towards the end of the breeding season when chances of new fledglings entering the population are less likely, and it is before winter when either deaths or emigrations could be occurring. The one to two month timeframe was deemed short enough to assume closure because if an individual was captured at the start of the period and the majority of its population is assumed sedentary (based on long-term re-sighting data, Appendix P), there is a high chance the individual would have remained in the population for two months. To determine the extent of positive bias (i.e. inflated estimates) induced by non-closure, the density estimates produced by the closed subset models were compared to the density estimates produced for longer time-periods described earlier.

4.2.4.3. Seed biomass modelling

Seed biomass was not included in models of *S. guttata* density, as it was necessary to minimise the number of parameters in the candidate sets due to sparse sightings or limited movement of birds between cameras at some sub-regions. Thus, seed biomass was modelled separately (Chapter 2) and visually compared with seasonal patterns of *S. guttata* densities. Seed biomass is likely to be more important than seed abundance, as *S. guttata* selectively forage on large seeds from a range of species (Chapter 3). The dataset from Chapter 2 was used to obtain patterns of seed biomass for the focal sub-regions: Hartley, Rockleigh and Springton. The soil surface and standing crop datasets were analysed separately due to the different methodologies used to sample them (Chapter 2). To account for the conversion of seed abundance (count data) to mass (Chapter 2) Tweedie compound poisson generalised linear mixed models (cpglmms) were used in the cplm package (Zhang 2013) in R version 3.5.1 (R Core Team 2016). Models assessed how seed biomass varied seasonally and with sub-region. Site was included as a random factor to account for the nested design of three sites within each sub-region (Zuur *et al.* 2009). The interaction of sub-region by season was modelled against seed biomass. The multcomp package (Hothorn *et al.* 2008) was used to obtain model estimates and confidence intervals of seed biomass at each level of the explanatory variables, and results were plotted using ggplot2 (Wickham 2009). Seed abundance data could not be obtained for some season by sub-region combinations as *S. guttata* were not found foraging (Chapter 3).

4.3 Results

4.3.1 Patterns of *S. guttata* and seed resource fluctuations

Camera encounters of *S. guttata* were generally highest in spring and summer, and lowest in winter (Figure 4.3). Observational encounters followed a similar pattern, being higher in spring-summer than autumn-winter. There was a significant difference in observational encounters between summer and autumn ($P = 0.003$, df = 34) and summer and winter ($P = 0.009$, df = 34). There were no significant differences between summer and spring ($P = 0.09$, df = 34), autumn and winter ($P = 0.63$, df = 34), autumn and spring ($P = 0.32$, df = 34) or winter and spring ($P = 0.54$, df = 34). The temporal pattern of camera encounters averaged over sub-regions was very similar to temporal seed abundances averaged over sub-regions (Figure 4.3). Encounters peaked in March, decreased to near-zero between May–September and then increased again from October onwards. Standard errors were large for encounters in November and December due to small numbers of camera operating days and some high *S. guttata* numbers. However, observational encounters support the upward trend in *S. guttata* from November onwards (Figure 4.4). A substantial proportion of the camera encounters in November and December can be attributed to juveniles, immatures and sub-adults. However, from January through April camera encounters of juvenile, immature or sub-adult birds were low. Seasonal seed abundances did not vary significantly between 2015 and 2016 ($F_{1,\,10} = 1.35$, $P = 0.27$). Variations in monthly *S. guttata* encounters between years could not be explored, but yearly variations in density estimates are examined in Section 4.3.2.

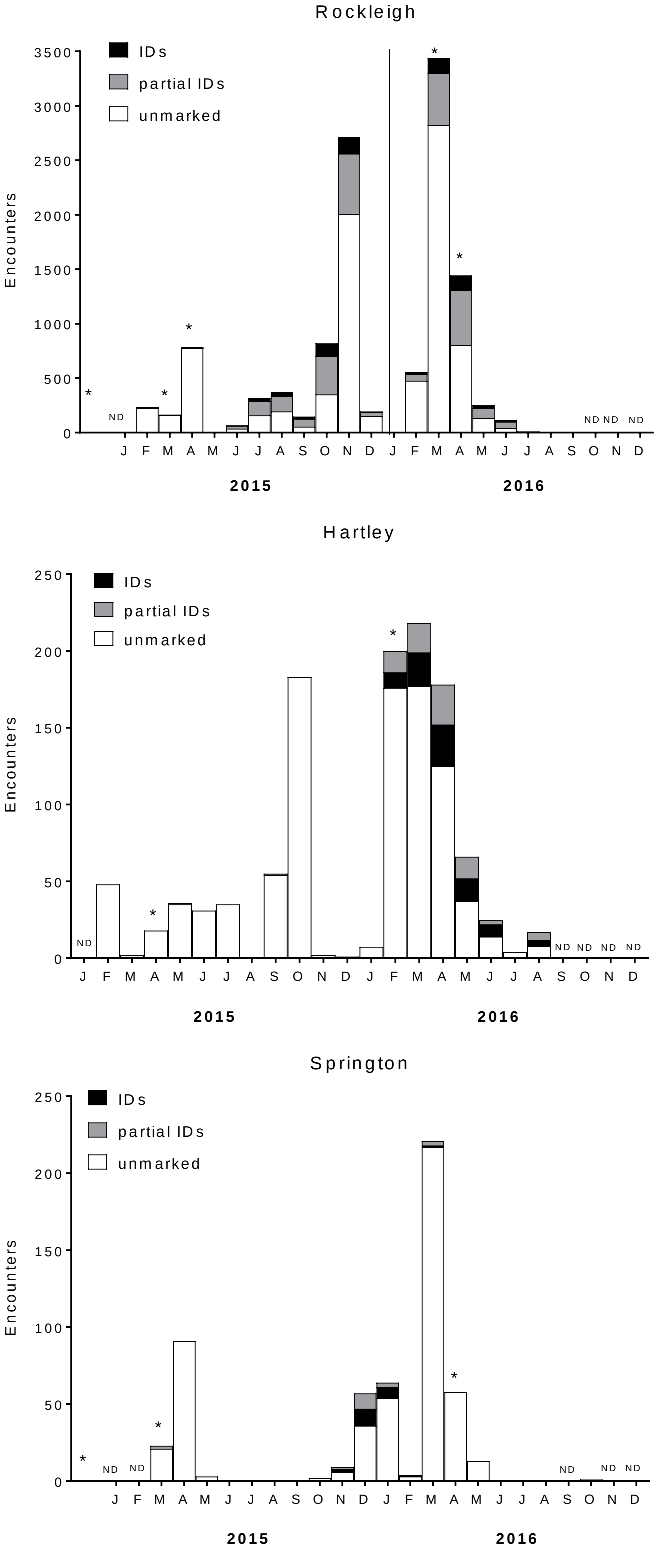

Figure 4-3 Remote sensing camera records for *S. guttata.*

The total number of encounters of fully-identified, partially-identified and unmarked *S guttata* at cameras for each of three sub-regions. 'ND' denotes no data due to non-operating cameras and '*' denotes tagging occasions. Encounters are not weighted by number of camera operating days.

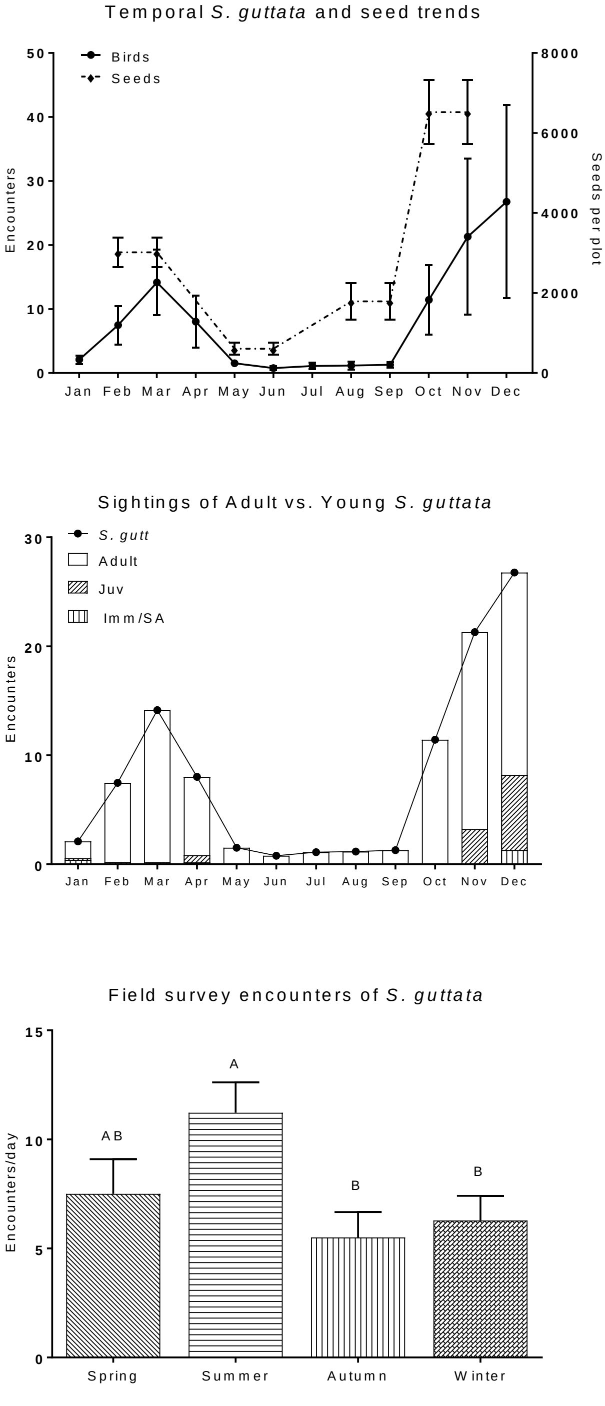

Figure 4-4 Mean monthly *S. guttata* encounters per camera day averaged for three sub-regions.

(Top) seasonal averages of total seeds sampled in plots. Seeds were sampled in a two-month period; the average for this period is displayed across both months. (Middle) the proportions of average encounters that were of adult birds, juveniles and immatures/sub-adults. Bottom: seasonal average observational encounters of *S. guttata*. Error bars represent SEMs, *n* = 15 study sites.

4.3.2 Population density modelling

Of the candidate model sets that included environmental and temporal variables, environmental variables (rainfall and temperature) were not good explanatories of *S. guttata* density at any of the three sub-regions. The model of best fit for explaining *S. guttata* density at Hartley in 2016 was H1; comprising the detection probability (g0) varying with month and *B* (the transience factor). Model H1 was the highest ranked and clearly favoured model from the candidate set, such that excluding any of the modelled variables resulted in a substantial reduction in model fit (Table 4.1). Thus, the strongest predictors of *S. guttata* density at Hartley were month and transience. H1 produced a density estimate of 0.023 birds/ha (95% CI = 0.016–0.035).

Table 4.1 AICc ranking of mark–resight spatial models of the density of *S. guttata* per ha, measured at three sites in Hartley during 2016 in the southern MLR.

Model	Model formula	AICc	Δ_i	w_i	logLik	K
H1	g0 ~ **MONTH + B, sigma ~ 1**	**2103.04**	**0.000**	**1**	**-1035.02**	**11**
H2	g0 ~ MONTH, sigma ~ 1	2134.29	31.25	0	-1052.75	10
H3	g0 ~ SEAS, sigma ~ SEAS	2180.32	77.28	0	-1079.49	8
H4	g0 ~ SEAS + ts, sigma ~ 1	2203.41	100.37	0	-1092.71	7
H5	g0 ~ SEAS, sigma ~ 1	2207.73	104.70	0	-1096.42	6
H6	g0 ~ TEMP + B, sigma ~ 1	2294.37	191.34	0	-1139.74	6
H7	g0 ~ TEMP, sigma ~ TEMP	2302.08	199.04	0	-1143.59	6
H8	g0 ~ TEMP + ts, sigma ~ 1	2305.51	202.48	0	-1145.31	6
H9	g0 ~ B + ts, sigma ~ 1	2430.43	327.39	0	-1207.77	6
H10	g0 ~ RAIN + B, sigma ~ 1	2430.91	327.87	0	-1208.01	6
H11	g0 ~ RAIN + ts, sigma ~ 1	2438.26	335.22	0	-1211.68	6
H12	g0 ~ RAIN, sigma ~ RAIN	2463.58	360.54	0	-1224.34	6
H13	g0 ~ B, sigma ~ 1	2477.29	374.26	0	-1232.65	5
H14	g0 ~ ts, sigma ~ 1	2477.30	374.26	0	-1232.65	5
H15	g0 ~ RAIN, sigma ~ 1	2485.12	382.08	0	-1236.56	5
H16	g0 ~ 1, sigma ~ 1	2529.43	426.39	0	-1260.07	4

Explanatory variables in candidate models are: SEAS = season; MONTH = the month in which and variables were measured; RAIN = daily rainfall (mm); TEMP = maximum daily temperature; *B* = a transience parameter; and ts = a parameter allowing variation in estimates based on tagging (t) and sighting data (s). The core parameters of the model are: g0 = detection probability and sigma = a parameter of animal movement; together g0 and sigma define the model for detection probability as a function of location. AICc = Akaike's Information Criterion with correction for small sample sizes, Δ_i = the difference between that model's AICc value and the AICc value of the model of best fit, w_i = Akaike weight, logLik = the log likelihood of the model, K = the number of estimated parameters. Candidate models with significant levels of empirical support ($\Delta_i < 2$) are shown in bold.

At Rockleigh in 2015, the best model for explaining *S. guttata* densities was R1.1; comprising detection probability (g0) and sigma varying with season. In 2016, the best model was R2.1; comprising detection probability (g0) and sigma both varying with *ts* (the marking-resighting factor). Both models were the highest ranked and clearly favoured model from their respective candidate sets, such that excluding any of the modelled variables resulted in a substantial reduction in model fit (Table 4.2). Model R1.1 indicates density in 2015 changed significantly between seasons, as detection probability and sigma (the movement parameter) were functions of season. In 2016, density did not change substantially between seasons, although the subset of data modelled was such that all but nine occasions fell within one season. Instead, model R2.1 allowed parameters to vary between marking and sighting occasions. R1.1 produced a density estimate of 0.023 birds/ha (95% CI = 0.021–0.025), while R2.1 estimated 0.062 birds/ha (95% CI = 0.053–0.074).

Table 4.2 AICc ranking of mark–resight spatial models of the density of *S. guttata* per ha measured at three sites at Rockleigh in 2015 and 2016 in the southern MLR.

Year	Model	Model formula	AICc	Δ_i	w_i	logLik	K
2015	**R1.1**	**g0 ~ SEAS, sigma ~ SEAS**	8296.97	0.00	**1**	-4139.28	**8**
	R1.2	g0 ~ SEAS + B, sigma ~ 1	8382.64	85.68	0	-4183.40	7
	R1.3	g0 ~ SEAS + ts, sigma ~ 1	8453.26	156.30	0	-4218.71	7
	R1.4	g0 ~ SEAS, sigma ~ 1	8475.82	178.86	0	-4231.24	6
	R1.5	g0 ~ TEMP + B, sigma ~ 1	10012.10	1715.14	0	-4999.37	6
	R1.6	g0 ~ TEMP, sigma ~ TEMP	10101.83	1804.86	0	-5044.24	6
	R1.7	g0 ~ TEMP, sigma ~ 1	10146.72	1849.76	0	-5067.89	5
	R1.8	g0 ~ RAIN + B, sigma ~ 1	11184.29	2887.33	0	-5585.47	6
	R1.9	g0 ~ RAIN, sigma ~ RAIN	11382.90	3085.93	0	-5684.77	6
	R1.10	g0 ~ B + ts, sigma ~ 1	11507.90	3210.94	0	-5747.28	6
	R1.11	g0 ~ B, sigma ~ B	11508.70	3211.73	0	-5747.67	6
	R1.12	g0 ~ B, sigma ~ 1	11513.42	3216.45	0	-5751.23	5
	R1.13	g0 ~ RAIN, sigma ~ 1	11572.55	3275.59	0	-5780.80	5
	R1.14	g0 ~ 1, sigma ~ 1	11855.61	3558.64	0	-5923.49	4
2016	**R2.1**	**g0 ~ ts, sigma ~ ts**	**4440.37**	**0.00**	**1**	**-2213.25**	**6**
	R2.2	g0 ~ TEMP, sigma ~ TEMP	4534.66	94.28	0	-2260.40	6
	R2.3	g0 ~ B, sigma ~ 1	5325.08	884.70	0	-2656.89	5
	R2.4	g0 ~ 1, sigma ~ 1	5373.39	933.02	0	-2682.27	4
	R2.5	g0 ~ SEAS, sigma ~ 1	5873.72	1433.35	0	-2931.21	5
	R2.6	g0 ~ B, sigma ~ B	6546.53	2106.15	0	-3266.33	6
	R2.7	g0 ~ RAIN + ts, sigma ~ 1	6587.30	2146.93	0	-3286.72	6
	R2.8	g0 ~ SEAS, sigma ~ SEAS	6685.09	2244.72	0	-3335.61	6

Explanatory variables are: SEAS = seasons; RAIN = daily rainfall; TEMP = max. daily temp.; *B* = transience; and ts = variation between tagging (t) and sighting (s). Core parameters are: g0 = detection probability and sigma = movement. Together g0 and sigma define the model. AICc = Akaike Information criterion corrected for small sample sizes, Δ_i = the difference between that model and the model of best fits AICc value, w_i = Akaike weight, logLik = the log likelihood of the model, K = the number of estimated parameters. Candidate models with significant levels of empirical support ($\Delta_i < 2$) are shown in bold.

The model of best fit for explaining *S. guttata* density at Springton in 2015 was S1; comprising detection probability (g0) varying with season and *ts*. This model was the highest ranked and clearly favoured model from the candidate set, such that excluding any of the modelled variables resulted in a substantial reduction in model fit (Table 4.3). This indicates *S. guttata* density at Springton changed seasonally and detection probability varied between marking and sighting occasions. S1 produced a density estimate of 0.352 birds/ha (95% CI = 0.251–0.493).

Table 4.3 AICc ranking of mark–resight spatial models of the density of *S. guttata* per ha, measured at three sites in Springton during 2015 in the southern MLR.

Model	Model formula	AICc	Δ_i	w_i	logLik	K
S1	**g0 ~ SEAS + ts, sigma ~ 1**	**3447.71**	**0.00**	**1**	**-1713.19**	**8**
S2	g0 ~ SEAS + B, sigma ~ 1	3539.06	91.35	0	-1758.86	8
S3	g0 ~ SEAS, sigma ~ 1	3580.22	132.51	0	-1781.11	7
S4	g0 ~ MONTH + ts, sigma ~ 1	3686.96	239.25	0	-1836.03	6
S5	g0 ~ MONTH + B, sigma ~ 1	3728.69	280.98	0	-1856.90	6
S6	g0 ~ RAIN + ts, sigma ~ MONTH	3739.23	291.52	0	-1862.17	6
S7	g0 ~ MONTH, sigma ~ MONTH	3770.87	323.16	0	-1877.99	6
S8	g0 ~ TEMP + ts, sigma ~ 1	3776.98	329.27	0	-1881.04	6
S9	g0 ~ MONTH, sigma ~ 1	3778.44	330.73	0	-1883.22	5
S10	g0 ~ B + ts, sigma ~ 1	3813.91	366.20	0	-1899.51	6
S11	g0 ~ ts, sigma ~ 1	3842.20	394.49	0	-1915.10	5
S12	g0 ~ RAIN + B, sigma ~ 1	3848.63	400.92	0	-1916.87	6
S13	g0 ~ RAIN, sigma ~ 1	3886.75	439.04	0	-1937.37	5
S14	g0 ~ RAIN, sigma ~ RAIN	3887.40	439.69	0	-1936.25	6
S15	g0 ~ TEMP, sigma ~ 1	3923.25	475.54	0	-1955.62	5
S16	g0 ~ B, sigma ~ B	3927.58	479.87	0	-1956.34	6
S17	g0 ~ B, sigma ~ 1	3927.94	480.23	0	-1957.97	5
S18	g0 ~ 1, sigma ~ 1	3969.43	521.72	0	-1980.07	4
S19	g0 ~ TEMP + B, sigma ~ 1	4242.52	794.81	0	-2113.81	6

Explanatory variables are: SEAS = season; MONTH = month; RAIN = daily rainfall; TEMP = maximum daily temperature; *B* = transience; and ts = variation between tagging (t) and sighting (s). The core parameters are: g0 = detection probability and sigma = animal movement; together g0 and sigma define the model for detection probability as a function of location. AICc = Akaike's information criterion corrected for small sample sizes, Δ_I = the difference between that model's AICc value and the AICc value of the model of best fit, w_i = Akaike weight, logLik = the log likelihood of the model, K = the number of estimated parameters. Candidate models with significant levels of empirical support ($\Delta_i < 2$) are shown in bold.

Models of a period for which the likelihood of closure was high (closed) produced density estimates that were different to those of a longer monitoring period for which closure was unlikely (open) (Figure 4.5). At Hartley, the closed model (February–March 2016; see Appendix O) produced a density estimate of 0.015 birds/ha (95% CI = 0.012–0.018), while the open model had a density estimate of 0.023 birds/ha (95% CI = 0.016–0.035). Though the confidence intervals of the closed and open models overlap, there is evidence to suggest a positive bias in the open density estimate as it is higher than the closed estimate (Figure 4.5). Similarly, at Rockleigh, the closed model (March–April 2016) produced a density estimate of 0.032 birds/ha (95% CI = 0.031–0.033; see Appendix D.iv.), which did not overlap with the open density estimates of 0.062 birds/ha (95% CI = 0.053–0.074). A positive bias was not apparent in the open 2015 estimates, which were lower than the closed estimates of the same population, though the high open estimate for Rockleigh in 2016 was likely due to positive bias. Notably, the density estimate produced for late spring at Rockleigh in 2015 (0.019 bird/ha, 95% CI = 0.017–0.020; Figure 4.5), which contains data collected more than five months from the main marking occasions, did not show a positive bias compared to the closed subset at Rockleigh (Figure 4.5). It was not possible to produce a closed model for Springton, as most marking occasions occurred several months earlier than the start of the camera monitoring period.

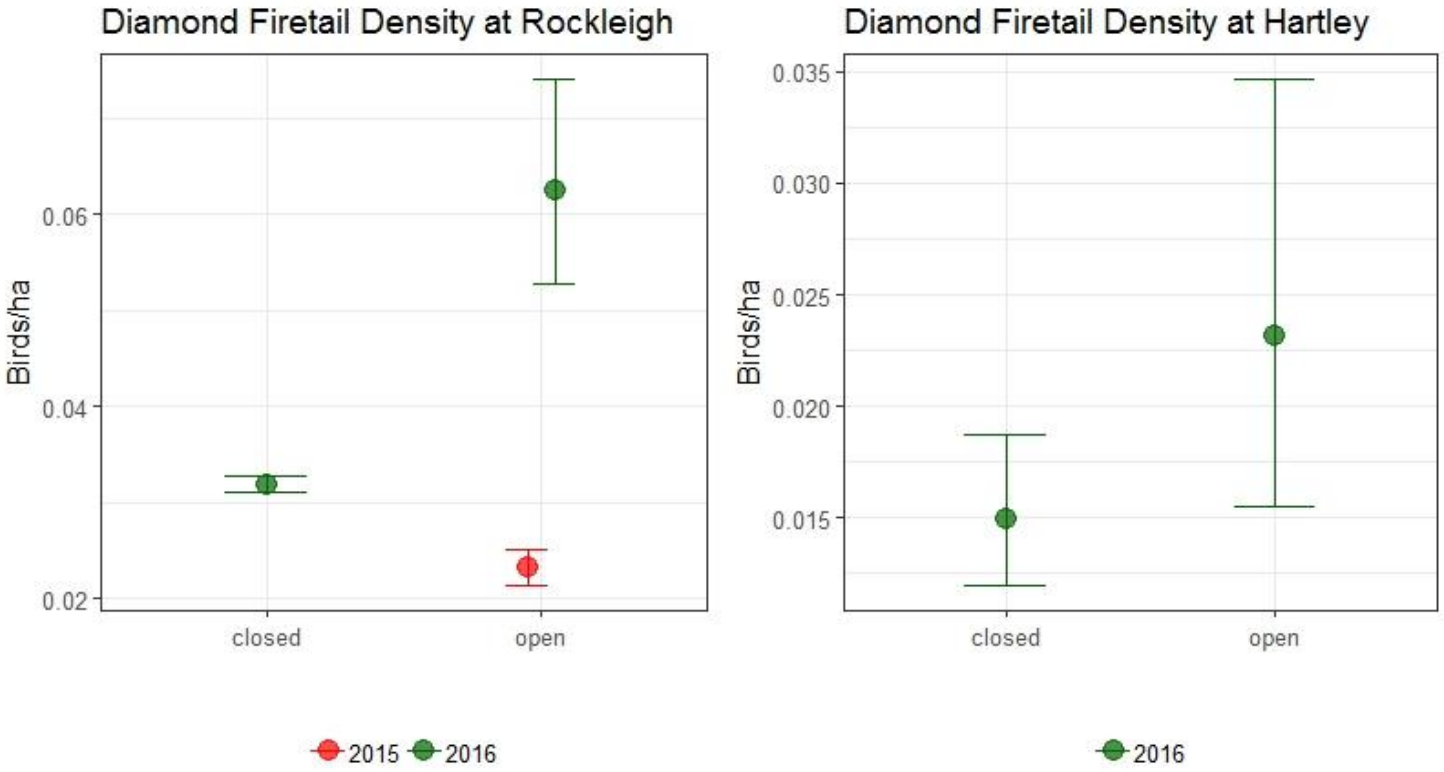

Figure 4-5 Density estimates from spatial mark-resight modelling of *S. guttata* at Rockleigh (left) and Hartley (right) for a two-month subset of resighting data with a greater likelihood of being closed (Rockleigh=Mar–Apr; Hartley=Feb–Mar) and subsets of resighting data spanning longer (open periods: Rockleigh 2015=Jun–Dec; Rockleigh 2016=Mar–Jun; Hartley=Feb–Aug) in the southern MLR. Error bars denote 95% confidence intervals.

4.3.3 Seed biomass and *S. guttata* density

A qualitative assessment of *S. guttata* density estimates per season derived from SEMR models compared with the model estimates of seed biomass (g) from cpglmms showed that seasonal patterns of *S. guttata* density and seed biomass were similar, for all three sub-regions (Figures 4.6 and 4.7). Seasonal densities of *S. guttata* were highest in late spring or summer, when total seed biomass was highest at most sub-regions (Figure 4.6). The numbers of *S. guttata* sightings were too low during late autumn at Rockleigh and late winter at Hartley in 2016 to produce density estimates. At Rockleigh and Springton, there were no re-sightings of tagged birds in late autumn 2015, so density estimates could not be produced. In late winter at Springton 2015 and at Rockleigh 2016, there were no sightings of any *S. guttata* on cameras. Instances where density estimates could not be produced were graphed as zeroes. At most sub-regions, total seed biomass decreased in late autumn and late winter compared to late spring or summer (Figure 4.7). Periods of low seed biomass corresponded with the seasons when there were too few or no resightings of *S. guttata* to model (Figure 4.6).

At Hartley in 2016, *S. guttata* densities during late summer were 0.015 birds/ha (95% CI = 0.012–0.019). In late autumn, densities were lower (0.0064 birds/ha, 95% CI = 0.0058–0.0069) and during late winter, resightings were too low to produce density estimates (Figure 4.6). At Rockleigh in 2015, *S. guttata* had a low late winter density (0.0092 birds/ha, 95% CI = 0.0091–0.0093). This increased during late spring, with 0.019 birds/ha (95% CI = 0.017–0.020). There were no resightings of tagged birds during late autumn 2015 at Rockleigh. In 2016 at Rockleigh, *S. guttata* densities were higher than 2015, being 0.032 birds/ha (95% CI = 0.0310–0.0327) in late summer. Resightings during late autumn 2016 were too low for densities to be calculated, while there were no sightings of *S. guttata* during late winter 2016 (Figure 4.6). At Springton in 2015, there were no re-sightings of tagged birds during late autumn and no sightings of *S. guttata* during late winter, so densities could not be calculated. Late spring populations had a density of 0.035 birds/ha (95% CI = 0.029–0.042; Figure 4.6).

Seed biomass on the soil surface was highest during late summer in both years (>3 g m^{-2} at Rockleigh and Springton; >1.2 g m^{-2} at Hartley) and decreased during late autumn at all three sub-regions (Figure 4.7). At Rockleigh in 2015 and Rockleigh and Springton in 2016, soil surface seed biomass continued to decrease to less than 1.54 g m^{-2} during late winter.

However, at Hartley in 2015, soil surface seed biomass was particularly low during late autumn (0.046 g m^{-2}) and increased again during late winter to 1.23 g m^{-2} (Figure 4.7). Standing crop seeds were highest during late spring 2015 (≥1.0 g m^{-2}) and late summer 2016 (≥0.72 g m^{-2}) at all sub-regions, and dropped into late autumn when seed biomass was lowest (<0.1 g m^{-2} in 2015 and <0.08 g m^{-2} at Rockleigh and Springton in 2016). At all sub-regions during 2015, seed biomass increased in late winter and was higher than for late summer (Figure 4.7). In 2016, seed biomass increased slightly between late autumn and late winter at Rockleigh and Springton, but did not reach biomasses as high as those observed during late summer. At Springton and Rockleigh, late autumn and late winter were both seasons with substantially lower total seed biomass compared to late spring or late summer. At Hartley in 2015, late autumn seed biomass was substantially lower compared to late summer or late winter.

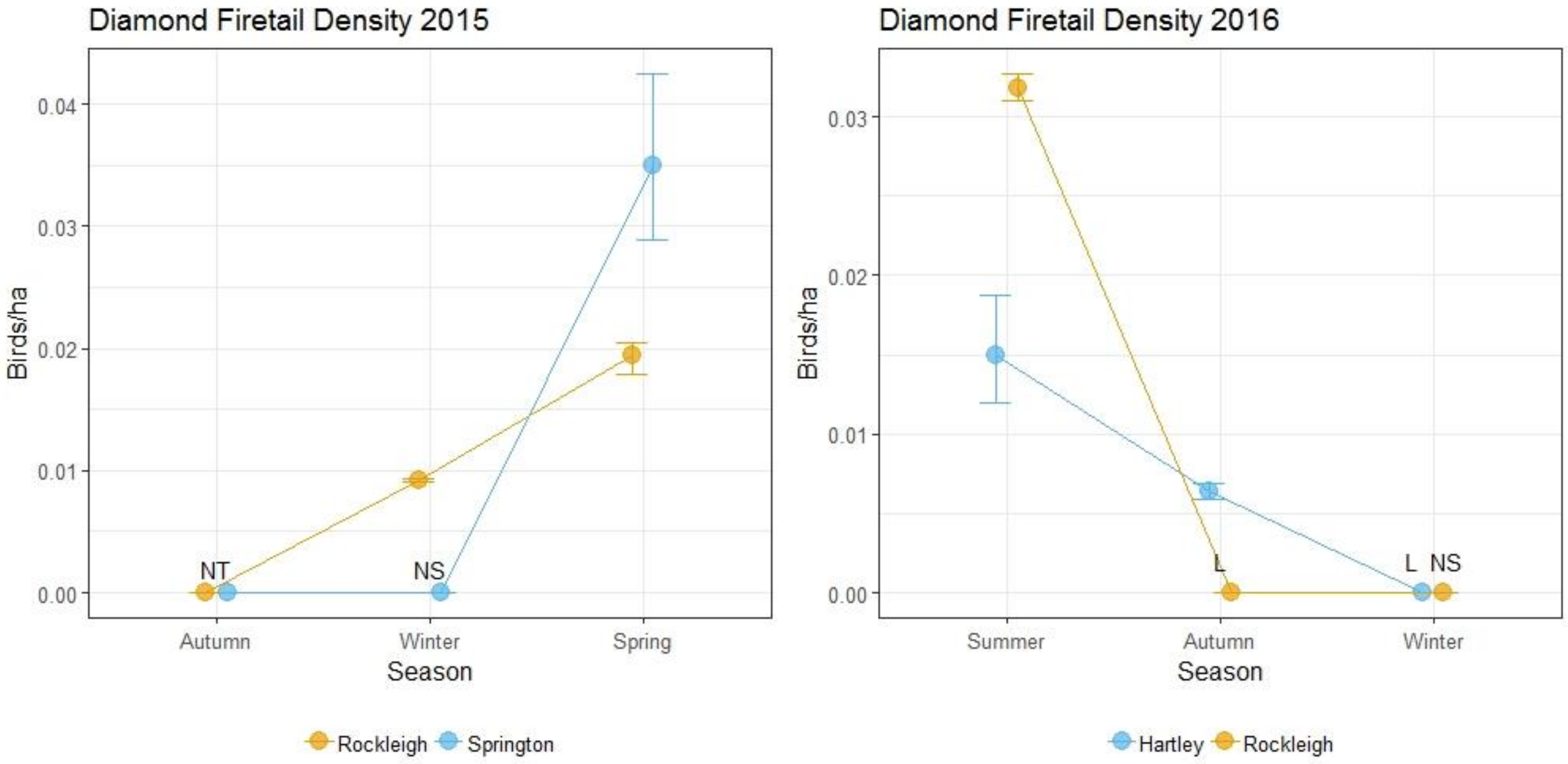

Figure 4-6 Density estimates from spatial mark-resight models of *S. guttata* in three seasons in 2015 (left) at Rockleigh and Springton and in 2016 (right) at Rockleigh and Hartley in the southern MLR. Error bars denote 95% confidence intervals. Where there were no birds recorded (NS); no re-sightings of tagged birds (NT); or too few re-sightings for models to run (L), points are displayed as zeroes.

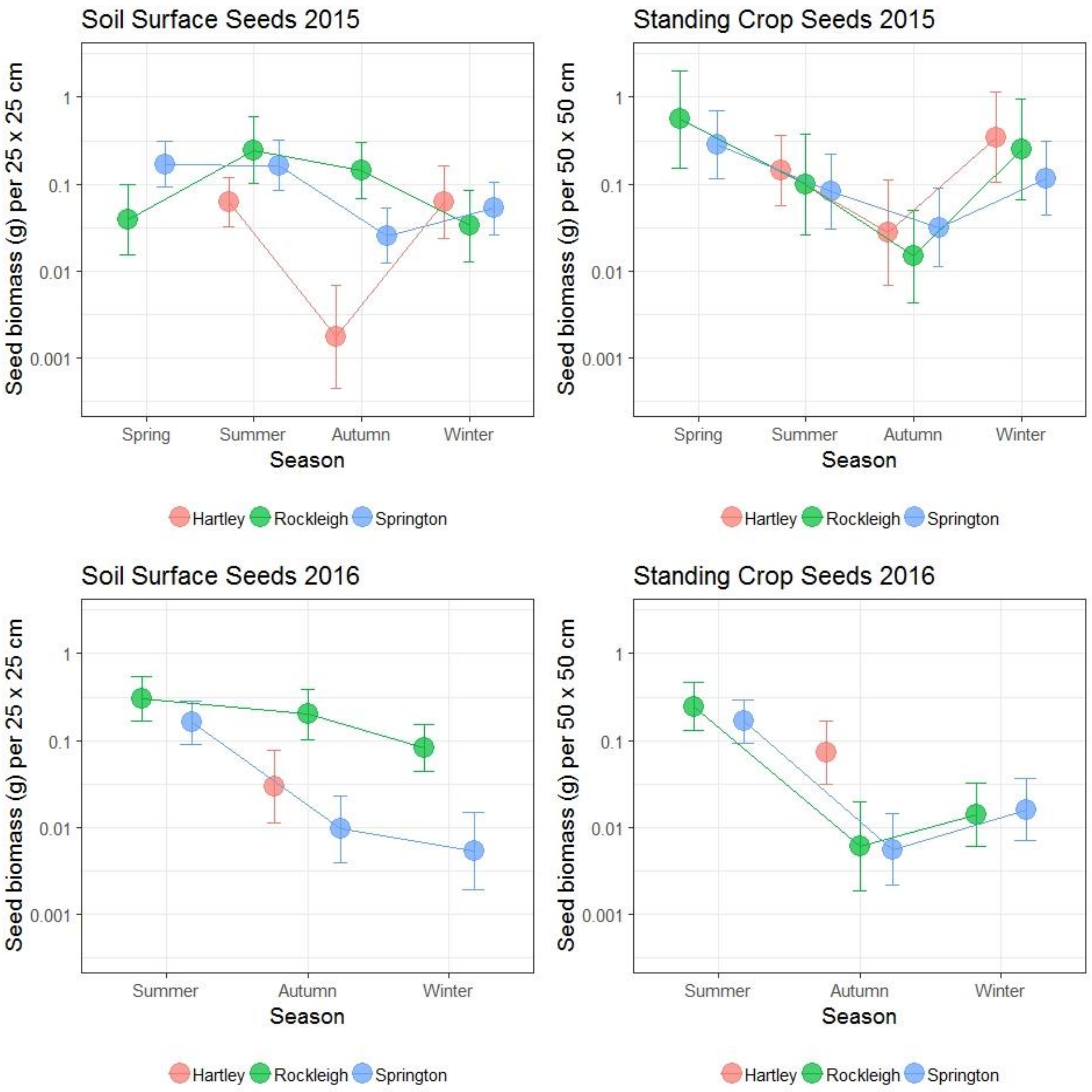

Figure 4-7 Seed biomass on the soil surface and in the standing crop of all seeding species in understorey quadrats during 2015 and 2016 across seasons at Hartley, Rockleigh and Springton in the southern MLR. Error bars denote 95% confidence intervals plotted as logarithmic functions that have not been back-transformed. Scale of *y*-axes is logarithmic.

4.4 Discussion

This study examined seasonal patterns of *S. guttata* densities in the southern MLR and their association with seasonal patterns of seed resources. Overall, monthly *S. guttata* encounters were strongly correlated with monthly seed abundances and seasonal *S. guttata* densities had similar patterns to seasonal seed biomasses. Indices of *S. guttata* and seed abundance were highest in late spring and summer and decreased into late autumn and winter when encounter rates were often too low to model. These findings highlight that *S. guttata* are relatively scarce in the southern MLR during late autumn and winter, when seeds are in short supply. Therefore, decreased seed availability during late autumn and winter may be limiting *S. guttata* numbers in the southern MLR.

4.4.1 Factors affecting *S. guttata* fluctuations

Population densities of *S. guttata* were either significantly lower in late autumn and winter than in late spring or summer, or could not be modelled because there were no or too few resightings. Between July and September, no *S. guttata* were recorded on any cameras at Rockleigh in 2016 and Springton in 2015 and 2016, and encounter rates were very low at Hartley. Finches are also known to drink from small water sources such as puddles or dew (G Hodder 2016 pers. obs.), available during winter, which may have lowered visitation rates to troughs where cameras were set up. Camera encounter rates may have subsequently increased in spring and summer because *S. guttata* water requirements increased and alternative water sources decreased, resulting in higher visitation rates to the troughs. In addition, small troughs may be a safer option than farm dams during spring and summer, as perceived predation risk may increase at larger water sources, particularly those without cover (Valeix *et al.* 2007). Thus, availability of water is somewhat mediated by risk. Daily drinking rates for granivores have been found to increase with hotter weather in semi-arid South Africa (Lee *et al.* 2017) and the Sonoran Desert, Arizona (O'Brien *et al.* 2006). Increased water requirements may have also attracted a wider range of individuals to troughs during hot or dry conditions. However, desert water sources were not found to be an attractant to migratory birds at a landscape scale in the Sonoran Desert (Lynn *et al.* 2006). In the present study, observational encounters of *S. guttata*, which were independent of water troughs, were also lower during autumn and winter compared with spring and summer. Furthermore, rainfall and temperature were not identified as predictors of *S. guttata* density in any mark-resight models. Lastly, mark-resight models correct for visit frequency by estimating 'detection probability', thus compensating for individuals visiting troughs more frequently than others (McClintock *et al.* 2009; McClintock and White 2009). Therefore, any increases in visit frequency by tagged birds should not have biased density estimates. These points suggest that patterns in *S. guttata* numbers recorded at cameras were representative of abundances in the immediate habitat rather than their use of water troughs.

Seasonally low *S. guttata* abundances may be due to predation, which is known to affect other bird species in the MLR (Colombelli-Negrel and Kleindorfer 2009; Ford *et al.* 2001; Lambert and Kleindorfer 2006). For example, 71.4% of superb fairy-wren (*Malurus cyaneus*) nests measured in four conservation parks in the MLR between 2004 to 2007 were predated (Colombelli-Negrel and Kleindorfer 2009). For *S. guttata*, nest predation is known to be a threat in the northern parts of the southern MLR, with 91–100% predation rates during the breeding seasons in 2004 and 2005 (McGuire and Kleindorfer 2007). However, in eastern populations of this region, successful fledglings were frequently observed during and after the breeding season (G Hodder 2015, 2016 pers. obs.). Overall, *S. guttata* densities were higher during the breeding season in spring–summer, with a high proportion of camera encounters attributed to fledged young birds during spring in particular. This indicates that nest predation was not causing low recruitment in south eastern MLR *S. guttata* populations, and does not explain near-zero encounter rates in autumn and winter. Cat predation on adult or fledged *S. guttata* has been historically recorded (Marshall 1932) and Read (1994) theorised this may be a driver for *S. guttata* declines in the MLR. However, many studies have found that cat predation on birds in Mediterranean systems is highest during spring and summer rather than autumn and winter (Baker *et al.* 2005; Barratt 1997; George 1974). Overall, evidence for the role of predation contributing significantly to low autumn and winter numbers of *S. guttata* is scant, although further research is required to explicitly test its contribution.

Seasonal variation in the availability of food appears to be the primary driver of fluctuations in *S. guttata* densities. Low food availability for other bird species leads to emigrations (e.g. Boyle *et al.* 2011), diet-switching (e.g. Howe *et al.* 2000; Rutz and Bijlsma 2006) or mortality (e.g. Kennedy and Dewey 2001). For example, red-necked phalaropes (*Phalaropus lobatus*) were unable to switch to alternative invertebrate prey species in response to water diversions at Mono Lake, California, resulting in reduced body condition and eventually death (Rubega and Inouye 1994). An analysis of atlas and bird-count data from eastern Australia found *S. guttata* to be strongly sedentary (Forshaw *et al.* 2012). In the present study, there was no evidence of *S. guttata* emigrating to another sub-region, through camera or field observations. However, seasonal *S. guttata* movements have been reported for some parts of central and western Victoria (Wilson and Leach 1928). A 1976 study reported *S. guttata* as a late–autumn–spring visitor to Sandy Creek in the MLR, but was absent for the remainder of the year (Rix 1976, as cited in Forshaw *et al.* 2012). In contrast, a study radio-tracking *S. guttata* at Monarto in the southern MLR between May–August found individuals did not leave their habitat patches of 0.96–16.63 ha regardless of month or number of tracking days, despite seed resources dropping significantly after late autumn rains (*n* = 6; Ankor 2005). Similarly, tagged *S. guttata* re-visited the same resource points year-round at all three sub-regions studied here (Appendix P). This suggests some southern MLR populations are winter residents and must switch to another food source or perish. While unable to switch from a grain-based diet, *S. guttata* did change diets from one of predominantly grass seeds in summer to sheoak seeds during winter (Chapter 3). However, sheoaks have been extensively cleared across the MLR (Bickford and Gell 2005; Joseph 1982) and consequently, their seed is relatively scarce (Chapter 2). Non-migratory *S. guttata* in the southern MLR are therefore likely to be experiencing food scarcity leading to high winter mortality.

4.4.2 Density of *S. guttata* populations

Density estimates for *S. guttata* in the southern MLR were low (0.023 birds/ha–0.062 birds/ha) compared with other regions. A population on the western slopes of the Great Divide in New South Wales had a density of 0.20 birds/ha (Kennedy and Overs 2001), while a site near Armidale had 0.25–1.18 birds/ha (Ford and Bell 1981). The woodlands of the MLR are on the western periphery of Australia's south-eastern woodland distribution and are separated from their eastern counterparts by semi-arid woodlands (Paton *et al.* 1994). As such, the region is a 'biological island', with isolated species populations on the outermost reaches of their continental range. The MLR has therefore experienced woodland bird extinctions before other areas. For example, the swift parrot (*Lathamus discolor*), glossy black-cockatoo (*Calyptorhynchus lathami*) and regent honeyeater (*Anthochaera phrygia*) have all been lost from the MLR but remain in (declining) populations in eastern-states woodlands (Garnett *et al.* 2011; Paton *et al.* 1999). By comparison, the east of Australia supports more extensive woodlands that permit a level of buffering for small populations due to potential re-colonisation from adjacent regions (Paton *et al.* 2004). This relative connectivity in the east may explain higher *S. guttata* densities in NSW. However, densities as low as 0.01–0.06 birds/ha were recorded near Armidale during a drought in the early

1980s (Ford *et al.* 1985). This is more in line with those observed in the MLR (0.023 birds/ha at Hartley 2016 and Rockleigh 2015, and 0.062 birds/ha at Rockleigh in 2016). A theoretical minimum viable population estimate of 2,590 birds was previously calculated for the southern MLR *S. guttata* population, for the purpose of setting a target for habitat restoration (Reed *et al.* 2003, as cited in Rogers 2011). Rogers (2011) reported that 14,050 ha of lower rainfall grassy woodlands remain in the region, giving a minimum of 0.18 birds/ha for a viable population. Thus, the low densities at Hartley and Rockleigh point to unsustainable populations with a precarious long-term existence in the region.

In contrast to the Rockleigh and Hartley density estimates, a substantially higher density of 0.352 birds/ha was estimated for Springton. This is likely to be an overestimate, as density estimates increase when detectability is low (Augustine *et al.* 2018; Efford and Fewster 2013) and Springton had low detection probabilities and sparse re-sightings. In addition, the higher density estimate for Rockleigh in 2016 is likely an over-estimate due to positive bias from resighting data captured long after initial tagging dates (Kissling and Garton 2006). Despite these evident biases, the lack of increasingly positive bias in long-term density estimates at Rockleigh in 2015 and the relative similarity between closed and open estimates at Hartley suggest that any bias caused by non-closure at these sub-regions did not affect density estimates greatly. Nonetheless, closure across a year or two-year period in these populations is biologically improbable, as evidenced by the nature of the data (Appendix P) and may have decreased the precision of estimates.

The low numbers of *S. guttata* tagged in some years, despite substantial trapping effort, is indicative of low population numbers. Data from Springton in 2016 and Hartley in 2015 could not be modelled due to few camera resightings. These periods corresponded with particularly low soil surface seed biomass. During late autumn at Hartley in 2015 soil surface seed biomass dropped to near-zero and was significantly lower than at any other sub-region in late summer and late autumn, bringing the total seed availability down. Coinciding with this, there were no resightings of tagged birds at Hartley in 2015. Similarly, at Springton in 2016, soil surface seed biomass was significantly lower than at Rockleigh in all seasons and lower than at Hartley during late autumn. These correlations suggest that low periodic seed availability led to low local *S. guttata* numbers throughout the year, providing further evidence of a link between food resources and *S. guttata* abundance.

4.4.3 Caveats and limitations

This study has provided evidence that temporal *S. guttata* numbers are correlated with temporal seed availability. However, due to sparse resightings, particularly around winter, only three sub-regions were able to be modelled. As *S. guttata* were measured near-continuously across two years, assumptions of population closure were violated over stretches spanning most of a year, although density estimates for closed periods of two months have been produced. To obtain unbiased estimates of seasonal *S. guttata* densities across their whole range in the MLR, future studies would need to increase trapping events to four distinct periods at the start of each season, though this would be very labour-intensive. Cameras should be installed from the date of trapping and run for periods of 1–2 months within which closure can be assumed (Pollock 1982). A larger array of cameras within the landscape would also increase the amount of information about individual bird movements and improve model estimates.

Spatially-explicit density modelling of colour-tagged wild bird populations could be improved by building a probability model that assigns weights to partial identifications of colour-tags. In this study, there were large numbers of partially-identified *S. guttata* compared with full identifications. Though relatively safe assumptions were made about the identity of some partially-tagged birds to improve the number of resightings, many remained unidentifiable. Encounters of these unidentified birds could only be tallied for each occasion per detector and did not contribute substantially to models. Thus, there is potential to increase the accuracy of models by utilising information about partial identifications more effectively. Probability models would assign a likelihood of true identity of partially-tagged individuals based on the known number of tag combinations to which it might belong. The large numbers of partial identifications relative to full identifications could have caused some failed variance calculations or maximisation errors in some models (these models were removed from candidate sets), so a probability model may improve computational efficiency. In addition, arranging two motion sensor cameras per detector site: one on either end of the capture space facing inwards, could allow both legs of a colour-tagged individual to be recorded simultaneously. Matching images from both cameras by time and date could improve the numbers of identified birds, although it is likely to be challenging.

Future studies should consider the use of radio-trackers to obtain known fate data for small cohorts of *S. guttata*. When the fate of a bird is known, there is no uncertainty around detection probability or whether the bird is in an observable or unobservable state (White and Burnham 1999). Known fate models do not rely on regular re-sightings of tagged individuals for parameter estimation, so sparsity of re-sightings is not an issue. Rather, the status of each bird is known at each sampling occasion, so precision is high even with small sample sizes (White and Burnham 1999). The use of radio-trackers would therefore somewhat alleviate the limitations of capturing birds from a sparse population. In addition, any potential bias of detecting birds at resource points would be removed.

4.4.4 Summary

This study has provided evidence that *S. guttata* numbers fluctuate in response to seasonal changes in seed resources, such that low food resources during late autumn–winter lead to sparse *S. guttata* densities. As some populations of southern MLR *S. guttata* are year-round residents, the maintenance of these low numbers is likely due to high autumn and winter mortality. However, increased mobility of birds during autumn and winter cannot be ruled out as an explanation for lower densities. Juveniles would be more susceptible to starvation than adults, as they have higher energy demands (Weathers and Sullivan 1989). Shorter winter day-lengths during which to forage and colder nights (Lehikoinen 1987; Meijer *et al.* 1996) would compound these issues. If recruitment of new breeding birds into the population is lower than the loss of adults, a slow but steady decline would be expected. Such declines have been observed for MLR *S. guttata* (Paton *et al.* 1994). To test whether low food availability is limiting *S. guttata* survival, in particular the survival of juveniles through winter to the following breeding season, survival rates at a food-supplemented population should be compared to survival rates at a non-supplemented population. Overall, low seed biomass and correspondingly low *S. guttata* densities during late autumn–winter are concerning and targeted species management should focus on improving seed resources, particularly during winter.

Statement of authorship

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Name of Principal Author	Grace Hodder		
Contribution to the paper	Conceptualised and designed the experiment, collected and analysed data, interpreted the results and wrote the manuscript.		
Percentage contribution	85%		
Signature		Date	16/12/2019

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Contribution to the paper	Assisted in study conceptualisation and design, and commented on draft manuscript.		
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Contribution to the paper	Assisted in study conceptualisation and design, and commented on draft manuscript.		
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Contribution to the paper	Assisted in data analysis.		
Signature		Date	16/12/2019

Chapter 5. Temporally patchy food resources affect survival of a vulnerable, granivorous finch

Photo by Tom Hunt 2015

5.1 Introduction

Population growth occurs when recruitment – the addition of new individuals into a population – is greater than mortality. Recruitment is therefore a fundamental process in population dynamics and is highly variable in response to a range of biotic and abiotic factors (Caswell 2000; Williams *et al.* 2002), such as changes in conditions. Recruitment rate is determined by the number of breeding adults, clutch size, number of successful fledglings and subsequently the number of juveniles that survive to breeding age (Anders *et al.* 1997; Clutton-Brock 1988). For many species that breed annually, each of these determining factors occurs at a different time of year, making them prone to seasonal effects (Magrath 1991). Over the short-term, variation in recruitment can directly impact population size. However, longer-term effects on population size occur when one or more of the processes contributing to recruitment is repeatedly compromised, affecting population structure (Pulliam 1988). Seasonal fluctuations, such as changes to the availability of food and shelter (Fretwell 1972), can alter recruitment rate by impacting on the underlying processes that occur during seasons of scarcity (Lack 1954; Lack 1966; Watson and Moss 1970). For spring-breeding species, food or shelter shortages during winter can limit the number of juveniles surviving to the following spring to breed (e.g. McCleery and Perrins 1985; Smith *et al.* 1980; Tinbergen *et al.* 1985). For example, habitat degradation and food limitation affected seasonal survival of lesser snow geese (*Anser caerulescens caerulescens*) goslings in Manitoba, resulting in reduced reproductive output (Williams *et al.* 1993).

In the Mount Lofty Ranges (MLR), South Australia, predominantly annual (>75%) invasive grasses now dominate the understorey (Chapter 2). In contrast, 90% of the grass species native to the region are perennials (Davies 1997). Annual and perennial grasses have very different patterns of seed production (Arredondo *et al.* 1998; Corbin and D'Antonio 2004). This significant shift in understorey composition has changed the length and timing of seed production (Chapter 2). As a result, seed availability fluctuates significantly across the year, with scarce seed in late autumn and early winter (Chapter 2). Fluctuations in seed resources affect the diet of the granivorous diamond firetail (*Stagonopleura guttata*) such that this species relies almost solely on sheoak seeds (*Allocasuarina verticillata)* when grass seeds are scarce (Chapter 3). However, *A. verticillata* has been heavily affected by clearance and now has a limited distribution (and seed supply) throughout the range of *S. guttata* (Chapter 3), jeopardising the availability of this key resource into the future.

Unsurprisingly, the persistence of *S. guttata* in the MLR is tenuous, with estimated densities of between 0.023 and 0.062 birds/ha (Chapter 4). An analysis of the state and trajectory of southern MLR *S. guttata* estimated a theoretical minimum viable population size of 2,590 individuals (Rogers 2011). The area of grassy woodlands in the MLR is predicted to be 14,050 ha (Rogers 2011) which, based on the density estimates from Chapter 4, would support just 323–871 individuals. Even if historical mapping underestimated potential habitat (i.e. scattered trees), *S. guttata* numbers are still likely to fall below the minimum viable estimate. Mirroring the seasonal patterns of seed resources, *S. guttata* abundance indices are very low in late autumn through winter (Chapter 4), suggesting high dispersal or mortality. If mortality is the cause of low winter numbers, survival of juveniles from the spring/summer breeding season through winter is at risk. Juveniles may be more susceptible to food scarcity, being less experienced than adult birds at foraging, and may therefore experience a disproportionately high mortality rate when food is scarce. Juvenile survival is a fundamental factor in recruitment, and low winter survival would reduce the numbers surviving to breed. A lack of new recruits into the breeding population would alter population structure and may be contributing to long-term population declines among this species.

This study tests the hypothesis that a scarcity of naturally occurring seed during late autumn and winter is affecting the survival of *S. guttata* over winter, particularly juveniles. Specifically, this study examines whether: i) year-round food supplementation increases *S. guttata* survival; ii) *S. guttata* individuals rely on supplemented food year-round or only during months of scarce seed resources; and iii) food-supplementation increases the survival of juveniles to breeding age.

5.2 Methods

5.2.1 Study area and sampling design

This study was conducted in the southern MLR over a three-year period from winter 2013 to winter 2016. During this period, the survival of *S. guttata* individuals was measured using capture-resight techniques at six sub-regions (Karinya, Springton, Rockleigh, Monarto, Hartley and Milang) located along the eastern scarp of the southern MLR. Each sub-region was 10–23 km apart, far enough to exclude regular movement of *S. guttata* individuals between sub-regions based on re-capture distances of <10 km in 99.5% of banded birds (Higgins *et al.* 2006) (Figure 5.1). Each sub-region contained three study sites located 1–8 km apart (*n* = 18 sites; Figure 5.1 and 1.3 in the *General Introduction*). Sites comprised patches of remnant or revegetated open eucalypt woodland with stands of *A. verticillata* and *Callitris gracilis* and predominantly weedy understoreys. To test the hypothesis that food scarcity during winter is affecting *S. guttata* survival, supplement seed was provided at half of the sub-regions (at each site at Milang, Monarto and Springton) for approximately two years. Water was provided at all 18 sites for this period.

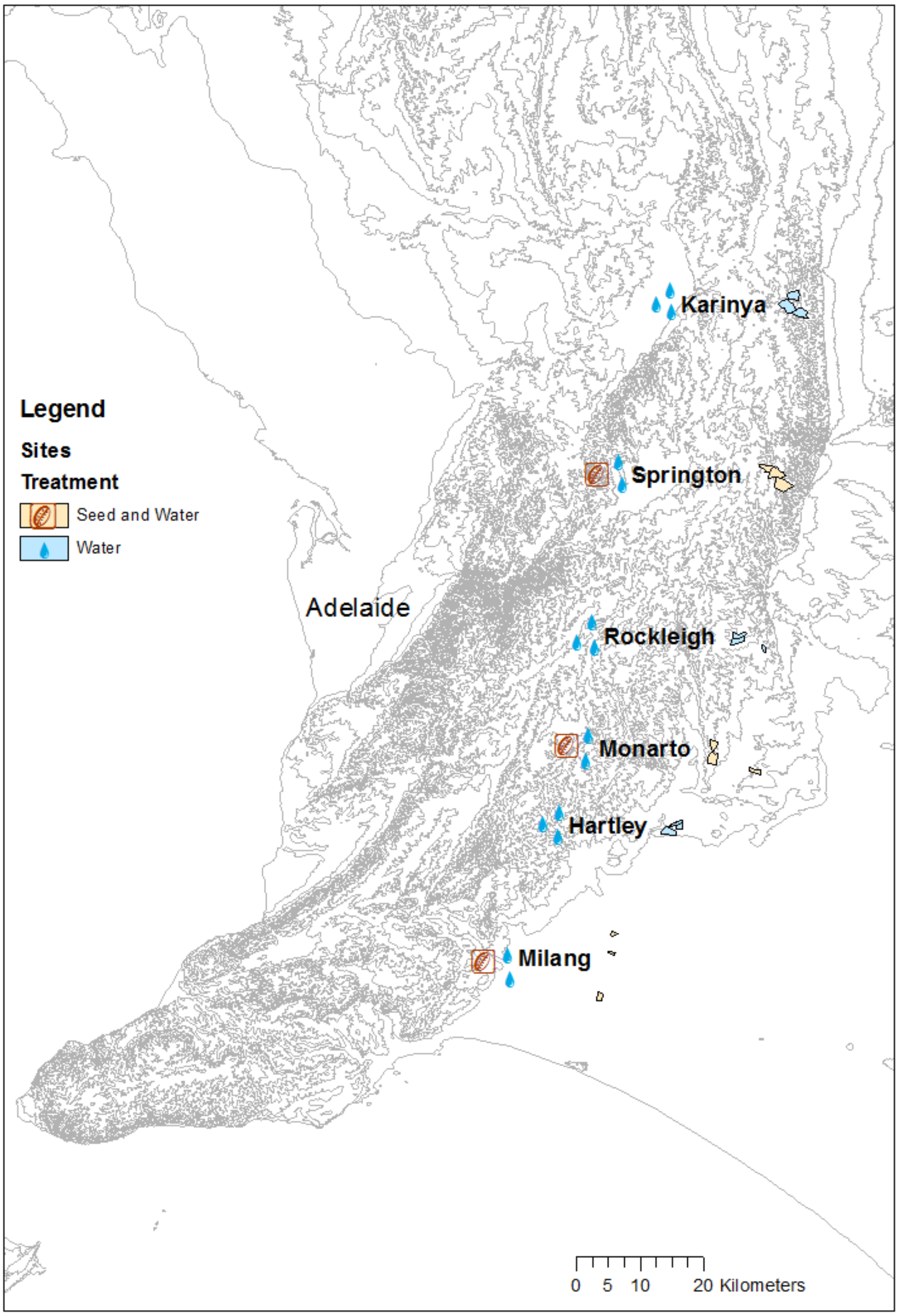


Figure 5-1 The Mount Lofty Ranges, South Australia, depicted with grey contour lines, and an overlay of the 18 study sites (pale blue and pale orange polygons) labelled by sub-region. Seed (brown symbols) was supplemented at all three sites at Milang, Monarto and Springton.

5.2.2 Sampling methodology

5.2.2.1. Seed and water supplementation

Resource stations containing water points (at all sites) and feeders (at nine sites only) were established in areas frequented by *S. guttata* (G Hodder 2014 pers. obs.), adjacent to vegetation to provide cover. Water points consisted of a 200 L drum attached to a trough made from galvanised iron guttering approximately 40 cm in length (Figure 5.2). A float valve and pipe regulated water flow from the drum to the trough. At some sites, a pre-existing water trough (for stock, or established by the landowners) was used in place of a purpose-built station. Water points provided a point of attraction for *S. guttata* at which they could be observed and recorded. Feeding stations were established next to water stations (within ~10 cm) at all sites within alternate sub-regions from south to north: Milang, Monarto and Springton. Feeding stations consisted of a 60 L Dome Rubbish Bin filled with mixed finch seed (containing a mix of Japanese millet *Echinochloa esculenta*, Shirohie millet *Echinochloa utilis*, yellow panicum *Panicum miliaceum*, red panicum *Panicum rigidulum*, wheat *Triticum aestivum*, plain canary seed *Phalaris canariensis*, linseed *Linum usitatissimum*, canola rapeseed *Brassica napus* and fine shell grit) (Figure 5.2). A slit was cut into the lower outer-edge of each bin to allow a slow flow of seed out of the bin and onto a plastic tray, fitted around the outside of the bin. Trays were positioned such that seed flow stopped once a small pile of seeds built up at the slit, and resumed once seed was removed by foragers (Figure 5.2; Figure 5.3).

Fences made from pig and chicken-wire were built around each resource station, secured by steel star droppers. The fences prevented kangaroos, stray livestock and rabbits from accessing seed and water. Resource stations containing feeders were entirely enclosed by weldmesh wire frames (50 x 50 x 4 mm). This prevented competition from large seed-eating birds, but allowed smaller birds such as peaceful doves (*Geopelia placida)* and red-rumped parrots (*Psephotus haematonotus)* to access seed (Figure 5.2). Water and seed were topped up manually approximately every four weeks, or as necessary.

Figure 5-2 A resource station with provisioned seed and water (left). A weldmesh cage with a roof encloses a small tank, trough, seed tray and seed bin. A resource station with provisioned water only is surrounded by a pig-wire fence (right).

Table 5.1 A timeline for research activities undertaken at each of four sub-regions (each with three sites) in the southern MLR between 2013 and 2016. Shaded squares indicate the months during which: trapping and tagging of *S. guttata* occurred (numbers represent number of trapping days), resource stations with provisioned water were installed and running ('x' indicates the addition of provisioned seed), cameras were installed and running, and dawn-dusk surveys were undertaken at feeders.

	Year	**2013**								**2014**												**2015**												**2016**											
Sub-region	*Month*	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
Hartley (three sites) Water only	Trapping/tagging																								6										3										
	Resource stations														▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
	Camera monitoring																						▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨			
	Dawn-dusk surveys																																												
Monarto (three sites) Seed & water	Trapping/tagging	1					2			1		2	3		2		3				1	1				1			1	1			2		1										
	Resource stations														▨	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Camera monitoring																						▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨			
	Dawn-dusk surveys															▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨						
Rockleigh (three sites) Water only	Trapping/tagging																				1		2		2											2	1								
	Resource stations														▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
	Camera monitoring																						▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨			
	Dawn-dusk surveys																																												
Springton (three sites) Seed & water	Trapping/tagging													2			1			3					2												2								
	Resource stations														▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
	Camera monitoring																							▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨			
	Dawn-dusk surveys																											▨																	

5.2.2.2. Trapping and tagging

Trapping was attempted at all sites within each sub-region, beginning in 2013. However, *S. guttata* were scarce in the environment and trapping large numbers of individuals at all sub-regions was difficult. Three trapping days at Milang yielded only five captures, and no *S. guttata* were captured at Karinya until the third year of study, when 27 birds were captured and tagged. Therefore, trapping effort was focused on the four sub-regions, where the most birds were caught, allowing survival of cohorts to be measured over time. As such, this chapter presents data from Hartley, Springton, Rockleigh and Monarto. Nine trapping days at Hartley yielded 45 tagged *S. guttata*, ten trapping days at Rockleigh yielded 121 tagged *S. guttata*, 15 trapping days at Springton yielded 40 tagged *S. guttata* and 22 trapping days at Monarto yielded 76 tagged *S. guttata* (Table 5.1). A trapping day consisted of erecting 6–12 mist-nets at dawn throughout a ~20 ha area of suitable habitat surrounding resource stations or known *S. guttata* hotspots. Nets were monitored regularly until late-afternoon or weather conditions became unsuitable (too hot, windy or raining). Each captured *S. guttata* was banded on the left leg with a uniquely numbered metal band provided by the Australian Bird and Bat Banding Scheme and three plastic coloured bands, one on the left leg (tarsus) and two on the right tarsus. The colour used on the left tarsus identified the sub-region, and when coupled with the two on the right tarsus enabled individual birds to be distinguished without the need for recapture. The age, weight and condition of the primary wing feathers were recorded for each individual. Age (juvenile, immature, sub-adult or adult) was determined by examining plumage and beak colouration (Forshaw *et al.* 2012). Birds were then released.

Figure 5-3 The view from a motion-sensor camera attached to a water tank, facing a water trough (left) where New Holland honeyeaters *Phylidonyris novaehollandiae* are bathing, and a feeder (right) where several *S. guttata* are feeding on the seed spilling out onto the tray.

5.2.2.3. Camera monitoring

One motion-sensor wildlife camera was established at each resource station, attached to either the water drum, or a star picket where drums were absent. A combination of Reconyx HC500 HyperFire Infrared Trail Cameras and Moultrie M-990i Infrared Digital Game Cameras were used. Cameras were deployed after resource stations were established, and remained in place for approximately 20 months (unless a camera malfunctioned, in which case it was removed and replaced with another; Table 5.1). Cameras were placed approximately 15 cm above the height of the trough, facing horizontally along its length. Sticks and rocks were strategically placed in the trough to attract *S. guttata* into a favourable position to view colour band combinations. In addition, the trough edges acted as perches such that if a bird moved from one edge to another, the colour-tags on each leg could be photographed in succession. Cameras were secured using tie-down (Occy) straps and were tilted slightly downwards by sticks wedged between the camera and drum. Cameras were set to record images, in bursts of three in quick succession once triggered by motion, with no delay in between bursts. The PIR sensitivity was set to high and vegetation was removed from the immediate 2 x 2 m area surrounding the cameras, to reduce false triggers. Cameras were left to record continuously, fitted with rechargeable batteries and 16 or 32 GB SD cards. Cameras were checked approximately every 4–8 weeks, and their batteries and SD cards were replaced as necessary. This resulted in approximately 2–4 weeks of continuous footage for every 4–8 week period, with occasional camera malfunctions resulting in inadequate footage (24 occasions from 242 camera checks).

5.2.2.4. Feeder surveys

Surveys of *S. guttata* foraging behaviour at feeders were undertaken to measure the amount of energy consumed from supplemented seed at different times of the year. At Monarto, a dawn–dusk survey was undertaken monthly at one site for two years during July 2014–June 2016 so caloric intake of individuals could be followed through time. At Milang and Springton however, six initial surveys in June, July and August 2015 did not record any *S. guttata* feeding on provisioned seed. As such, additional observations of feeders were conducted at these sites during manual tracking surveys (see Chapter 3), though no evidence of *S. guttata* eating provisioned seed was found. Camera images from Milang and Springton also showed no evidence of supplemented seed consumption by *S. guttata*, although other species ate the seeds. As such, Milang and Springton were treated as non-supplemented for analyses and no further feeder surveys were undertaken at these sites.

Surveys commenced at dawn and were conducted by two observers positioned far enough from the feeder so as not to disturb visiting birds. The feeder was observed continuously from dawn until dusk, with short breaks taken in turn. As such, at least one observer was monitoring the feeder at all times. For every tagged *S. guttata* visiting the feeder, its colour-tag combination, time of arrival, the time it left, and its behaviour (foraging, resting, preening, or alert) during the visit were recorded. In addition, the number of untagged *S. guttata*, their age (juvenile, immature, sub-adult or adult) and the time spent at the feeder were recorded. The second observer recorded the foraging rates of individual *S. guttata* by measuring the time taken to eat ten seeds (including picking up the seed, de-husking, mandibulating and swallowing). Observer two repeated measurements on each tagged individual as many times as possible, while maximising the number of measurements made on every tagged individual that visited the feeder throughout the course of the day. In addition, foraging rates of untagged birds with a focus on juveniles and immatures were recorded.

5.2.3 Camera image processing

Camera images were examined and those without *S. guttata* were discarded. For each image containing a colour-tagged individual, the colour combination was recorded where possible (either fully or partially identified), along with the site, date and time the photograph was taken. The number of untagged individuals in each frame was also recorded as well as the age class of all tagged and untagged birds. There were no sightings of tagged individuals at sub-regions other than where they were first captured, so sub-regions were deemed independent.

5.2.4 Statistical analysis of patterns

5.2.4.1. Summary statistics of survival

Trends in young and adult *S. guttata* survival were examined at Hartley, Monarto, Rockleigh and Springton. These analyses complemented mark-resight survival modelling by providing information about sub-regions that could not be modelled due to sparse resightings (see Section 5.3.2). The minimum number of days that *S. guttata* were known to be alive throughout the study, calculated as the time of capture to the last known sighting was square-root transformed to meet the assumptions of normality. Unpaired, parametric *t*-tests were performed on the transformed data using GraphPad Prism version 7 for Windows, (La Jolla California USA) to assess differences in longevity between sub-regions (*n* = number of tagged individuals). The same analysis was performed for young birds (*n* = number of tagged juveniles, immatures or sub-adults). In addition, the number of juveniles known to have survived their first year was compared for supplemented (Monarto) and non-supplemented sites (Hartley, Springton and Rockleigh) using Fisher's exact tests.

5.2.4.2. Mark-resight modelling of survival

To obtain survival estimates of *S. guttata*, mark-resight models were built using the RMark package (Laake 2013) in R version 3.5.1 (R Core Team 2016). This approach models encounters (resightings) of tagged individuals, incorporating the sightings of untagged and partially-identified, tagged individuals. Poisson-log normal mark resight models (McClintock *et al.* 2009) were employed because the exact number of tagged individuals in the population at every sampling occasion was unknown and sampling was with replacement. Unlike spatially-explicit capture-recapture models (used in Chapter 4; Efford 2018), these models can be used to estimate apparent survival (Phi φ, an estimate of actual survival corrected for resighting probability) when sampling is under the robust design (McClintock and White 2009). However, they do not account for the spatial element of camera arrays, which is advantageous for density analyses (Chapter 4). Poisson-log normal mark-resight models estimate the following core parameters: mark-resight probability (alpha α), individual heterogeneity (sigma σ), the number of unmarked individuals in the population

(U), the probability of transitioning from an observable state to an unobservable state (gamma double prime ϔ) and the probability of remaining at an unobservable state (gamma prime ϓ). For this study, apparent survival (Phi φ) was the main parameter of interest and was examined in relation to time, while all other core parameters were kept constant through time.

Response variables comprised capture histories of tagged individual resightings, counts of unmarked individuals and counts of unidentified, tagged individuals. One sampling occasion spanned a month-long period within which at least one motion sensor camera was recording data for a sub-region. This resulted in 17 sampling occasions for each sub-region. Population closure was assumed within but not between occasions, following the robust design. Counts of unmarked individuals comprised the maximum number recorded together per month. The number of unidentified, tagged individuals recorded > 2 minutes apart per month, per sub-region were capped at the total number possible given the number of fully identified individuals. The number of tagged *S. guttata* known alive and in the populations at the first sampling occasions were also provided to the model. Capture histories were plotted using ggplot2 in R version 3.5.1 (R Core Team 2016; Wickham 2009), with points weighted by the number of resightings per month.

Sub-regions were modelled separately, due to variation in trapping and sighting occasions. Sparse resightings of smaller numbers of tagged birds at Hartley and Springton produced models with large variances and thus unsensible estimates. Resightings of young birds were too sparse to model juvenile, immature or sub-adult survival independently. Therefore, only the results for Monarto (supplemented) and Rockleigh (not supplemented) are presented. For these two sub-regions, the largest cohorts of captured *S. guttata* (47 individuals captured prior to October 2014 at Monarto, and 109 individuals captured between March 2015 and February 2016 at Rockleigh) were modelled. This approach was necessary because the addition of smaller cohorts (12 or fewer individuals) did not provide enough information to warrant the additional complexity required by their inclusion in the models. Two models were run each for Monarto and Rockleigh: a null model (all parameters kept constant) and a model constraining apparent survival by seasonal groups (spring/summer and autumn/winter; the predictor variable). Seasons were grouped by relative abundances of seed and *S. guttata* (see Chapters 2 and 4). There were computational issues with running more complex models due to a high level of individual heterogeneity among tagged birds. The null model and the season-constrained model was compared using Akaike's Information

Criterion corrected for small sample sizes. Model estimates of apparent survival and their confidence intervals were extracted using RMark and displayed graphically.

5.2.4.3. Energy intake from supplement seed

To determine whether *S. guttata* at Monarto were relying wholly on supplemented seed or were also foraging naturally, their daily energy (kJ) intake from supplemented seed was calculated. To determine the number of seeds consumed per day by individuals, their foraging rates were averaged monthly and multiplied by the time they spent foraging at the feeder. This value was then multiplied by the average kJ contained in a standard millet seed (0.074 kJ) (Price 1983) to determine approximate daily caloric intake. An allometric scaling equation for passerines was used to determine average Field Metabolic Rate (FMR) (Nagy 1987). The average body mass of captured *S. guttata* (18.03 g ± 1.30 SD) was used in this equation to determine the FMR of an MLR *S. guttata*: 77.99 kJ/day. Individual daily kJ intakes at the feeder were divided by the FMR to determine the proportion of the expected daily energy intake that was met by the supplemented seed.

The foraging rates of young (juvenile, immature or sub-adult) were also compared with those of adults. Sufficient replicate data were collected on six different young birds and 13 different adult birds. Individual foraging rates were averaged and the standard deviation among birds was calculated. Welch's *t*-test was used to compare foraging rates of adult and young. Analyses were undertaken using GraphPad Prism version 7.

5.2.4.4. Linear mixed modelling of energy intake

Linear Mixed Models were employed to assess temporal patterns of energy intake at the feeder using the lme4 package in R version 3.5.1 (Bates *et al.* 2015; R Core Team 2016). The response variable – the proportion of expected daily kJ intake obtained from supplemented seed – was modelled against the fixed factors: month, season and year, with individual (ID) as the random effect to account for variation among birds. Because month and season are not independent, two separate models were run (Month*Year and Season*Year), and their relative fits were compared using Akaike's Information Criterion corrected for small sample sizes (Appendix Q). The response variable was cube root transformed to obtain a distribution closer to normal to satisfy model assumptions. Normal Quantile-Quantile and residuals versus fitted estimates plots were used to check the following assumptions: explanatory variables were linearly related to the response variable and errors had constant variances, were independent and normally distributed (Appendix Q).

Likelihood Ratio Tests were used to examine the interaction effect (of month by year, and season by year) for each model. To visually compare patterns of supplemented seed intake and natural seed biomass, seed biomass at Monarto (as per Chapter 2) was graphed (*n* = number of quadrats measured at Monarto per season) alongside model estimates of seasonal energy intakes. There were no foraging *S. guttata* encountered at Monarto during winter in the first year and seed biomasses were not measured in spring year two (see Chapter 2 for details).

5.3 Results

5.3.1 Capture histories

Tagged individuals at Monarto (food supplemented) were often resighted across the three years of study (Figure 5.4), particularly the larger cohorts of nine, 13 and 16 birds tagged in 2013 and 2014. Smaller cohorts tagged in 2015 (2–12 birds) or 2016 (3 birds) were only resighted within a short period post-capture. Nineteen of the 31 juveniles tagged at Monarto were resighted as adults in subsequent years.

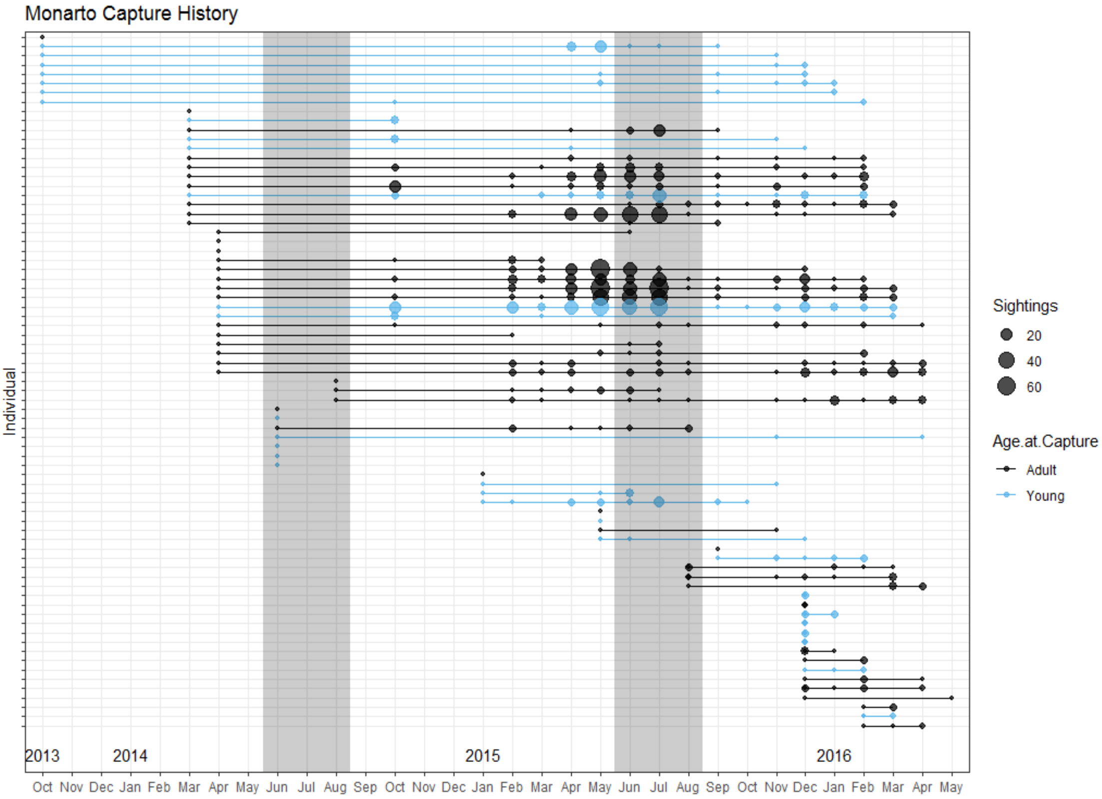


Figure 5-4 The capture and resighting history of *S. guttata* tagged at three sites at Monarto (n = 76) during October 2013–May 2016. Young at capture are in blue, adults in black. Circle size represents the number of independent resightings per month. Dark horizontal lines follow individuals resightings through time. Winter months are grey.

At Rockleigh (not supplemented), capturing *S. guttata* proved difficult prior to 2015, when a large cohort (60 birds) was tagged in April (Figure 5.5). Despite relatively high resighting rates among this cohort post-capture, 57 of these birds were not resighted after March 2016. A second large cohort (49 birds), captured in March 2016, were only resighted within a short period post-capture.

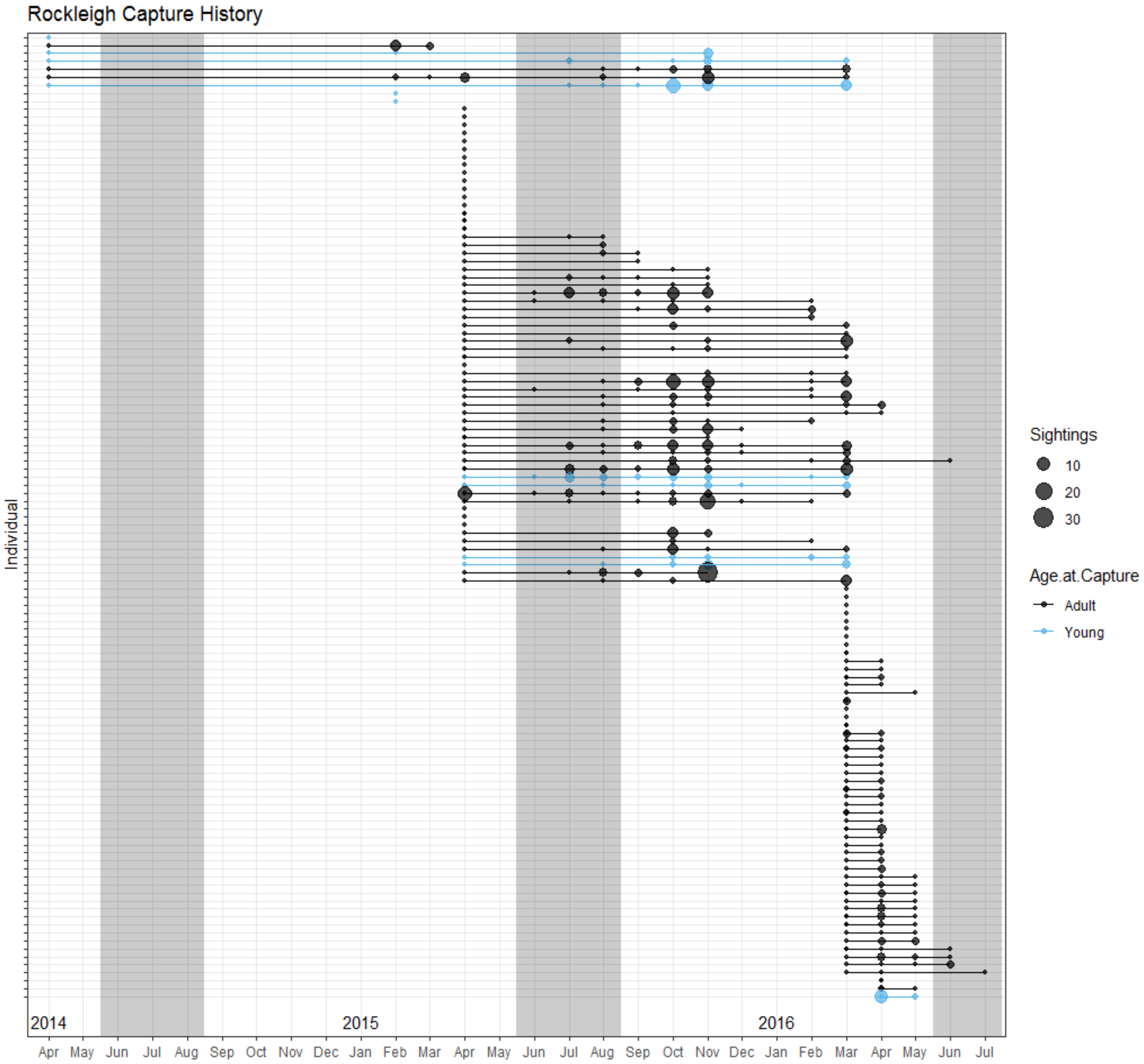


Figure 5-5 The capture and resighting history of *S. guttata* tagged at three sites at Rockleigh (n = 121) during April 2014–July 2016. Young at capture are in blue, adults in black. Circle size represents the number of independent resightings per month. Dark horizontal lines follow individuals resightings through time. Winter months are grey.

Capturing *S. guttata* at Hartley (not supplemented) was difficult. Few birds were captured until February 2016, when a cohort of 36 individuals was tagged (Figure 5.6). However, only three individuals from this cohort were resighted beyond four months post-capture, and 19 individuals were never resighted.

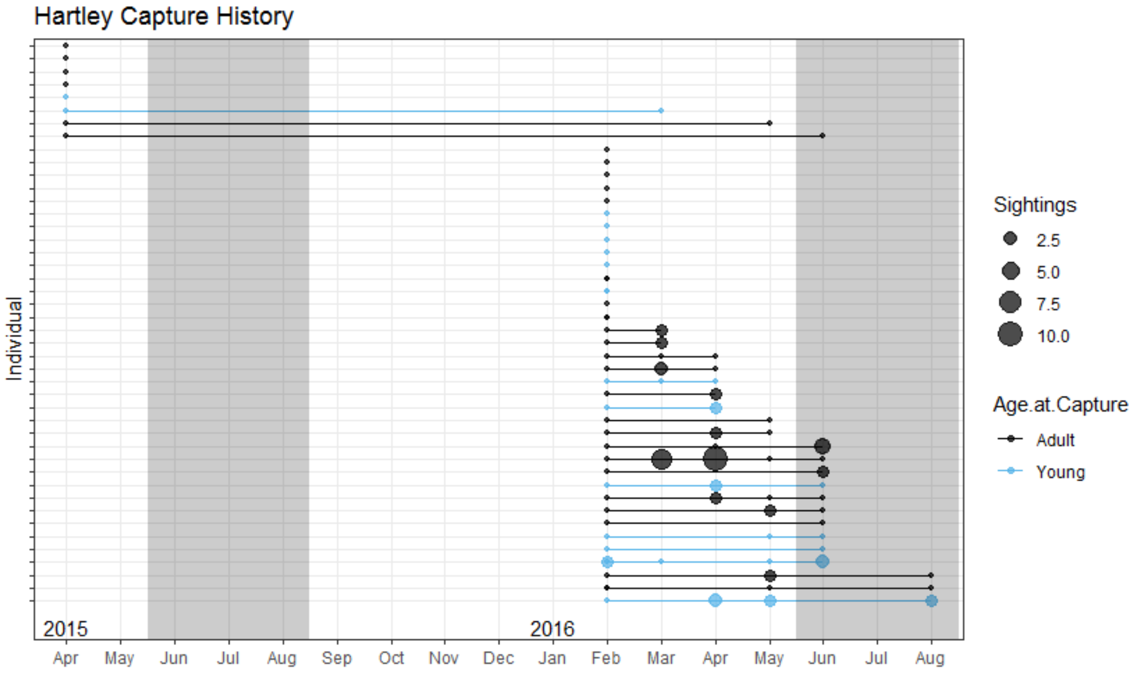


Figure 5-6 The capture and resighting history of *S. guttata* tagged at three sites at Hartley (*n* = 44) during April 2015–August 2016. Young at capture are in blue, adults in black. Circle size represents the number of independent resightings per month. Dark horizontal lines follow individuals resightings through time. Winter months are grey.

Stagonopleura guttata captures at Springton (not supplemented) were staggered across the three years, with cohorts of 2–22 birds tagged in all years (Figure 5.7). However, 29 of the 40 captured *S. guttata* were never resighted despite extensive search effort.

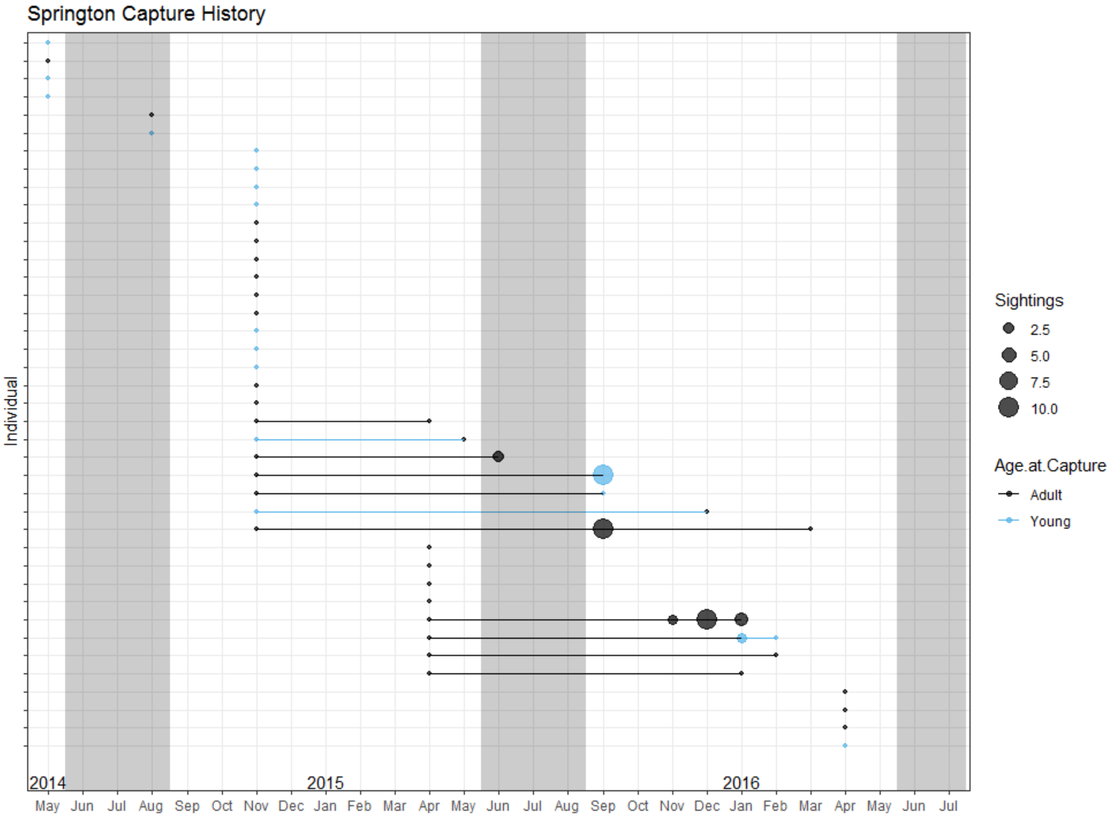


Figure 5-7 The capture and resighting history of *S. guttata* tagged at three sites at Springton (*n* = 40) during May 2014–July 2016. Young at capture are in blue, adults in black. Circle size represents the number of independent resightings per month. Dark horizontal lines follow individuals resightings through time. Winter months are grey.

5.3.2 Summary statistics of survival and behaviour

5.3.2.1. Survival

Tagged *S. guttata* at the three supplemented Monarto sites survived longer, on average, (358.10 ± 38.15 days) than those at the nine non-supplemented sites (Rockleigh: 165.40 ± 18.37 days; Hartley: 79.48 ± 16.39 days; Springton: 68.43 ± 23.19 days; Table 2). The number of days that *S. guttata* were known to be alive at Monarto was higher than at Rockleigh which had the second highest mean survival (unpaired *t*-test, $P = 0.0002$, df = 190). Mean survival at Rockleigh was higher than Springton and Hartley (unpaired *t*-tests, $P = 0.0003$, df = 154; $P = 0.02$, df = 158 respectively; Table 5.2). The percentage of tagged *S. guttata* that survived their first winter post-capture was higher at supplemented sites (78.5%; Table 5.2) than non-supplemented sites (Rockleigh = 40.7%, Springton = 20.0% at and Hartley = 15.9%). Similarly, the number of tagged birds that survived their second winter post-capture was higher at Monarto (64.6%) compared with Rockleigh (28.5%), Springton (2.5%) and Hartley (0%), and again for birds surviving through a third winter post-capture (Table 5.2).

Table 5.2 Summary survival statistics of tagged *S. guttata* at four sub-regions in the southern MLR from 2013–2016. The percentages of the number of tagged birds known to be alive after each subsequent winter post-capture, along with the average number of days tagged birds were known to be alive.

Sub-region	No. tagged birds	% known to be alive after:			Mean days known alive ± se
		1st winter	2nd winter	3rd winter	
Monarto (supplemented)	76	78.5	64.6	4.1	358.10 ± 38.15
Rockleigh (not supplemented)	121	40.7	28.5	0.0	165.40 ± 18.37
Springton (not supplemented)	40	20.0	2.5	0.0	68.43 ± 23.19
Hartley (not supplemented)	44	15.9	0.0	NA	79.48 ± 16.39

5.3.2.2. Survival of young

There was no difference in the number of days that young *S. guttata* were known to be alive between Monarto (337.60 ± 61.18) and Rockleigh (338.50 ± 88.79; unpaired *t*-test $P = 0.83$, df = 41; Table 5.3). However, Monarto and Rockleigh had longer known survival of young than Springton (36.00 ± 28.87) (unpaired *t*-test, $P < 0.01$, df = 44,41 respectively) and Hartley (76.67 ± 24.4) (unpaired *t*-tests $P < 0.03$, df = 45,24; Table 5.3). In addition, the proportions of young that were known to have survived their first winter versus those with unknown fates was clearly different between supplemented and non-supplemented sites (Fisher's exact $P = 0.0002$; Figure 5.8).

Table 5.3 Summary statistics of survival of tagged young (juvenile, immature or sub-adult) *S. guttata* at four sub-regions in the southern MLR from 2013–2016.

Study Area	No. young birds tagged	% known alive after 1st winter	Mean days known alive ± se
Monarto (supplemented)	31	73.9	337.60 ± 61.18
Rockleigh (not supplemented)	11	63.6	338.50 ± 88.79
Springton (not supplemented)	14	07.1	36.00 ± 28.87
Hartley (not supplemented)	15	13.3	76.67 ± 24.4

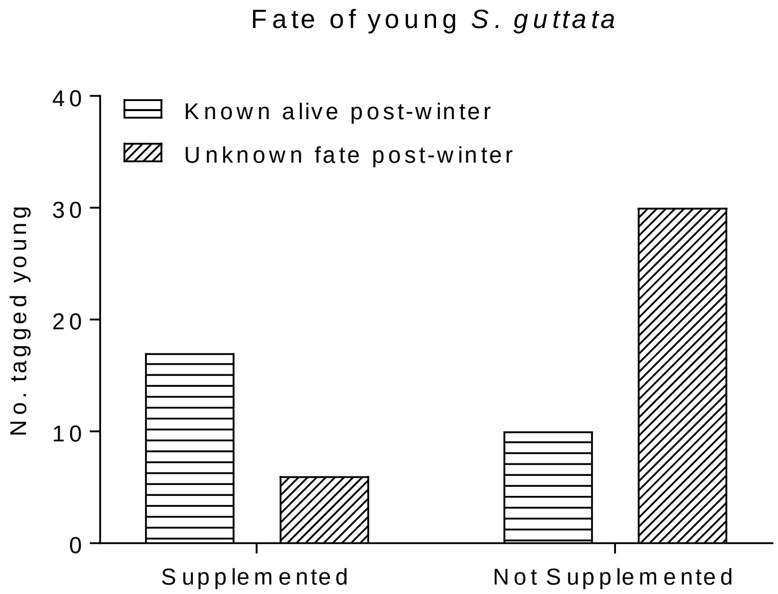


Figure 5-8 The number of tagged young *S. guttata* at supplemented sites ($n = 23$) versus non-supplemented sites ($n = 40$) that were known to survive their first winter, or were not sighted again after their first winter.

5.3.2.3. Foraging rates

Young *S. guttata* foraged for seeds at a significantly slower rate than adult birds, with young birds taking on average 35.8 ± 3.7 seconds to eat 10 seeds, and adults taking 22.9 ± 0.8 seconds (Welch's *t*-test $P = 0.02$, $t = 3.4$, df = 4.4; Figure 5.9).

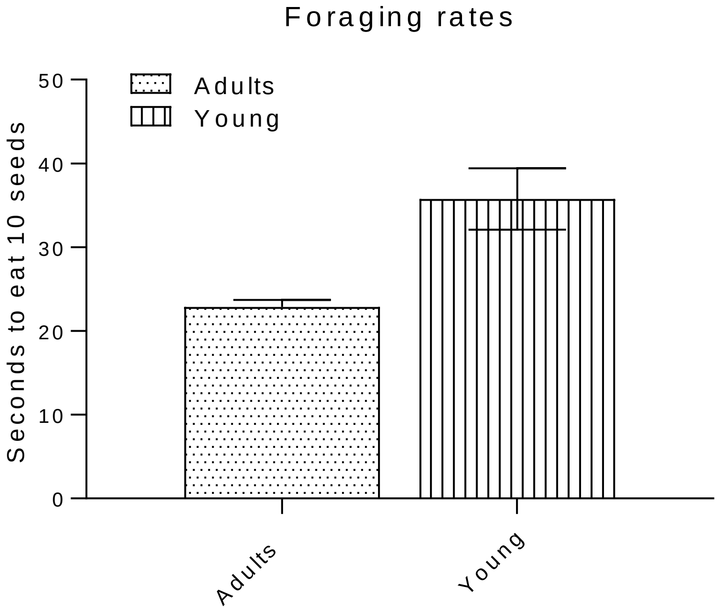


Figure 5-9 Mean ± se time taken to eat 10 seeds by adult (*n* = 13) and young (*n* = 6) *S. guttata* at a supplement feeder at Monarto, recorded during monthly observations across a two-year period.

5.3.3 Mark-resight modelling of survival

The null model was the highest ranked of the Monarto candidate set, and a better fit for explaining survival than the model constrained by season-groups (Table 5.4). This indicates that trends in apparent survival of *S. guttata* at Monarto are not well-explained by seasonal changes. In contrast, the model with apparent survival constrained by season-groups (SEAS) was the highest ranked of the Rockleigh candidate set, and a better fit for explaining survival than the null (Table 5.4). This indicates that trends in apparent survival of *S. guttata* at Rockleigh are better explained by seasonal groupings than by a time-constant model.

Table 5.4 AICc ranking of Poisson-log normal mark–resight models of *S. guttata* apparent survival at three seed supplemented sites and three unsupplemented sites in the southern MLR during 2013–2016. The model parameters: mean resighting rate (α), individual heterogeneity (σ), number of unmarked individuals (U), probability of remaining at an unobservable state (ϒ') and probability of transitioning from an observable state to an unobservable state (ϒ") were kept constant through time in all candidate models.

Candidate model	AICc	Δ_i	w_i	Dev.	K
Monarto (supplemented)					
Survival φ (~1)	**2066.4**	**0.00**	**0.998**	**2054.1**	**6**
Survival φ (~SEAS)	2079.1	12.68	0.002	2064.7	7
Rockleigh (not supplemented)					
Survival φ (~SEAS)	**1712.3**	**0.00**	**0.991**	**1697.9**	**7**
Survival φ (~1)	1721.7	9.39	0.009	1709.4	6

Phi (φ) is constrained by SEAS = seasonal groupings according to environmental variables and trends in *S. guttata* numbers (autumn/winter and spring/summer). AICc = selection criterion for small sample sizes, Δ_i = the difference between that model's AICc value and the AICc value of the model of best fit, w_i = Akaike weight, Dev. = the model deviance, K = the number of estimated parameters. Candidate models with empirical support are shown in bold.

The time-constant model estimated high survival at both Monarto (φ = 0.95 ± 0.012 SE) and Rockleigh (φ = 0.90 ± 0.019 SE), though this was higher at Monarto based on 95% confidence intervals (Figure 5.10 a). The mark-resight model estimates of apparent survival in spring/summer and autumn/winter at Monarto and Rockleigh are similar, and generally high (Figure 5.10 b). The Monarto autumn/winter survival estimate had large confidence intervals, likely due to the estimate being close to the parameter boundary and when back-transformed from the logit scale, become large. Therefore, the model perceives no difference in survival during spring/summer (φ = 0.90 ± 0.02 SE) compared with autumn/winter (φ = 0.99 ± 0.01 SE) at Monarto, though standard errors are small (Figure 5.10 b). However, at Rockleigh, spring/summer survival (φ = 0.97 ± 0.02 SE) is higher than autumn/winter survival (φ = 0.85 ± 0.03 SE), with the large difference in Akaike weightings of this model and the null model indicating a difference between the two seasonal groups (Table 5.4, Figure 5.10 b)

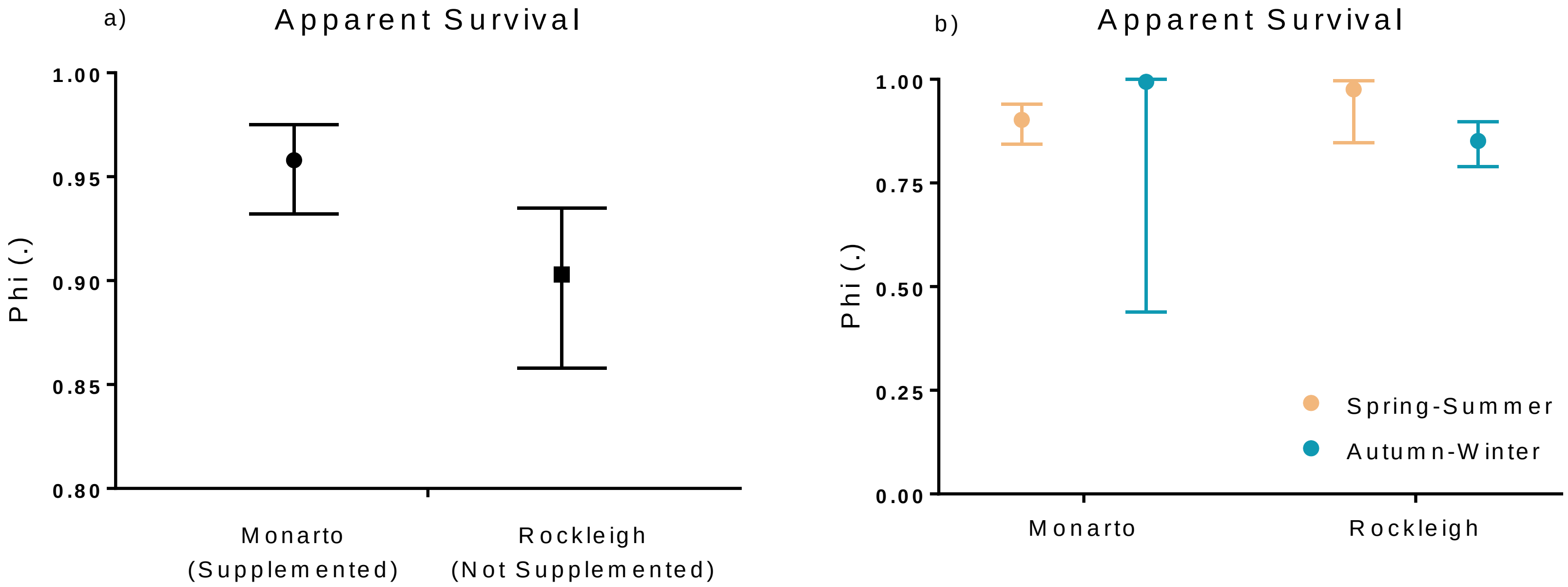


Figure 5-10 Poisson-log normal mark-resight model estimates of apparent survival of cohorts of *S. guttata* at seed supplemented sites (Monarto) and unsupplemented sites (Rockleigh) across an approximate three-year period (Oct 2013–May 2016). (a) null model estimates, (b) survival constrained by seasonal groups. All other parameters were kept constant, error bars denote 95% confidence intervals.

5.3.4 Energy intake from supplement seed

The Linear Mixed Model of seasonal changes in energy intake from the Monarto feeder was higher ranked than the model of monthly changes to energy intake as indicated by the Akaike weight, *w*i (Appendix Q). Likelihood ratio tests showed that the interactions between year and either month or season were significant in both models (Month:Year LRT = 36.93, $P < 0.001$, df = 11; Season:Year LRT = 21.63, $P < 0.0001$, df = 3). Therefore, energy intake at the feeder varied between years dependent on the month or season, and temporal changes to energy intake were best explained by seasons rather than months.

There were clear monthly and seasonal changes to the amount of energy (standardised relative to *S. guttata* daily requirements; SRDR) obtained from the supplement feed, with lower intakes in summer of both years and spring compared with autumn and winter in the first year. There was a steady increase in the energy obtained from supplemented seed from summer (0.41 kJ day^{-1} SRDR in year 1; 0.42 kJ day^{-1} SRDR in year 2) through autumn (0.63 kJ day^{-1} SRDR in year 1; 0.57 kJ day^{-1} SRDR in year 2) to winter (0.99 kJ day^{-1} SRDR in year 1; 0.72 kJ day^{-1} SRDR in year 2) (Figure 5.12). However, spring energy intakes varied considerably between years (0.53 kJ day^{-1} SRDR in year 1; 0.95 kJ day^{-1} SRDR in year 2). The energy obtained from supplemented seed averaged across the two years showed an inverse seasonal pattern to naturally occurring seed patterns throughout Monarto (Figure 5.11a, b).

Monthly modelling of standardised *S. guttata* energy intake at the feeder allows a finer-scale visualisation of temporal trends (Figure 5.12). Energy intake gradually increased month by month in both years from January (< 0.5 kJ day^{-1} SRDR) to July (~1.0 kJ day^{-1} SRDR). Intake in October–November were higher in year two (~1.0 kJ day^{-1} SRDR) than year one (~0.4 kJ day^{-1} SRDR). Intake dropped into December in both years (< 0.5 kJ day^{-1} SRDR) (Figure 5.12).

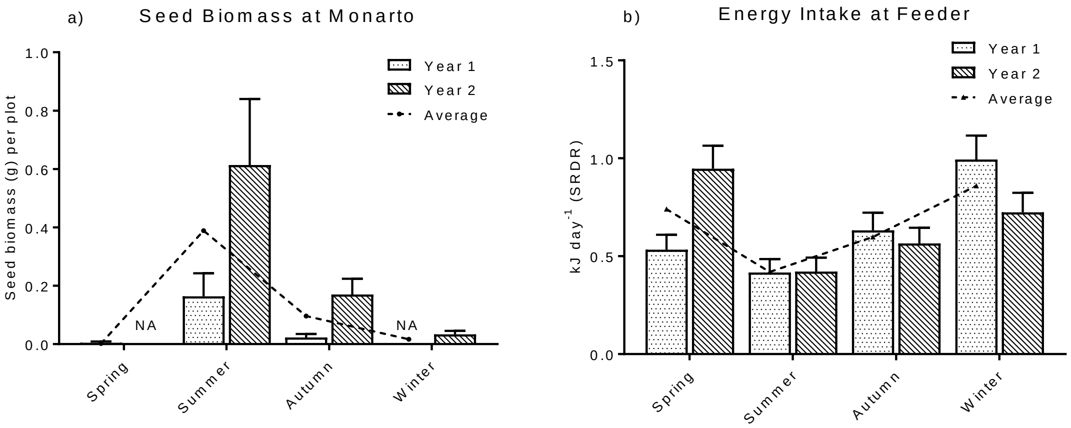


Figure 5-11 Average ± SEM seed biomass per plot (*n* = 115) measured at Monarto during 2014–2016 (a) & linear mixed model estimates of energy intake (b) from a Monarto supplement feeder, standardised relative to the average daily requirements (SRDR) of a passerine. Estimates and SEMs have been back-transformed to the raw scale.

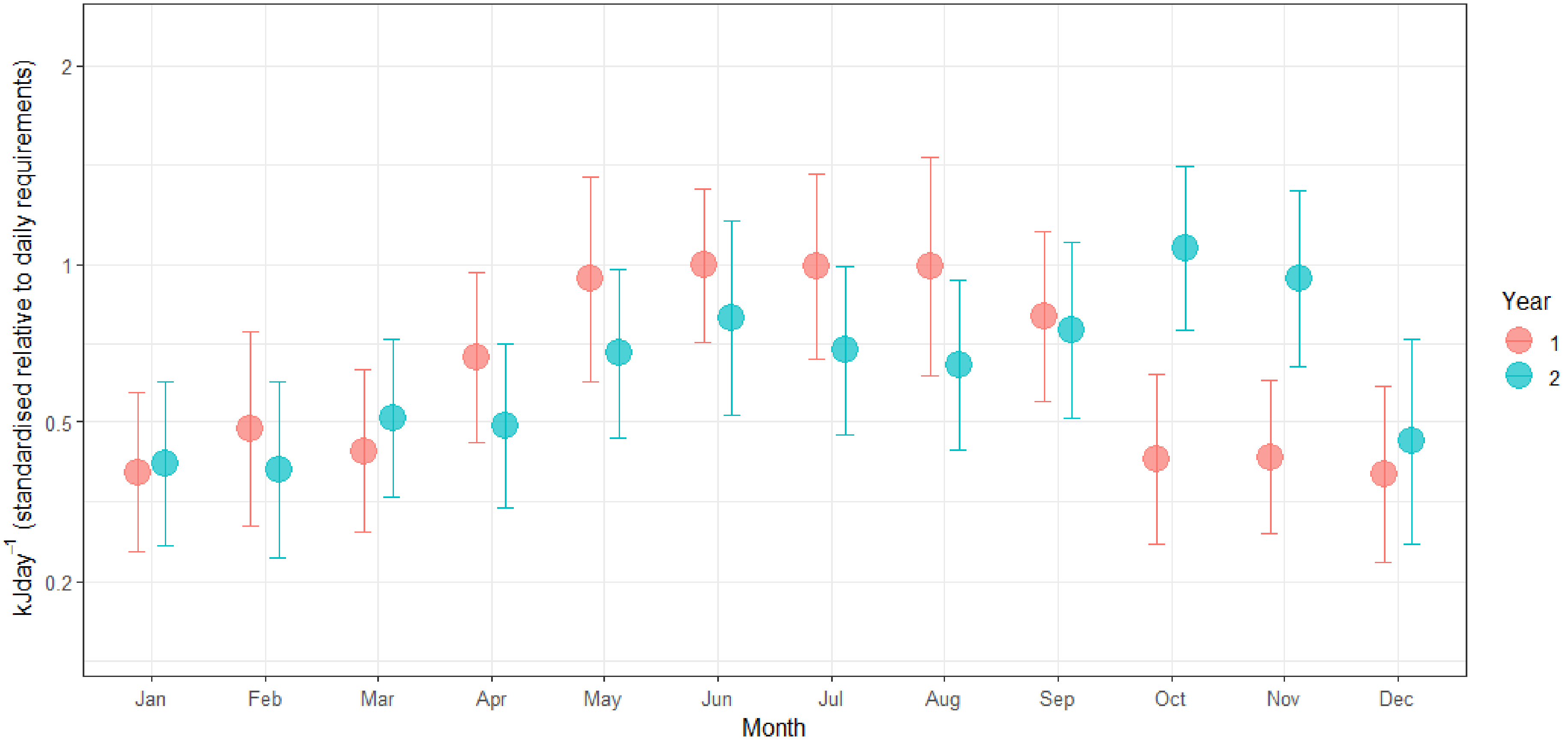


Figure 5-12 Linear mixed model estimates of the energy intake (kJ) of *S. guttata* from the supplement feeder at Monarto, standardised relative to the average daily requirements of a passerine of their size, modelled against month (x-axis) and year (coloured: red = year 1; teal = year 2). Error bards denote 95% confidence intervals, which are plotted as logarithmics and have not been back-transformed. Scale of y-axis = logarithmic.

5.4 Discussion

This study tested the hypothesis that a shortage of food is limiting the survival of *S. guttata* in the southern MLR, with a particular focus on the survival of first year birds through winter. Mark-resight analyses produced high overall apparent survival estimates (90–95%) across a three-year period that are consistent with annual survival estimates for other southern Estrildidae such as the crimson finch (*Neochmia phaeton)* (70–96%; Milenkaya *et al.* 2011) and the red-billed firefinch (*Lagonosticta senegala)* (89%; McGregor *et al.* 2007). Ashmole (1963) hypothesised that high adult survival among southern passerines was due to a lack of harsh winters, and contributed towards food limitation and favoured small clutch-sizes. Although high, time-constant survival estimates for *S. guttata* of all ages differed significantly between supplemented and non-supplemented sites, with lower survival at sites without provisioned seed. In addition, the mean number of days that tagged *S. guttata* were known to be alive was lower at all non-supplemented sites than supplemented sites. The number of young *S. guttata* that were known to have survived their first winter was higher at supplemented sites than non-supplemented sites, suggesting post-fledgling survival may be impacted by seed scarcity. Despite a limited number of true treated replicates due to *S. guttata* not taking seed at certain sub-regions, these findings provide evidence that supplemental food can improve the survival of *S. guttata*, implicating seasonal seed abundance as a limiting factor in the MLR.

5.4.1 Juvenile survival

The survival of juveniles from independence to breeding age is of critical importance for replacement rates, and therefore population longevity (Lack 1954, 1966). Juveniles are often more vulnerable than adults due to inexperience in avoiding predation (Anders *et al.* 1997), obtaining adequate food (Wunderle 1991), or lower body masses (Kennedy and Dewey 2001; Lima 1986), and their survival can be a weakness for species already at risk due to other threats such as habitat loss. In the isolated MLR *S. guttata* population, significantly more young *S. guttata* are known to have survived their first winter at seed supplemented sites than non-supplemented sites. Seed availability in the MLR in winter is scarce (Chapter 2) and obtaining adequate food within the shorter daylight hours may be challenging for juveniles that consume seeds at a slower rate than adults. Food has been documented as a limiting factor for juvenile survival in other avian species (Herrera 1998; Ward and Kennedy 1996; Zanette *et al.* 2003). For example, the survival of juvenile great tits (*Parus major*) is limited by the amount of beech seed present in winter (Perdeck *et al.* 2000). Similarly, greater snow geese (*Chen caerulescens*) in the arctic experience a rapid decline in the quality of plant foods during summer affecting juvenile survival and growth rates (Lindholm *et al.* 1994). Low juvenile survival has consequences on population dynamics (Dimond 2001). For example, the endangered burrowing owl (*Athene cunicularia*) experienced 11–48% declines in the numbers of breeding individuals directly following years of poor juvenile survival (Todd *et al.* 2003). As such, if winter survival of juveniles is food-limited among MLR *S. guttata,* the number of breeding adults in the following season is likely to be affected. Seed availability was consistently low across two years, suggesting that a periodic food scarcity occurs annually for these populations. Thus, future studies should examine the relationship between juvenile survival and subsequent adult breeding rates among *S. guttata*. A population viability analysis would identify whether recruitment matches mortality.

5.4.2 *Stagonopleura guttata* survival

The apparent survival of *S. guttata* was higher where seed was provisioned, suggesting that the survival of both adult and young birds is food limited. Apparent survival was higher during spring and summer than autumn and winter at supplemented sites, suggesting that supplementary food reduced the seasonal impact on apparent survival. Harsh winter conditions can often hamper resources, and what little is available can be severely depleted by birds (Pulliam and Enders 1971). Winter food has limited other temperate zone passerine populations (Källander 1981; Krebs 1971; Smith *et al.* 1980). Food supplementation during times of shortage slowed population declines for yellowhammers (*Emberiza citrinella*), robins (*Erithacus rubecula*) and dunnocks (*Prunella modularis*) in European farmland (Siriwardena *et al.* 2007), and significantly improved nutritional conditioning of downy woodpeckers (*Picoides pubescens*), Carolina chickadees (*Poecile carolinensis*), and white-breasted nuthatch (*Sitta carolinensis*) (Grubb and Cimprich 1990). Food supplementation enables certain species to survive in areas degraded by human development (Cannon 1999; Cannon 2000), and aid in the recovery of threatened species (Wilbur *et al.* 1974). At Monarto, many landholders have provided seed for *S. guttata* for decades (G Hodder 2018 pers. comm.). Given that this sub-region has low seed availability during winter and is affected by invasive annuals (Chapter 2), supplementary feeding may be enabling the persistence of *S. guttata* in this degraded area. While the survival modelling was limited in its application across the MLR, experimental supplementary feeding increased the number of resightings of both adults and juveniles, indicating that survival over winter is food limited. To increase population viability for *S. guttata*, natural winter food availability should be improved.

The coincidence of low seed availability, low density of *S. guttata* (see Chapter 4) and low survival probability during late autumn and winter suggest that food resources are impacting survival. However, correlation does not prove causation, and other factors may have influenced results. Birds may have been more mobile at certain sub-regions due to sparser or more scattered resources in the landscape, leading to a lower chance of detection at cameras. Similarly, the lure of food at the Monarto resource points may have caused local *S. guttata* to remain sedentary and thus increased the chance of detection. Regardless, the severe depletion of natural seed resources in late autumn and winter is concerning and indicative of seasonal food shortages across the region, with invasive annual grasses the likely cause. This study cannot prove that *S. guttata* have *not* adapted to altered seeding patterns and are in fact finding sufficient food resources elsewhere by becoming more mobile during winter months. Nor has this study demonstrated that any loss of individuals during winter is directly impacting population viability. However, the increase in overall survival probability in the presence of supplemented food is consistent with the hypothesis that food shortages are causing winter mortality.

Survival was lower at Rockleigh than Monarto, though still high (~90% overall survival probability). Rockleigh yielded the greatest number of tagged *S. guttata* and a high proportion of young birds surviving their first winter. In contrast, there were very low numbers of tagged and resighted birds at Hartley and Springton despite near-equal trapping efforts among sub-regions. It follows that Rockleigh is supporting a larger or more sedentary population than other areas. The foraging habitat at Rockleigh was a near-homogeneous grassland of *Ehrharta calycina*: perennial veldt grass (G Hodder 2016 unpub.). In contrast, Hartley and Springton comprised predominantly annual grasses with very few native perennials and small stands of *A. verticillata*. *Ehrharta calycina* is one of a small minority of perennial introduced grasses, whose seeds can germinate at any time of the year with adequate moisture (Smith *et al.* 1999) and do not mass-germinate in response to heavy rains like annual seeds (Houdet 2003; Chapter 2). Consequently, *E. calycina* produces abundant, large seeds (Fisher *et al.* 2009) throughout much of the year including autumn and winter (G Hodder 2016 unpub.). This is demonstrated in Chapter 2, where soil surface seed biomass at Rockleigh in late autumn was significantly higher than at other sub-regions, and consistently high in summer, autumn and winter. What's more, the seeds of *E. calycina* were frequently recorded in crops of *S. guttata* at Rockleigh, but not at other sub-regions (Appendix I). This emphasises that food quantity and year-round consistency are more important than food species (Chapter 3). The physiological traits of a perennial invasive have moderated the effects of landscape change for *S. guttata*. Nonetheless, a variety of native species provides nutritional diversity that a monoculture cannot.

5.4.3 Usage of supplement seed

Stagonopleura guttata did not rely solely on provisioned food at supplemented sites throughout the year. Instead, the amount of seed obtained from feeders varied seasonally, with summer seed consumption (<50% daily KJ) being lower than autumn and winter (approximately 100% of daily kilojoules). This indicates that *S. guttata* foraged naturally when local resources permitted, particularly during summer, including at sites where they were not accustomed to provisioned seed. Patterns of natural seed availability inversely corresponded to patterns of *S. guttata* seed intake at feeders, with a near-total reliance on supplement seed during winter when natural seed biomass was low. This further supports the hypothesis that food is limiting during winter. Interestingly, daily energy intakes from supplemented seed in late spring was significantly higher in the second year than the first. Low feeder intakes during spring year one suggest there may have been patches of seed available elsewhere that were not captured by sampling, and sample sizes were low (n = 10; Chapter 2). While seed biomass was not sampled in spring year two, the unusually high energy intake from the feeder implies natural seed was scarce. Winter was particularly cold during year two (monthly minimum temperatures were between -3.1^{o}C and -4.6^{o}C; Bureau of Meteorology 2019), which may have damaged autumn-germinating native perennials (Waters *et al.* 2001). These conditions are likely to have reduced spring seed production, forcing *S. guttata* to rely on supplementary seed. Overall, *S. guttata* used provisioned seed as a supplement to a natural diet, displaying a preference for natural foraging during times of relative abundance.

Stagonopleura guttata were only recorded consuming supplemented seed at Monarto sites, despite it being provided at Milang and Hartley near-continuously for over 15 months. Many *S. guttata* visited resource stations at Milang and Springton to drink from the water troughs, and often perched on the seed tray itself, but did not eat the seed. Boutin (1990) proposed that a lack of response by birds to food supplementation may be a result of competition or ineffective food delivery, though the regular presence of *S. guttata* at all seed trays and their ready consumption of seed at Monarto does not support this. Moreover, *S. guttata* were seldom deterred from feeders by other species (G Hodder 2015, 2016 pers. obs.). Natural seed availability was generally lower at Milang and Springton than at other sub-regions (Chapter 2), so it is unlikely that *S. guttata* were obtaining enough food from the landscape. Landowners at Monarto have a history of feeding wild birds (G Hodder 2016 pers. comm.), therefore the consumption of cultivated bird seed may be a learned behaviour among *S. guttata*. Behaviour that allows individuals in a population to exploit new resources is known as "innovative behaviour", and plays an important role in rapid macro-evolutionary adaptation (Greenberg 2003). Alternatively, the response to supplemented seed at Monarto may be influenced by group size. Foragers in groups are expected to locate resources more easily (Clark and Mangel 1986) and assess resource quality more efficiently (Beauchamp 2005). Individuals in larger groups may also be more willing to take risks (Stowe *et al.* 2006). During the observations of foraging flocks (which were independent of resource points), birds were observed in pairs or singly at Milang and Springton more often than at Monarto, where larger groups were observed.This combination of sparse local populations, smaller group sizes, and possible lack of innovative behavioural response highlights the vulnerability of *S. guttata* to alterations in natural food resources and their inability to rapidly adapt to such changes.

5.4.4 Caveats and limitations

While this study has shown that apparent *S. guttata* survival was higher where food was supplemented, there is a chance that the lure of food disproportionately increased visitation to resource points, which would confound results. However, mark-resight models correct for visit frequency (known as detection probability) by modelling mean resighting rates as fixed effects and individual heterogeneity as random effects (McClintock *et al.* 2009; McClintock and White 2009). Resighting probabilities do not need to be high to accurately estimate survival, rather sample size of marked animals is more important (Kordjazi *et al.* 2016). Therefore, any increases in visit frequency should not have biased survival estimates. There is, however, a chance that the lure of food increased the *proportion* of tagged birds that visited supplemented resource points. However, an exclusively granivorous diet requires extra-dietary water to aid digestion of dry seed matter (Joseph 1985). Foraging observations of *S. guttata* in the field revealed that individuals accessed nearby water frequently after a foraging bout (G Hodder 2015 pers. obs.). Resource points often provided the only source of water within a site during the warmer months. As such, if *S. guttata* were foraging within proximity of a resource point during this time they are likely to have used it for water. Thus, all tagged birds foraging within sites in summer should theoretically have been captured on camera, regardless of whether they were visiting for food or water. Therefore, similar proportions of the local tagged population are likely to have been recorded at supplemented and non-supplemented sites during warmer months at least However, during the cooler months, birds may have been less inclined to visit resource points with water only due to the presence of smaller and safer water sources in the landscape. Thus the additional lure of provisioned seed cannot be eliminated as having influenced resightings of tagged birds.

5.4.5 Summary

This study found that apparent survival of *S. guttata* in the southern MLR was high (90–95%) over a three-year period in two sub-regions. However, these sub-regions also had the highest rates of capture and resightings compared with the other four, where *S. guttata* appeared sparse. It is therefore likely that the populations in the two sub-regions for which survival could be modelled were the largest of the six studied, inferring lower survival for *S. guttata* elsewhere in the southern MLR. Despite high survival across seed supplemented and unsupplemented populations, a higher proportion of tagged birds were known to have survived multiple winters when food was supplemented. In addition, more juveniles are known to have survived their first winter to breeding age at supplemented sites than at non-supplemented sites. The comparatively slow foraging rates of juveniles compared with adults has highlighted their particular vulnerability during times of food scarcity. In the MLR, these leaner times coincide with the transition of independent fledglings from the spring/summer breeding season into young breeding adults. As such, this study highlights the numbers of breeding adults and therefore population replacement rates as potential limiting processes for MLR populations. To improve juvenile survival through to adulthood, as well as the survival of adults, it is essential that the grassy woodlands of the MLR are managed to create consistent, year-round food resources for *S. guttata*.

Chapter 6. General Discussion

6.1 Processes affecting *Stagonopleura guttata*

This study followed *Stagonopleura guttata* population dynamics and food seed composition and abundance through time during 2013–2016. As such, the correlation between food resource fluctuations and the timing of different demographic and behavioural processes in *S. guttata* were examined. A conceptual model of these processes is described below, revealing a confluence of factors that are likely to cause a critical pinch-point for the species.

In spring, exotic annual grasses that now dominate the understorey of much of the MLR produce abundant seed (Chapter 2). During this time, *S. guttata* start pairing off to begin breeding, and were often observed performing courtship displays or collecting nesting material (G Hodder 2016 pers. obs.). The abundance of weedy grass seeds provides easily accessible food and may help to reduce the foraging time of adults engaging in breeding activities (Litzow and Piatt 2003). Despite this, *S. guttata* ate weedy grass seeds in lower proportions to their availability in spring and summer. The seeds of the weedy grasses found in the MLR contain less protein than many native grass seeds (Yeoh and Watson 1981), and commonly lack amino acids such as lysine, alanine, methionine and leucine (Allen and Hume 1997; Yeoh and Watson 1981). A granivorous diet is prone to protein deficiency and can lack essential amino acids (Allen and Hume 1997). In contrast, the suite of native MLR grasses provide complementary nutritional profiles, with different species offering different amino acids (Yeoh and Watson 1981). Thus, while weedy species provide ready calories, a variety of native grass seeds provides a broader complement of nutrients, critical for egg and female development, and nesting to fledging young (Chapter 3). This was reflected in the diet preferences of *S. guttata*, with native grasses remaining prominent in their diet during spring.

By summer, most exotic annuals have dropped their seed in temperate climates (Shirtliffe *et al.* 2000) and were abundant on the soil surface in the MLR during this time (Chapter 2). This rapid mass-seeding is likely to produce more seed during summer than an understorey dominated by perennials, as perennials produce seed sparingly over longer periods (Arredondo *et al.* 1998; Bazzaz *et al.* 1987; Corbin and D'Antonio 2004). *Stagonopleura guttata* can make multiple breeding attempts from spring to autumn (Higgins *et al.* 2006) when resources are abundant (Zann and Straw 1984). As such, the abundance of weedy seeds during spring and summer could stimulate more breeding attempts than would occur if the understorey was dominated by perennial grasses and forbs, although the nutritional profile of these seeds may be lacking.

Independent fledglings were frequently observed in all monitored populations in the southern MLR between late spring and late autumn, with most fledglings appearing during summer, and the occasional juvenile present into early winter (G Hodder 2015, 2016 pers. obs.). Overall population densities and encounter rates of *S. guttata* were relatively high until early autumn, with an increase in encounter rates from November onwards associated with more frequent sightings of young birds (Chapter 4). This suggests that *S. guttata* often produced clutches that led to successfully fledged juveniles, and therefore nest predation may not be a major limiting factor in the southern MLR. However, this requires testing with nest survival studies. Large foraging flocks of young and adult birds were observed at some sub-regions during summer and autumn (G Hodder 2015, 2016 pers. obs.). Thus, there was a spike in local numbers of *S. guttata* in summer and autumn due to the addition of young from the breeding season. This spike coincides with breaking autumn rains that appeared to bring about mass germination of weedy annual seeds on the soil surface. Subsequently, seed biomass significantly dropped into late autumn (Chapter 2), at a time when new fledglings added pressure on food resources.

A further confluence of factors during late autumn and winter add strain on resources. Juvenile birds forage more slowly than adults, taking longer to de-husk and swallow seed kernels (Chapter 5). In addition, juveniles have a lower body weight (G Hodder 2016 unpub.) and need to eat more to build body mass (Kennedy and Dewey 2001; Lima 1986). The colder conditions from late autumn into winter demand more energy to keep warm, thus individuals with lower body mass can suffer during colder seasons (Lehikoinen 1987; Meijer *et al.* 1996). Simultaneously, the days become shorter in the temperate MLR from autumn onwards, reducing the daylight hours for foraging. Densities of *S. guttata* and encounter frequencies drop significantly into late autumn and winter, suggesting either high mortality or high dispersal. However, no tagged birds were ever recorded at a different sub-region than the one in which they were captured, yet individuals revisited the same two or three resource points within a sub-region (these points ranged between 1–8 km apart) across multiple years. This suggests that at least some individuals within populations were residents (Chapters 4 and 5). Therefore, low autumn-winter numbers most likely reflect mortality, with young birds being more susceptible to low winter survival. Supporting this, more juveniles are known to have survived their first winters at seed-supplemented sites (Chapter 5).

The survival of fledglings to breeding age is critical for recruitment (Lack 1954, 1966). Low juvenile survival through winter compromises the numbers of young adults that are added to the breeding population. If the number of new breeding birds is lower than the rate of loss of adults then the population declines over time. This would be reflected by a slow but steady decline for the MLR population that would not fully replace its numbers with each new generation, a pattern that has been observed since the 1980s (Paton *et al.* 1994; Paton 2018 unpub.). Similar patterns have been recorded in Neotropical migrant bird populations, where post-fledging mortality was high and juvenile survival was lower than the replacement levels needed to counter adult mortality (Anders *et al.* 1997). As such, there appears to be a food resource pinch-point in late autumn and winter that intercepts the passage of independent fledglings to breeding adults. To determine whether juvenile survival is critically low for maintenance of the MLR population, a Population Viability Analysis should be undertaken across the region.

6.2 Management recommendations

Habitat rehabilitation should be a major focus of biodiversity management (Fischer and Lindenmayer 2007; Recher 1999). This thesis has demonstrated a consequence of modification and fragmentation—the invasion of exotic annual grasses and their competitive dominance in modified grassy ecosytems—that is contributing towards ongoing declines of a vulnerable species. There was a strong association between the mass-germination of seeds from these dominant annuals and a six-fold reduction in seed biomass after breaking rains (Chapter 2). Over 70% of the (scarce) seed biomass available to granivores in late autumn was attributed to native perennial seeds that had not yet germinated. The seeds of perennials can germinate at any time of the year with adequate moisture (Smith *et al.* 1999), do not germinate as readily as annuals, and tend to have periods of dormancy or lower seed viability (Houdet 2003; Reynolds *et al.* 2001). Thus, an understorey of native perennial grasses and forbs would produce seeds that would not readily become unavailable to foraging birds due to germination.

Perennials re-sprout vegetatively and are largely evergreen; consequently there are many perennial grass species whose seed production is not restricted to single, short seasons (G Hodder 2016 unpub.). As such, many native grass species produce seeds more consistently and over longer periods of the year than common annual grasses. To examine this, the phenologies of a suite of native and introduced grasses and forbs were measured across three years at study sites (G Hodder 2016 unpub.). This research identified some key native plant species that complement one another with their timing of seed production, together providing year-round seed for granivores. These species include C4 grasses such as: *Enneapogon nigricans* (provides seed from April to December), *Setaria constricta* (May to January), *Panicum effusum* (July to May), and *Aristida behriana* (August to March). The addition of C3 grasses such as: *Austrostipa drummondii* (provides seed from September to February), *Austrostipa nitida* (September to February) and *Rytidosperma caespitosum* (November to January), would ensure that adequate seed production occurred in spring, replacing the spring mass-seeding by exotic annual grasses with a more moderate supply. Thus, management of *S. guttata* in the southern MLR should focus on the rehabilitation of native perennials in the understorey, particularly the suite of species identified above.

As a supplement to grass seeds, *S. guttata* relied heavily on sheoak seeds (namely *Allocasuarina verticillata*) during winter months. Their diet switched from grass seeds to the seeds of *A. verticillata* during this time (Chapter 3). The area of occupancy of woodlands associated with *A. verticillata* has been reduced by 78% in the MLR since the arrival of Europeans (Rogers 2011). This species was selectively cleared for firewood, agricultural and ornamental purposes (Doran and Hall 1983) and has experienced fragmentation and contractions throughout the region (Bickford and Gell 2005; Joseph 1982). Moreover, extant populations are subject to limited recruitment due to grazing by over-abundant kangaroos, and historically by European rabbits (*Oryctolagus cuniculus*) and livestock (Bird *et al.* 2012). Despite its restricted distribution, *A. verticillata* stands were present at nearly all 18 study sites where resident *S. guttata* were monitored. *Stagonopleura guttata* were recorded taking *A. verticillata* seeds from open cones on the tree and from those fallen on the ground (Chapter 3). Seeds were recorded as present in open cones from February through until September (G Hodder 2016 unpub.), with cones opening in response to long periods of high temperatures and low humidity in January or February (Hueneke 1976). Thus, *A. verticillata* provide important resources during times when grass seeds are scarce. As such, the extant distribution of *S. guttata* in the southern MLR may be somewhat dependent on the extant distribution of *A. verticillata*. In addition, the kernels of *A. verticillata* seed are high in protein (43–44%; Crowley and Garnett 2001a), valuable to a granivorous diet that is prone to protein deficiency (Allen and Hume 1997). Rehabilitation of *A. verticillata* throughout its former range would increase food resources during critical periods for *S. guttata*, assist in halting their declines and may serve to expand their current range.

6.3 Future improvements

The study of rare species in the wild is often challenged by small sample sizes, a significant time cost required for data collection, and a paucity of prior species-specific knowledge to guide the approach (Thompson 2004). As such, there were some limitations to this research; namely, sparse encounters of tagged *S. guttata*, their aversion to provisioned seed, and the failure to collect simultaneous measurements of food resources and *S. guttata* trends due to the time-intensive field work. Despite this, this research has added to our understanding of the southern MLR *S. guttata*, of which there was limited prior knowledge (Higgins *et al.* 2006). This thesis has quantitatively assessed the seed species available to MLR granivores, identified a gap in these resources, improved the understanding of *S. guttata* diet, estimated the density of southern MLR populations, and estimated survival in an in-field supplementation trial. There are a suite of learnings arising from this research upon which future research of the species should be based. Many of these have been briefly discussed in previous chapters but will be elaborated upon here.

The sparsity of tagged *S. guttata* encounters, particularly during winter and early spring, limited the amount of information that could be included in density models and caused computational issues. To obtain more robust density estimates and to enable seasonal comparisons, four distinct trapping-sighting periods (one within each season) should be defined. These periods should be restricted to a timeframe within which a closed system can be more reliably assumed. Trapping would need to occur intensively at the start of each period to trap enough individuals. This would be challenging during the colder months when *S. guttata* are less inclined to visit concentrated water sources but might be achieved with sufficient assistance from bird-banders. To maximise the effort required to tag enough individuals at each sub-region, fewer sub-regions may need to be studied. Camera data collection should be limited to the sighting periods only (Pollock 1982). To assist with model computation and increase the amount of information in the density models, a larger array of cameras should be established if resources permit. Additionally, any emigration may have been confounded with survival rate. It may be possible to account for emigration by replacing the survival parameter in the closed sampling periods with a product of survival and site fidelity (Conn *et al.* 2004). Alternatively, as discussed in Chapter 4, the use of small radio-trackers on a sample of tagged *S. guttata* would eliminate many of the issues surrounding sparsity and the assumption of closure. In addition, radio-tracking would provide information on emigration and mobility. This technology was not available within funding constraints at the start of this study.

Despite the provision of seed at nine study sites, *S. guttata* only ate supplementary seed at the three Monarto sites. This meant that the treatment could not be replicated at a landscape scale. The history of landowners feeding seed to wild birds in the Monarto area indicates that the consumption of cultivated bird seed is a learned behaviour that takes more than two years to acquire. Future studies of the effects of food supplementation on these populations would first need to ensure *S. guttata* had learnt to exploit supplemented seed. Local landholders could be encouraged to maintain domestic bird feeders prior to future studies, but this raises ethical issues about the broader application of feeding wild birds (Jones 2011). In addition, confounding variables arise from teaching finches to take supplement seed, due to the interference with their natural behaviour. Alternatively, there may be landholders in other parts of the region that already feed *S. guttata*, that could be identified using a survey or by advertising. A longer-term approach, and one that naturally follows from this study, is to restore large areas with an understorey of native perennial grasses and *A. verticillata* then measure the extent that *S. guttata* forage among these restored areas during late autumn and winter. Survival of populations that use restored habitat and of populations in habitat dominated by weedy exotics could be measured and compared. Frahns Farm, 550 ha of disused farmland at Monarto, is currently being rehabilitated with the variety of the native grasses recommended above and *A. verticillata*. This property could provide a basis for such a study.

A substantial amount of field time was required to collect adequate data on *S. guttata*. Amidst this field schedule, it was difficult to collect sufficient numbers of seed samples at enough time-points for the inclusion of these data into density or survival models. Modelling seed resource fluctuations together with *S. guttata* population dynamics would quantitatively examine the relationship between the two, whereas this thesis was only able to visually compare these trends. A more effective study design would incorporate seed resource measurements into the trapping-sighting periods described above. To achieve this, bird-banding days should be followed immediately with seed sampling and bird tracking days. However, repeating these steps across multiple sub-regions within a reasonable timeframe and obtaining enough replicates to account for the large variation in seed abundance and composition could prove challenging. To increase the efficiency of this fieldwork, seed resource sampling could focus on total abundance or biomass only, rather than identifying individual species. A dustpan and broom could be used to sample the soil surface seeds to reduce sieving time, and seed heads from different species could be bagged together to save time in the field. However, future research on finch seed resources should winnow the seeds to extract the kernels, thus measuring the resources consumed by finches more precisely. While this research has contributed substantially to the current understanding of *S. guttata*, several improvements have emerged and should be incorporated into future research.

6.4 Further research

Overgrazing by non-native or overabundant herbivores is known to affect understorey plant composition (Dorrough *et al.* 2004) and seed-resources (Crowley and Garnett 2001b) in many Australian systems. Under heavy livestock grazing, a compositional change from warm-season perennial grasses to cool-season annuals is commonly reported (e.g. Dorrough *et al.* 2006; Moore 1965). Similarly, heavy rabbit and kangaroo grazing has been found to limit the growth and abundance of native perennial grasses (Grice and Barchia 1992; Norbury *et al.* 1993). An increase in nitrates in these systems is observed concurrent with the switch to dominant annual species, which in turn promotes the growth of weedy annual grasses and forbs in areas that experience winter rainfall (Moore 1965). Kangaroo numbers have increased throughout southern and semi-arid Australia since 1978 (Department for Environment and Water 2018), with severe implications for ecosystem health (Alexander 1997). As such, large tracts of temperate Australian woodland is affected by overgrazing that exacerbates the invasion of annual grasses and forbs. Moreover, overgrazing is likely to further reduce the amount of seed produced during late autumn and winter, and may have contributed to the low seed biomasses observed in the present study. The interaction between overgrazing and plant community composition, and its effect on seed availability, requires further research. Holistic research into the restoration of grassy understorey ecosystems to obtain desirable composition should build on tested practical methods (e.g. Cole and Lunt 2005; Gibson-Roy *et al.* 2010; Prober and Thiele 2005).

The chemical content of natural foods is complex, and the value of each food type is dependent on other available food types to maximise nutritional complementarity (Clark 1982). Some prior research exists on the nutrient content of various native and non-native grasses (e.g. Allen and Hume 1997; Yeoh and Watson 1981). For example, Houston *et al.* (1995) reported that several essential amino acids could be deficient in the seeds of the weedy annual *Panicum mileaceum*. Similarly, many of the weedy annual grasses from the Pooid genera found in the southern MLR, such as *Hordeum* spp, *Bromus* spp, *Lagurus ovatus* and *Vulpia myuros,* have low alanine, methionine and leucine (Yeoh and Watson 1981). Weedy annual *Avena* spp have low glutamine while *Bromus* spp have low cysteine and arganine (Yeoh and Watson 1981). In contrast, native perennials such as *Chloris truncata*, *Enneapogon nigricans* and *Eragrostis* spp have consistently higher glutamine and methionine than other grass genera. The nutrient profile of native perennial *Rytidosperma* spp differ again, having high alanine, methionine and leucine, while native perennial *Austrostipa* spp have high aspartic acid, glycine, arginine and lysine (Yeoh and Watson 1981). Based on amino acid profiles alone, granivores would need a variety of grass types to avoid nutrient deficiencies. In particular, a mix of native perennial *Rytidosperma* spp, *Austrostipa* spp, *Aristida* spp, *E. nigricans* and *C. truncata* would provide a suite of nutrients that are low in the weedy annual grass seeds currently available to MLR *S. guttata*. However, management would benefit from a targeted study of the nutrient profiles of the seeds eaten by *S. guttata*, in particular a comparison of a weed-dominated versus native-dominated diet.

6.5 Wider application of results

Exotic annuals have out-competed native perennials in many systems around the world and are problematic across the woodlands of the wheat-sheep belt in Australia (D'Antonio and Vitousek 1992). Throughout this region, similar patterns of decline are occurring among woodland birds, particularly ground-foragers (Ford *et al.* 2001). For example, the painted button-quail (*Turnix varius*), a ground-foraging seed-eater and insectivore, has declined across the New South Wales sheep-wheat belt since the clearance of 80–90% of the region’s native vegetation, in a similar manner to *S. guttata* (Reid 1999). Invasive annual grasses are likely to reduce access to the ground-layer for painted button-quails, as well as reducing the amount of perennial native seeds available in winter (Garnett and Franklin 2014). It is also likely that invasive annuals are affecting the food resources of other avian species across the temperate zone. Seed resources have also been found to regulate avian granivore density in other ecosystems world-wide (e.g. Pulliam 1983; Schluter 1988; Thompson *et al.* 1991), although most of this research is concentrated on arid, semi-arid or tropical environments. For example, seasonal and annual fluctuations in the abundance of granivorous birds were impacted by seed supply in an Argentinian desert (Blendinger and Ojeda 2001) and the density of granivorous finches on the Galapagos Islands was strongly regulated by seed availability, particularly during times of scarcity (Boag and Grant 1984). As such, the present study adds to the broader knowledge of granivore-seed dynamics from the perspective of a temperate ecosystem.

It is not only granivorous birds in this range that are likely to be suffering from food shortages. Granivorous native mammals such as *Notomys* spp, *Rattus* spp and *Pseudomys* spp, that inhabit parts of temperate Australia, must also be affected by the strain on seed resources during late autumn and winter. Almost 30% of world-wide mammalian extinctions since 1600 AD have occurred in Australia (McKenzie and Burbidge 2002), with a concentration of extinctions among conilurine rodents in semi-arid woodlands of southern Australia (Smith and Quin 1996). A range of conflicting causes of these extinctions have been proposed (e.g. Fisher *et al.* 2003; McKenzie *et al.* 2007), one of which is pastoralism (Morton 1990), though it is clear that these extinctions do not have a single causal factor. However, competition from grazing by introduced and overabundant herbivores is known to affect rodents in temperate systems (Burbidge and McKenzie 1989; Morton 1990). This is likely to be exacerbated by the loss of seeds in late autumn-winter through mass-germination in understoreys dominated by annual species, leading to resource scarcity. The present study on *S. guttata* therefore serves as a case study for the way in which plant composition changes can alter food resources for granivores other than birds.

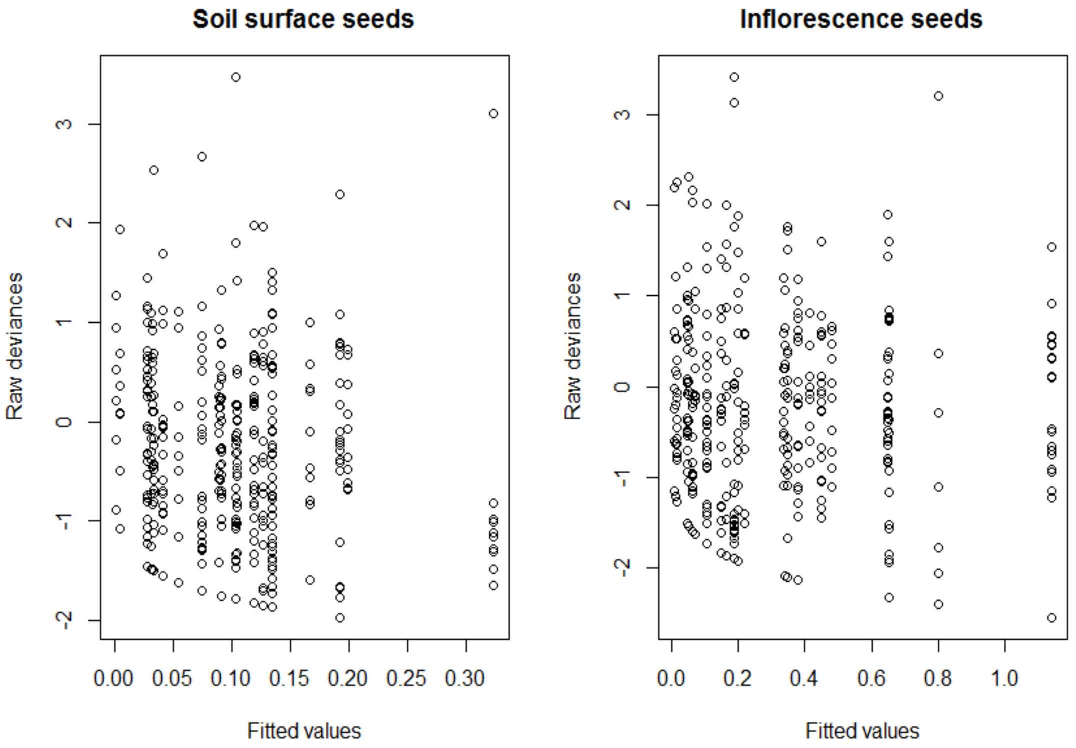
6.6 Conclusion

The world is experiencing a period of mass extinction, with the current rate of decline predicted to remain stable or to increase into the future (Geyle *et al.* 2018). Arguably, habitat loss due to changes in land use has been the most influential factor in avian biodiversity loss. However, it is the complex interactions of fragmentation, degradation and related processes that surmount to extinctions, rather than single factors. Identifying the specific combination of threats contributing to a species' decline requires focussed, single-species research. This thesis supports the hypothesis that the invasion of exotic grasses in the understorey has changed seeding patterns for *S. guttata* in the southern MLR, resulting in food shortages at critical times of the year. Several pieces of evidence support this: a scarcity of seeds after breaking autumn rains, a mirroring of seasonal *S. guttata* diets with environmental resources, a correlation between *S. guttata* and seed biomass fluctuations, and higher survival in areas where seed was supplemented. The confluence of periodic seed shortages and increased pressures on food intercept the passage of new juveniles into the breeding population, compromising population replacement rates. Overall, seed availability is limiting for southern MLR *S. guttata* during late autumn and winter, and management should therefore focus on reinstating consistent year-round food resources. Currently, similar research from other temperate woodlands is limited. However, these interacting processes are likely to affect granivores across temperate agricultural regions that have experienced compositional shifts in Australia and world-wide.

Appendices

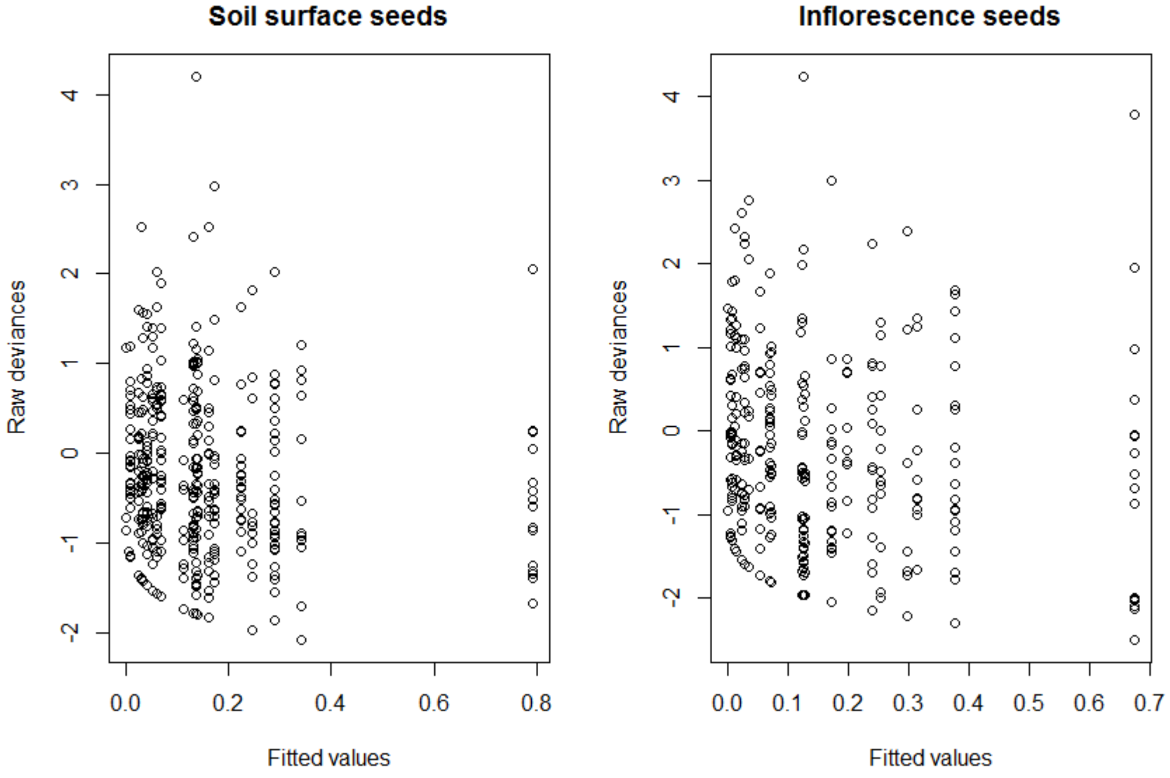
Appendix A: Total seed biomass modelling using compound-Poisson generalised liner mixed effects models – assumption checks and diagnostics plot

Appendix A.i.: First year data modelled against four sampling seasons, three study areas and forage vs. random plots



APPENDIX A.i: Raw deviances plotted against fitted values of the global compound-Poisson generalised linear mixed-effects model of the effects of season, study area and forage vs. random on the total soil (left) and inflorescence (right) seed biomass in plots sampled between 2014 and 2015.

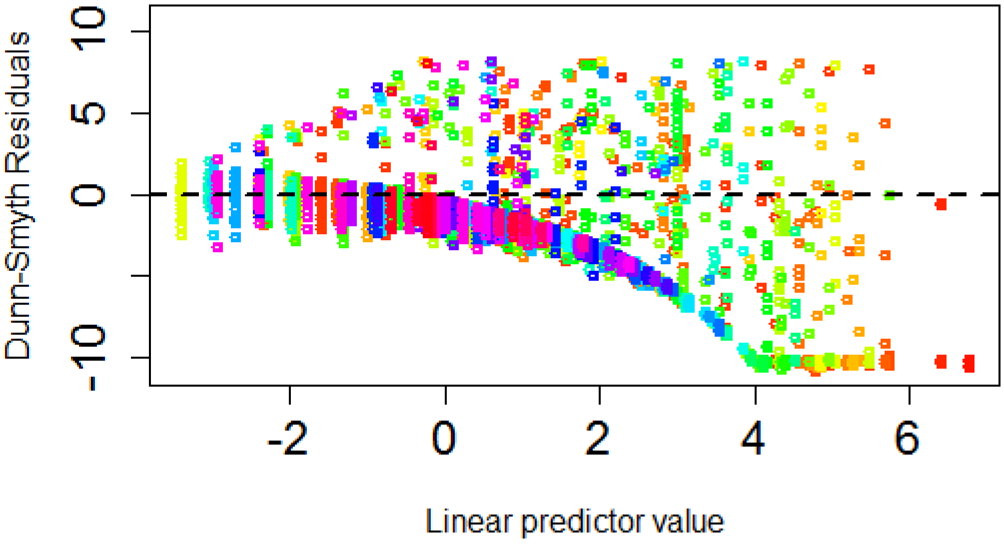
Appendix A.ii.: Two-year data modelled against three sampling seasons, five study areas and two years



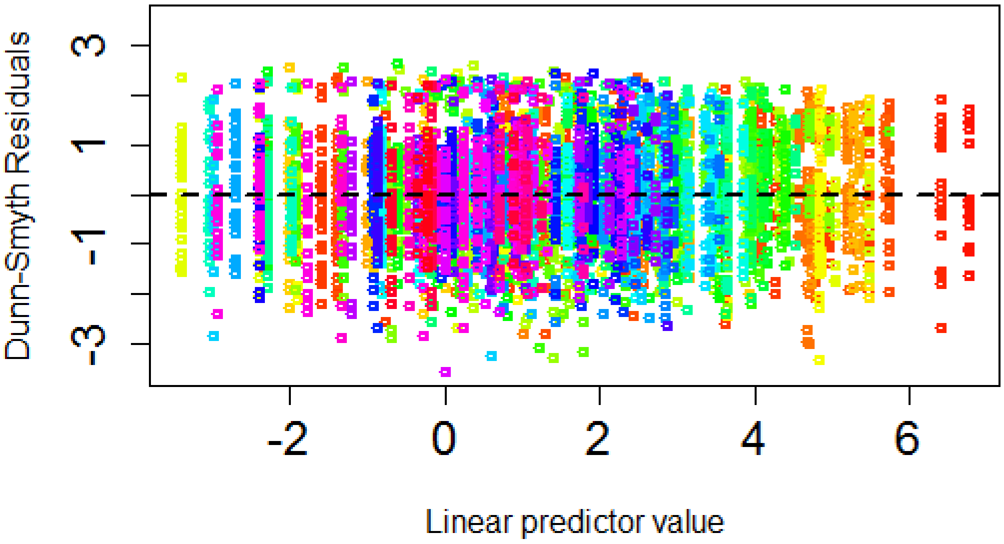
APPENDIX A.ii.: Raw deviances plotted against fitted values of the global compound-Poisson generalised linear mixed-effects model of the effects of season, study area and year on the total soil (left) and inflorescence (right) seed biomass in plots where *S. guttata* foraged between 2014 and 2015.

Appendix B: Seed species composition modelling using multivariate generalised linear models – assumption checks and diagnostics plots

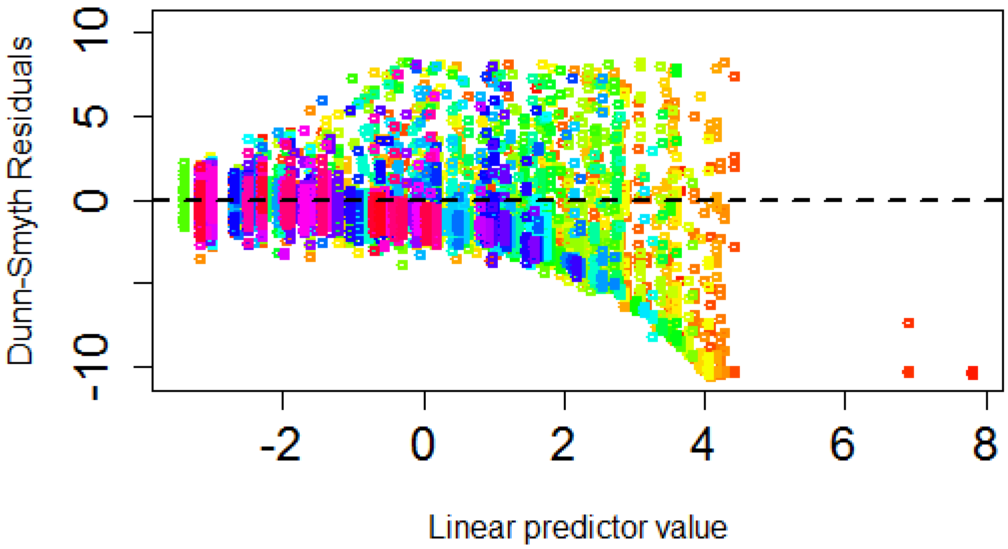
APPENDIX B.i.: Two-year abundance data modelled against three sampling seasons, three study areas and two years



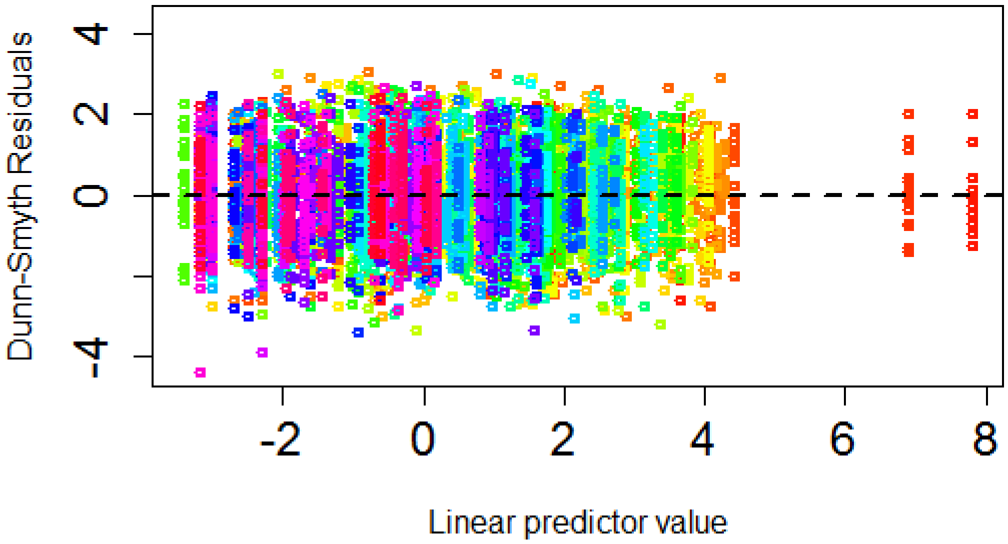
APPENDIX B.i.a: Dunn-Smyth residuals plotted against fitted values of the global multivariate generalised linear model, fitted with a Poisson distribution, of the effects of season, study area and year on the inflorescence seed species abundance and composition sampled from plots where DFTs foraged in the MLR between 2015–2016.



APPENDIX B.i.b.: Dunn-Smyth residuals plotted against fitted values of the global multivariate generalised linear model, fitted with a negative binomial distribution, of the effects of season, study area and year on the inflorescence seed species abundance and composition sampled from plots where DFTs foraged in the MLR between 2015–2016.

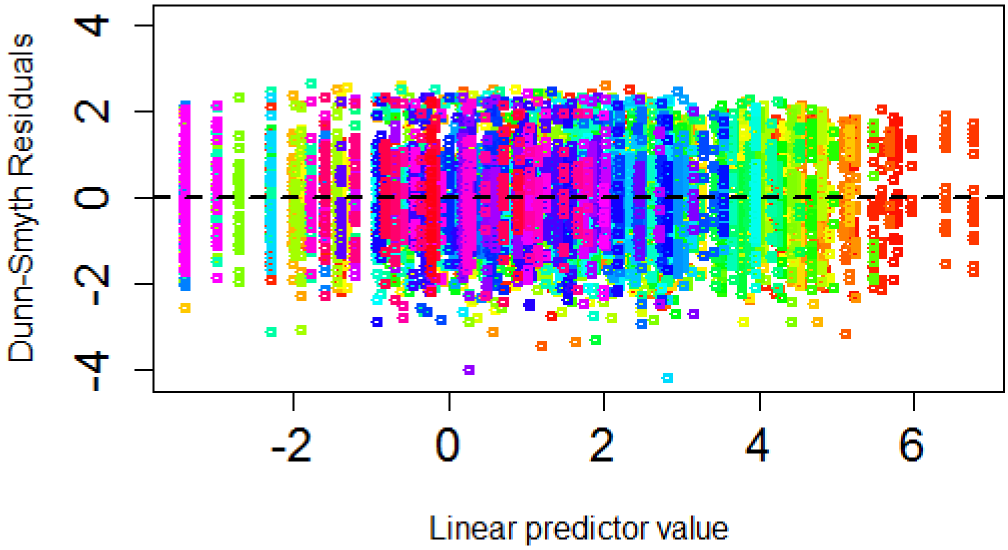


APPENDIX B.i.c.: Dunn-Smyth residuals plotted against fitted values of the global multivariate generalised linear model, fitted with a Poisson distribution, of the effects of season, study area and year on the soil surface seed species abundance and composition sampled from plots where DFTs foraged in the MLR between 2015 – 2016.

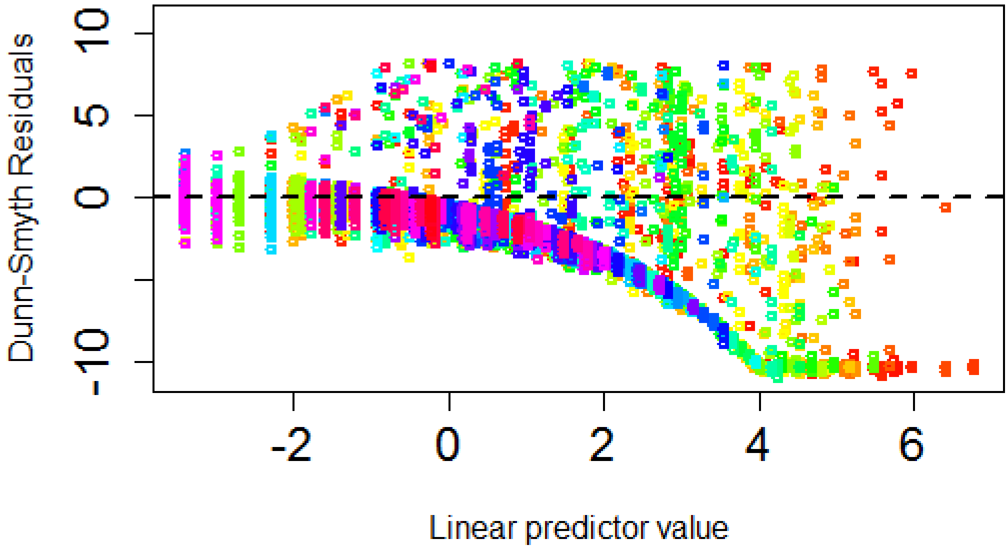


APPENDIX B.i.d.: Dunn-Smyth residuals plotted against fitted values of the global multivariate generalised linear model, fitted with a negative binomial distribution, of the effects of season, study area and year on the soil surface seed species abundance and composition sampled from plots where DFTs foraged in the MLR between 2015 – 2016.

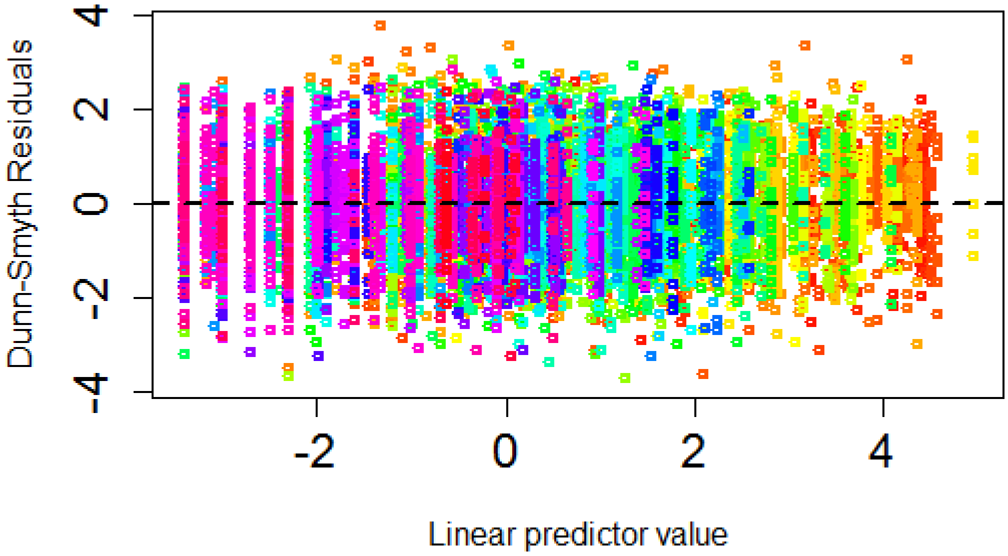
Appendix B.ii.:First year abundance data modelled against four sampling seasons, three study areas and forage vs. random plots.



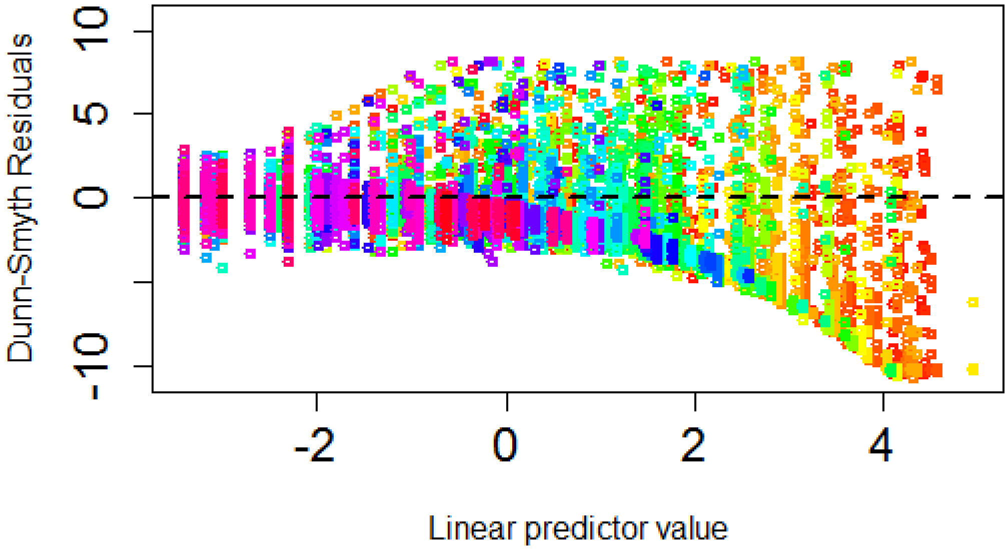
APPENDIX B.ii.a: Dunn-Smyth residuals plotted against fitted values of the global multivariate generalised linear model, fitted with a negative binomial distribution, of the effects of season, study area and ‘forage’ vs. ‘random’ plots on inflorescence seed species abundance and composition sampled from plots in the MLR between 2014 – 2015.



APPENDIX B.ii.b: Dunn-Smyth residuals plotted against fitted values of the global multivariate generalised linear model, fitted with a Poisson distribution, of the effects of season, study area and ‘forage’ vs. ‘random’ plots on inflorescence seed species abundance and composition sampled from plots in the MLR between 2014 – 2015.

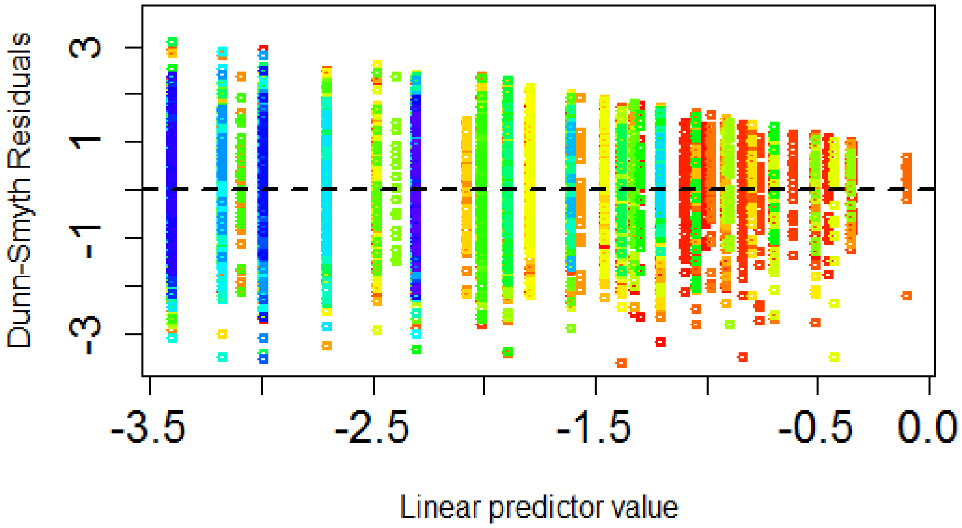


APPENDIX B.ii.c: Dunn-Smyth residuals plotted against fitted values of the global multivariate generalised linear model, fitted with a negative binomial distribution, of the effects of season, study area and ‘forage’ vs. ‘random’ plots on soil surface seed species abundance and composition sampled from plots in the MLR between 2014 – 2015.

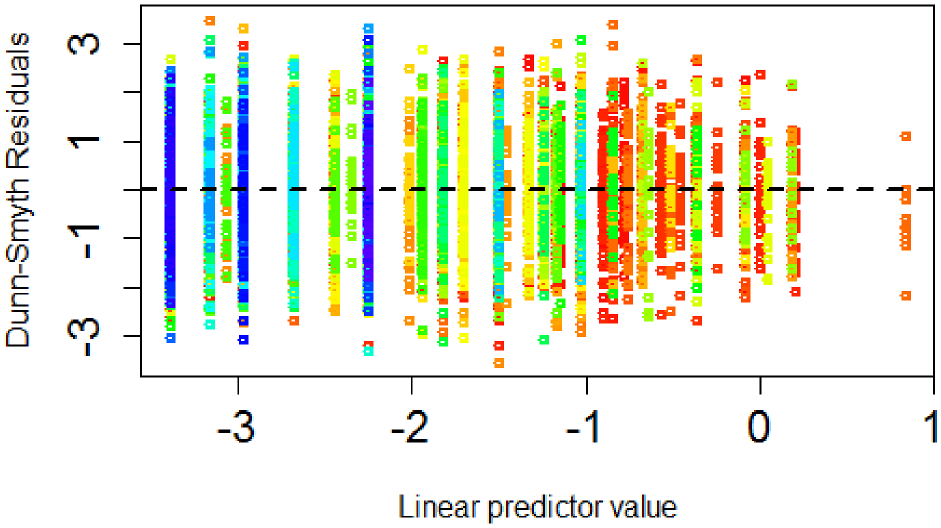


APPENDIX B.ii.d: Dunn-Smyth residuals plotted against fitted values of the global multivariate generalised linear model, fitted with a Poisson distribution, of the effects of season, study area and ‘forage’ vs. ‘random’ plots on soil surface seed species abundance and composition sampled from plots in the MLR between 2014 – 2015.

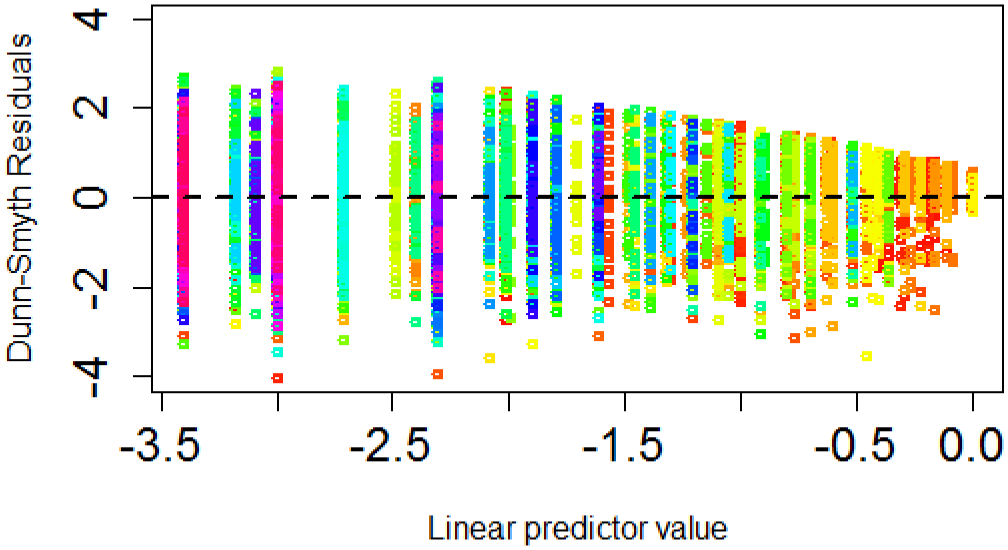
APPENDIX B.iii.: First year presence/absence data modelled against four sampling seasons, three study areas and forage vs. random plots



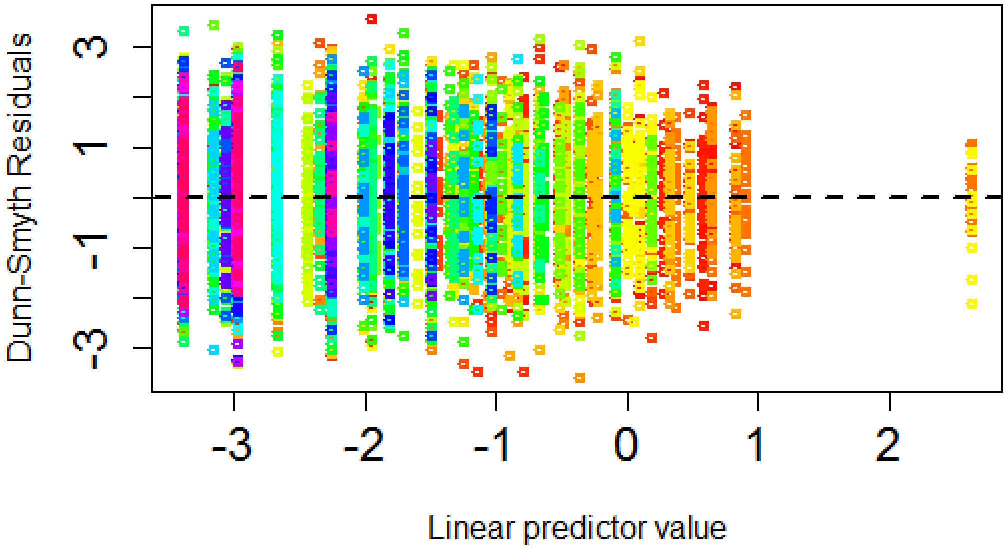
APPENDIX B.iii.a: Dunn-Smyth residuals plotted against fitted values of the global multivariate generalised linear model, fitted with a negative binomial distribution, of the effects of season, study area and 'forage' vs. 'random' plots on the presence-absence of inflorescence seed species sampled from plots in the MLR between 2014–2015.



APPENDIX B.iii.b: Dunn-Smyth residuals plotted against fitted values of the global multivariate generalised linear model, fitted with a binomial distribution with a complementary log-log link, of the effects of season, study area and 'forage' vs. 'random' plots on the presence-absence of inflorescence seed species sampled from plots in the MLR between 2014–2015.



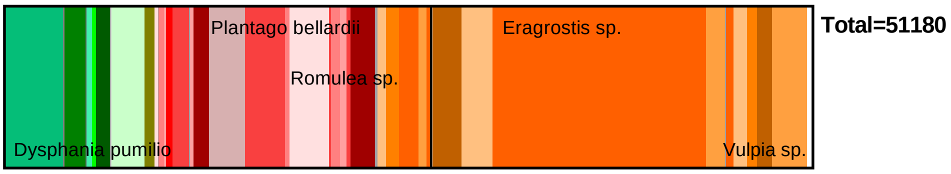
APPENDIX B.iii.c: Dunn-Smyth residuals plotted against fitted values of the global multivariate generalised linear model, fitted with a negative binomial distribution, of the effects of season, study area and 'forage' vs. 'random' plots on the presence-absence of soil surface seed species sampled from plots in the MLR between 2014–2015.



APPENDIX B.iii.d: Dunn-Smyth residuals plotted against fitted values of the global multivariate generalised linear model, fitted with a binomial distribution with a complementary log-log link, of the effects of season, study area and 'forage' vs. 'random' plots on the presence-absence of soil surface seed species sampled from plots in the MLR between 2014–2015.

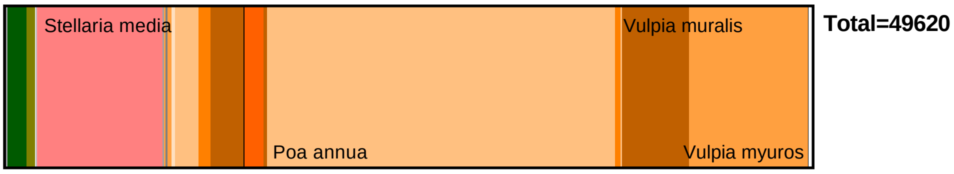
Appendix C: Proportions of Seed Species Available Seasonally

Proportion of seed species in the environment seasonally. Species are colour-coded by plant origin (native=greens, non-native=reds/oranges) and plant form. From left to right on profiles, species are ordered: native forbs, native grasses, native sheoaks, weed forbs, weed grasses, weed sheoaks. Total number seeds in plots displayed on profile right. Prominent species are labelled. Data are pooled over sites, areas and years.

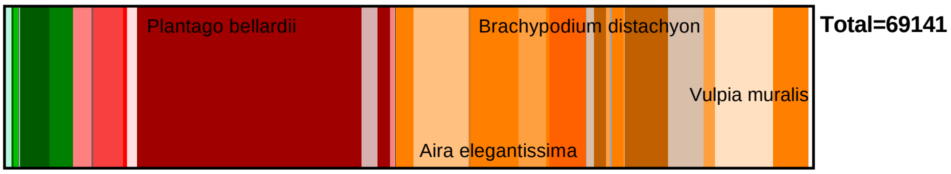


Summer Resources

Autumn Resources



Winter Resources



Spring Resources

Appendix D: Individual species abundance responses

Appendix D.i.: Individual species abundance responses to levels of Sub-region, Season and ‘Forage’ vs. ‘Non-forage’ quadrats. Abundances were counts of all seeds from grasses, forbs, small shrubs or sheoaks found on the soil surface within 25 x 25 cm plots sampled from 15 study sites in the eastern MLR between 2014—2015. Multivariate modelling was performed using manyglm. Study sites were pooled within levels of Sub-region. ‘*’ denotes a significant difference in abundance of a seeding species within levels of a factor, at alpha = 0.05. Arrows represent the direction of the significant trend.

Species	**Subregion**	*Hartley*	*Monarto*	*Rockleigh*	*Springton*	*Karinya*	**Season**	*Spring*	*Summer*	*Autumn-Winter*	*Winter-Spring*	**FR**	*Forage*	*Random*	**Season: Subregion**	**Season: FR**
Actinobole uliginosum							*	↑								
Aira sp.																
Artotheca calendula	*				↑	↑										
Aristida behriana	*				↑	↑	*				↓	*		↑	*	
Austrostipa sp.	*			↑		↑									*	
Avena barbata	*				↑	↑	*			↓	↓				*	
Avena sativa	*	↑			↑		*		↑							
Avena sp.	*	↓		↓			*				↓				*	
Brachypodium distachyon	*					↑	*				↓				*	
Briza maxima	*				↑	↑	*				↓					
Bromus diandrus																
Bromus hordeaceus	*				↑	↑	*			↓	↓				*	
Bromus rubens	*			↑	↑	↑	*			↓						
Bromus sp.																
Casuarina glauca																
Compositae sp. L																
Compositae sp. S															*	
Conyza sp.																
Dysphania pumilio															*	
Ehrharta calycina	*			↑											*	
Ehrharta longiflora	*		↑		↑							*	↑		*	*
Ehrharta sp.	*	↓					*	↓	↓							
Elymus scabra																
Enneapogon nigricans	*				↑	↑										
Erodium sp.	*				↑	↑	*			↓	↓					

Euchiton involucratus																
Festuca sp.							*		↓	↓						
Gahnia deusta	*	↑														
Hordeum sp.	*	↑				↑										
Hypochaeris glabra	*				↑	↑	*	↑								
Hypochaeris sp.	*	↓	↓				*			↓	↓				*	*
Lagurus ovatus																
Lepidosperma sp.																
Lolium perenne																
Medicago arabica																
Medicago minima																
Medicago polymorpha																
Medicago sp.	*	↑	↑													
Medicago truncatula	*		↑													
Millotia sp.																
Other																
Pentaschistis airoides																
Pentaschistis sp.																
Plantago bellardii	*	↓	↓				*	↑								*
Plantago sp.																
Poa annua	*					↑	*				↑					
Romulea minutiflora	*				↑	↑	*	↑								
Romulea rosea	*				↑	↑	*	↑								
Romulea sp.	*				↑	↑	*	↓		↓						
Rytidosperma auriculatum	*					↑										
Rytidosperma caespitosum	*				↓		*			↓	↓					
Rytidosperma erianthum																
Rytidosperma setaceum																
Rytidossperma sp.							*		↑							
Senecio sp.	*			↑			*	↑								
Setaria constricta							*		↓	↓						
Silene sp.																
Stellaria media																
Stellaria sp.																
Trifolium angustifolium	*		↓	↓			*			↓	↓				*	
Trifolium arvense	*		↓	↓											*	

Trifolium campestre																
Trifolium subterraneum															*	*
Unknown spikey seed																
Vittidinia sp.																
Vulpia bromoides	*	↑		↑			*				↑					
Vulpia ciliata	*					↓	*			↓					*	*
Vulpia fasciculata	*	↑		↑											*	
Vulpia muralis	*		↓		↓		*		↓	↓						
Vulpia myuros							*	↑			↑					
Vulpia sp.	*	↓					*		↑							

APPENDIX D.ii.: Individual species abundance responses to levels of Sub-region, Season and ‘Forage’ vs. ‘Non-forage’ quadrats. Abundances were counts of all seeds from grasses, forbs, small shrubs or sheoaks contained in the standing crop within 50 x 50 cm plots sampled from 15 study sites in the eastern MLR between 2014—2015. Multivariate modelling was performed using manyglm. Study sites were pooled within levels of Sub-region. ‘*’ denotes a significant difference in abundance of a seeding species within levels of a factor, at alpha = 0.05. Arrows represent the direction of the significant trend.

Species	**Subregion**	*Hartley*	*Monarto*	*Rockleigh*	*Springton*	*Karinya*	**Season**	*Spring*	*Summer*	*Autumn-Winter*	*Winter-Spring*	**FR**	*Forage*	*Random*	**Season: Subregion**
Aira caryophyllea	*		↑			↑	*		↑						
Aira cupaniana							*	↑							
Aira elegantissima							*	↑							
Aira sp.															
Allocasuarina verticillata															
Arctotheca calendula															
Aristida behriana	*	↓		↓			*				↓				
Avena barbata	*		↓	↓			*	↑			↑				
Austrostipa blackii							*	↑							
Austrostipa erem-pub															
Austrostipa nitida															
Austrostipa pilata	*	↓			↓		*		↓	↓					
Austrostipa scabra															
Austrostipa setacea							*	↑							
Austrostipa stipoides															
Bromus distachyon				↑	↑		*			↓					
Bromus maxima	*				↑	↑	*			↓	↓				
Bromus minor															

Bromus diandrus															
Bromus hordaceus	*				↑	↑	*	↑							
Bromus madritensis															
Bromus rubens															
Bromus rub-mad	*	↑				↑	*	↑			↑				
Calandrinia calyptrata															
Casuarina glauca															
Chenopodium sp.															
Chloris truncata															
Dysphania pumilio	*	↑					*		↑						
Ehrharta sp.	*			↑	↑										
Ehrharta calycina															
Ehrharta erecta															
Ehrharta longiflora	*				↑		*				↑				
Ehrharta scabra															
Eragrostis sp.	*	↑					*		↑						
Enchylaena tomentosa															
Enneapogon nigricans	*				↑	↑									
Euchiton involucratus															
Euphorbia drummondii															
Festica rubra															
Festucas p.							*	↑							
Galenia sp.															
Hordeum sp.	*					↑									
Hordeum leporinum							*	↑							
Hypericum perforatum															
Hyphochaeris glabra	*				↑	↑	*	↑			↑				
Hypochaeris sp.															
Lagurus ovatus															
Lolium perenne	*					↑	*	↑			↑				
Marrubium vulgare															
Panicum effusum	*				↑	↑									
Pentaschistis pallida	*				↑		*	↑							
Stellaria media	*					↑									
Plantago sp.															
Poa annua							*				↑	*	↑		
Romulea sp.							*	↓							
Romulea minutiflora							*	↑							
Romulea rosea	*				↑	↑	*	↑							
Rytidosperma auriculatum							*	↑							
Rytidosperma caespitosum	*					↑	*	↑			↑				

Rytidosperma geniculatum															
Rytidosperma racemosum															
Rytidosperma setaceum	*		↑				*	↑							
Senecio sp.															
Setaria constricta															
Silene sp.															
Trifolium campestre															
Petrorhagia dubia	*				↑	↑	*			↓	↓				
Vittadinia sp.															
Vulpia fasciculata	*	↑		↑											
Vulpia bromoides							*				↓				
Vulpia ciliata							*	↑			↑				
Vulpia muralis	*		↓				*	↑			↑				
Vulpia myuros	*					↑	*	↑			↑				
Vulpia sp.							*			↓					
Trifolium arvense															
Trifolium angustifolium	*		↓	↓			*			↓	↓				
Plantago bellardii	*	↓	↓				*	↑							
Compositae sp.															
Lepidosperma sp.	*	↑													
Gahnia deusta	*	↑										*		↑	
Gahnia lanigera	*	↑													
Oxalis sp.															
Other															

APPENDIX D.iii: Individual species presence/absence responses to levels of Sub-region, Season and 'Forage' vs. 'Non-forage' quadrats. Species counted were all seeds from grasses, forbs, small shrubs or sheoaks found on the soil surface within 25 x 25 cm plots sampled from 18 study sites in the eastern MLR between 2014—2015. Multivariate modelling was performed using manyglm. Study sites were pooled across levels of Sub-region. '*' denotes a significant difference in presence/absence of a seeding species within levels of a factor, at alpha = 0.05. Ticks represent species presence.

Species	**Subregion**	*Milang*	*Hartley*	*Monarto*	*Rockleigh*	*Springton*	*Karinya*	**Season**	*Spring*	*Summer*	*Aut-Winter*	*Win-Sprin*	**FR**	*Forage*	*Random*	**SubR:Sea**	**Seas:FR**	**Area:FR**	**SR:Se:FR**
Actinobole uliginosum																			
Aira sp.																			
Allocasuarina verticillata																			
Arctotheca calendula	*	√			√	√	√	*	√	√									

Aristida behriana	*					√	√	*	√	√	√								
Atriplex semibaccata																			
Austrostipa nitida																			
Austrostipa sp.	*			√	√	√	√	*	√	√									
Avena barbata	*		√			√	√	*	√	√									
Avena sativa								*		√									
Avena sp.	*		√	√		√	√	*	√	√	√								
Brachypodium distachyon	*					√	√	*	√	√	√								
Briza maxima	*	√				√	√	*	√	√									
Bromus diandrus																			
Bromus hordeaceus	*					√	√	*	√	√						*			
Bromus rubens	*				√	√	√	*	√			√				*			
Bromus sp.																			
Calytrix sp.																			
Casuarina glauca																			
Chloris truncata																			
Compositae sp. L																			
Compositae sp. S																			
Conyza sp.																			
Cruciferaceae sp.																			
Dysphania pumilio	*		√		√		√												
Ehrharta calycina	*							*											
Ehrharta longiflora	*	√		√	√	√							*						
Ehrharta sp.								*			√	√							
Elymus scabra																			
Emex australis	*		√																
Enchylaena tomentosa																			
Enneapogon nigricans	*					√	√	*				√							
Eragrostis sp.																			
Erodium sp.	*					√	√	*	√	√									
Euchiton involucratus																			
Euphorbia drummondii																			
Festucas p.								*	√			√							
Gahnia deusta																			
Gahnia lanigera																			
Hordeum leporinum																			
Hordeum sp.	*		√				√												
Hypochaeris glabra	*			√		√	√	*	√										
Hypochaeris sp.	*	√	√		√	√	√	*	√	√	√								*
Lagurus ovatus																			
Lepidosperma sp.																			
Lolium perenne																			

Medicago arabica																			
Medicago minima																			
Medicago polymorpha																			
Medicago scutella																			
Medicago sp.	*		√	√															
Medicago truncatula	*			√															
Millotia sp.																			
Other																			
Pentaschistis airoides																			
Pentaschistis sp.																			
Plantago bellardii	*	√	√		√	√	√	*			√								
Plantago sp.																			
Poa annua	*						√	*				√							
Poa sp.																			
Romulea minutiflora	*					√	√	*	√										
Romulea rosea	*					√	√	*	√										
Romulea sp.	*					√	√	*		√	√	√							
Rytidosperma auriculatum	*						√												
Rytidosperma caespitosum	*	√						*	√	√									
Rytidosperma erianthum																			
Rytidosperma geniculatum																			
Rytidosperma setaceum																			
Rytidosperma sp.								*		√									
Sclerolaena sp.																			
Senecio sp.	*				√			*	√										
Setaria constricta																			
Setaria sp.																			
Silene sp.																			
Unknown spikey seed	*	√			√			*	√										
Stellaria media																			
Stellaria sp.																			
Trifolium angustifolium	*		√			√	√	*	√	√									
Trifolium arvense	*		√			√	√	*											
Trifolium campestre																			
Trifolium sp.																			
Trifolium subterraneum								*		√	√					*			
Unknown large seed																			
Unknown spikey seed 2								*											
Petrorhagia dubia																			

Vittidinia sp.								*											
Vulpia bromoides	*		√		√														
Vulpia ciliata	*	√	√		√	√		*	√	√		√							
Vulpia fasciculata	*		√		√	√		*		√									
Vulpia muralis	*	√		√				*	√			√							
Vulpia myuros								*	√			√							
Vulpia sp.	*	√	√					*		√									

APPENDIX D.iv.: Individual species presence/absence responses to levels of Sub-region, Season and 'Forage' vs. 'Non-forage' quadrats. Species counted were all seeds from grasses, forbs, small shrubs or sheoaks contained in the standing crop within 50 x 50 cm plots sampled from 18 study sites in the eastern MLR between 2014—2015. Multivariate modelling was performed using manyglm. Study sites were pooled across levels of Sub-region. '*' denotes a significant difference in presence/absence of a seeding species within levels of a factor, at alpha = 0.05. Ticks represent species presence.

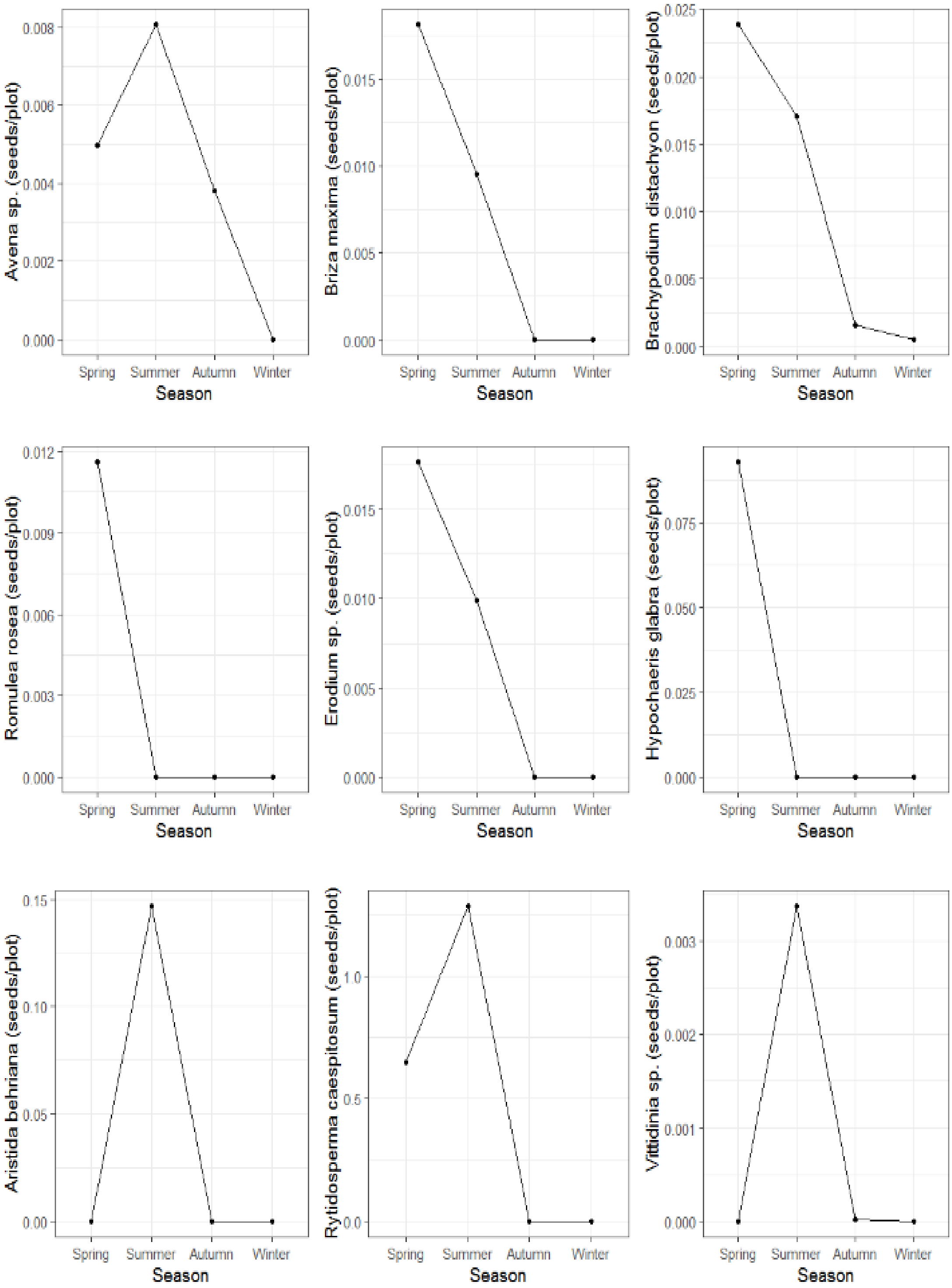
Species	**Subregion**	*Milang*	*Hartley*	*Monarto*	*Rockleigh*	*Springton*	*Karinya*	**Season**	*Spring*	*Summer*	*Aut-Winter*	*Win-Sprng*	**FR**	*Forage*	*Random*	**SubR:Sea**	**SubR:FR**
Actinobole uliginosum																	
Aira caryophylla																	
Aira cupaniana																	
Aira elegantissima																	
Aira praecox																	
Aira sp.																	
Allocasuarina verticillate																	
Arctotheca calendula																	
Aristida behriana																	
Atriplex suberecta																	
Atriplex semibaccata																	
Avena barbata																	
Avena sativa																	
Avena sp.																	
Austrostipa acrociliata																	
Austrostipa blackii																	
Austrostipa drummondii																	
Austrostipa eremophila.puber.																	
Austrostipa nodosa																	
Austrostipa pilata								*									
Austrostipa scabra																	
Austrostipa setacea								*									

Austrostipa stipoides																	
Austrostipa sp.																	
Austrostipa nitida																	
Brachypodium distachyon	*					√	√	*	√	√							
Briza maxima	*	√		√		√	√	*	√	√		√				*	
Briza minor								*	√			√					
Bromus diandrus								*									
Bromus hordaceus								*	√								
Bromus sp.																	
Bromus madritensis																	
Bromus rubens								*									
Bromus rubens.madritensis								*	√			√					
Calandrinia calyptrate																	
Calytrix sp.																	
Casuarina glauca																	
Chenopodium pumilio																	
Chenopodium sp.																	
Chloris truncata																	
Compositae sp.	*																
Conyza sp.																	
Cruciferae sp.																	
Dysphania pumilio																	
Ehrharta calycina																	
Ehrharta erecta																	
Ehrharta sp.	*							*									
Ehrharta longiflora	*	√				√		*	√			√	*	√			
Einadia nutans																	
Elymus scabra																	
Emex australis																	
Eragrostis sp.																	
Erodium sp.																	
Enchylaena tomentose																	
Enneapogon nigricans	*					√	√	*	√	√	√						
Euchiton involucratus																	
Euchiton sp.																	
Euphorbia drummondii																	
Festuca rubra																	
Festuca sp.								*	√								*
Galenia sp.																	
Hordeum sp.	*						√	*									

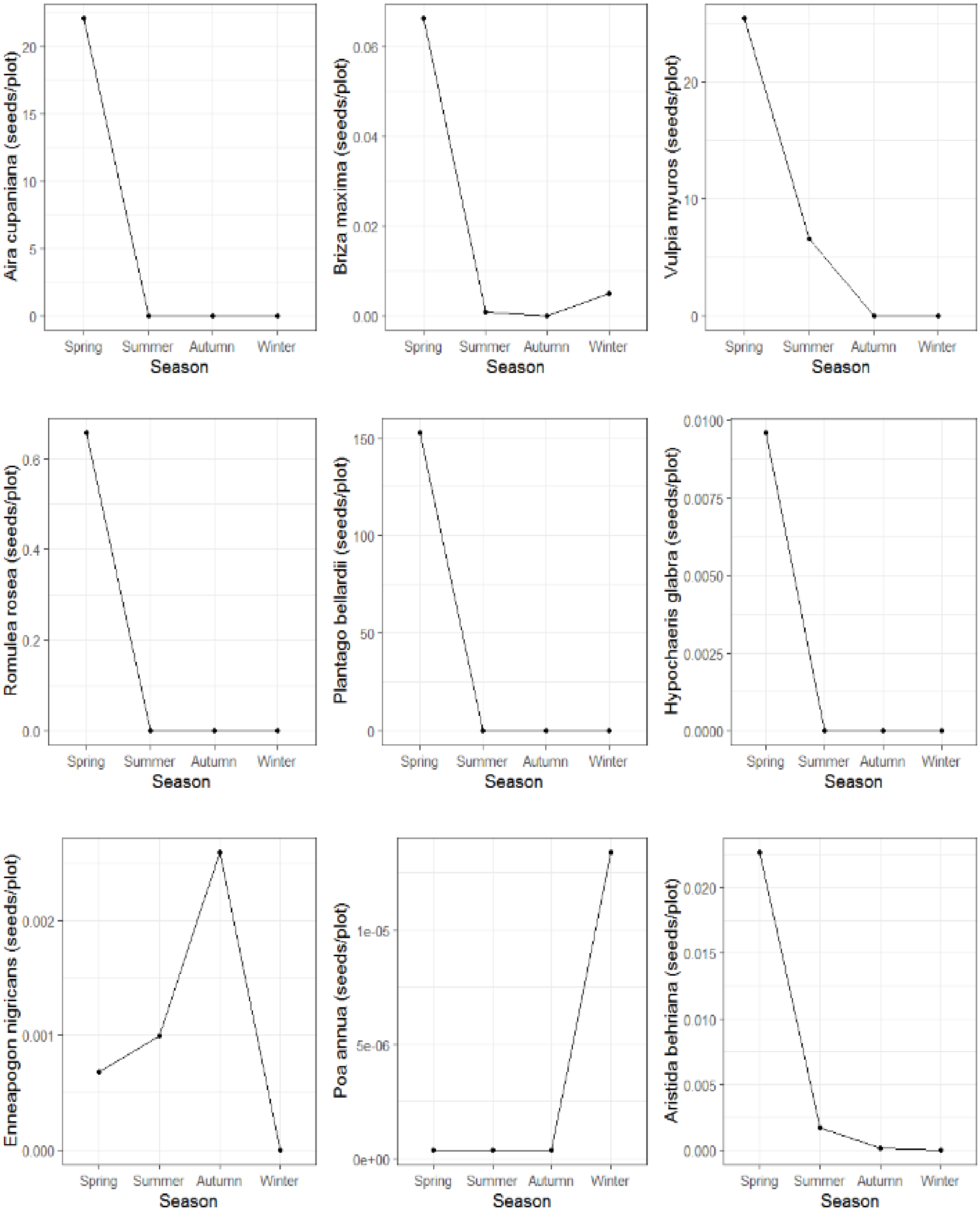
Hordeum leporinum	*							*	√								
Hydrocotyle sp.																	
Hypericum perforatum																	
Hypochaeris glabra								*	√			√					
Hypochaeris sp.																	
Lagurus ovatus																	
Lolium perenne	*		√				√	*	√			√					
Marrubium vulgare																	
Millotia sp.																	
Neurachne alopeculoidea																	
Panicum effusum																	
Pentaschistis airoides																	
Pentaschistis pallida	*					√		*	√	√							
Pentaschistis sp.																	
Petrorhagia dubia	*					√	√	*	√	√							
Podolepis sp.																	
Stellaria media	*						√						*	√			
Stellaria sp.																	
Plantago sp.																	
Poa annua	*						√	*				√	*				
Poa sp.																	
Polypogon sp.																	
Romulea sp.	*					√	√	*		√	√						
Romulea minutiflora								*	√								
Romulea rosea	*					√	√	*	√								
Rytidosperma auriculatum								*	√								
Rytidosperma caespitosum	*		√	√		√	√	*	√	√		√					
Rytidosperma erianthum																	
Rytidosperma geniculatum																	
Rytidosperma racemosum var racemosum																	
Rytidosperma setaceum	*			√	√												
Rytidosperma sp.																	
Sclerolaena sp.																	
Senecio sp.																	
Setaria constricta																	
Setaria sp.																	
Silene sp.																	
Sporobolus mitchelli																	
Themeda triandra																	

Trifolium campestre																	
Trifolium subterraneum																	
Vittadinia sp.																	
Vulpia fasciculata	*		√		√			*	√	√		√					
Vulpia bromoides								*				√					
Vulpia ciliata	*	√	√		√	√		*	√	√		√					
Vulpia muralis								*	√	√		√				*	
Vulpia myuros	*	√		√	√	√	√	*	√	√		√				*	
Vulpia sp.																	
Trifolium sp.																	
Trifolium arvense								*	√	√							
Trifolium angustifolium	*					√	√	*	√	√	√						
Plantago bellardii								*	√	√							
Compositae sp.																	
Lepidosperma sp.																	
Gahnia deusta																	
Gahnia lanigera																	
Medicago arabica																	
Medicago minima																	
Medicago polymorpha																	
Medicago scutellata																	
Medicago trunculata																	
Medicago sp.																	
Oxalis sp.																	
Unknown spikey seed																	
Spikey Hedgehog seed																	
Unknown 21mm seeds																	
Unknown hard Acacia																	
Other																	

Appendix E. Seasonal seed abundances of some individual species.

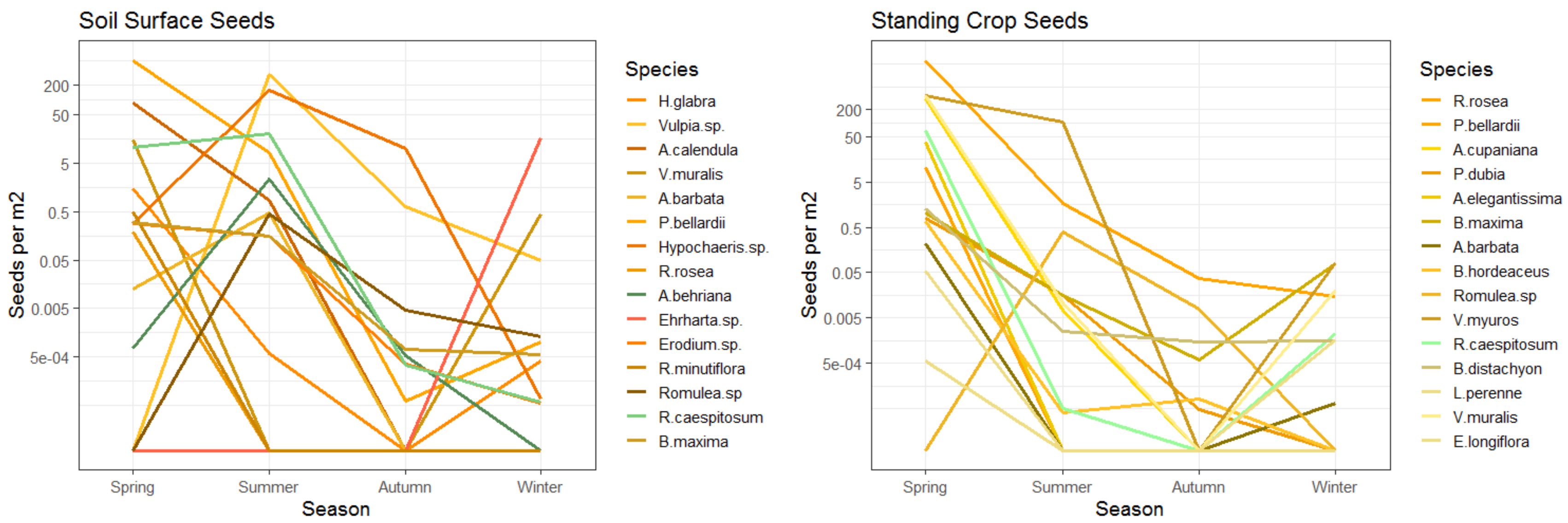


Appendix E.i.: The number of seeds on the soil surface per 25 x 25 cm plot as estimated using manyglm modelling of seed species abundances against seasons, three sub-regions and forage versus non-forage quadrats sampled from the eastern MLR between 2014 and 2015. Plotted species abundances changed significantly between seasons. Top row: weedy annual grasses, middle row: weedy annual forbs, bottom row: native perennial grasses and a shrub.



Appendix E.ii.: The number of seeds in the standing crop per 50 x 50 cm plot as estimated using manyglm modelling of seed species abundances against seasons, three sub-regions and forage versus non-forage quadrats sampled from the eastern MLR between 2014 and 2015. Plotted species abundances changed significantly between seasons. Top row: weedy annual grasses, middle row: weedy annual forbs, bottom row: native perennial grasses.

Appendix F: Seasonal patterns of some individual species'seed abundances across Year 1



Appendix F: The 15 species of grass, forb, small shrub or sheoak that contributed most to changes in the soil surface seed abundance (left) and in standing crop seed abundance (right) plotted against seasons. Seed samples were from $n = 434$ quadrats taken from 9 study sites (3 in each of 3 sub-regions) in the eastern MLR in 2014–2015. Seed species categories are colour-coded: gold = annual weedy grass, orange = annual weedy forb, red = weedy perennial grass, green = native perennial grass. Y-axis is logarithmic. Species abundances were modelled against sub-regions, sampling season and the forage vs. non-forage treatment using multivariate negative binomial generalised linear models. Graphs represent model estimates of species responding significantly to season alone, averaged across sub-region and forage/non-forage quadrats.

Appendix G: Presence or absence of seeding species

The presence or absence of individual seeding species of grasses, forbs, small shrubs and sheoaks sampled across one year and four seasons differed significantly with season, dependent on the study area and on whether they were sampled from forage or non-forage quadrats, just as their respective abundances did. This was true for the composition of the seeds on the soil surface (p=0.001) and for the composition of seeds in the standing crop (p=0.001). The model that best fitted the one-year presence/absence dataset was a three-way interaction (Area by Season by Year). The presence/absence dataset varied with season, area and forage/non-forage in much the same way as its counterpart abundances dataset. The amount of variation in the presence/absence dataset that was explained by the predictors: season and area, was very high compared with other predictors and their interactions. A large amount of the variation in the presence-absence composition of seeding species on the soil surface was attributed to season (Deviance=2510.4) and area (Deviance=1350.5), rather than the forage versus non-forage predictor (Deviance=167.8) or any interactions. Similarly, a large amount of the variation in the presence-absence composition of seeds in the standing crop was attributed to season (Deviance=1262.5) and area (Deviance=853.1) rather than to the forage versus non-forage predictor (Deviance=178.3) or any interactions.

In addition to these collective (“global”) patterns of presence-absence composition of seeding species, which were dependent on the interactions of predictors, there were again many individual species whose presence or absence was significantly affected by either season or area alone. There were 27 species present or absent on the soil surface dependent on the level of area, and 36 species present or absent depending on the level of season. Almost all species that had abundances affected by area on the soil surface, were also present or absent depending on the area. A similar pattern occurred for species on the soil surface affected by season. However, in both of these cases, the presence or absence of individual species was more susceptible to changes in area and season than their individual abundances. The presence or absence of just one species on the soil surface, *E. longiflora*, was affected by the forage versus non-forage predictor, and its abundance was also affected by this same predictor. The presence of *E. longiflora* was positively associated with forage quadrats rather than non-forage quadrats (p=0.001).

In contrast, there were more seed species in the standing crop with abundances that were affected by the season and area predictors, rather than their presence or absence in the standing crop seed bank alone. Twenty-two species were present or absent in the standing crop dependent on area alone, while 33 species were present or absent dependent on season alone. For the most part, the species with abundances that were affected by these predictors were also present or absent dependent on the same predictors. There were three species that were present or absent in the seed abundance seedbank dependent on whether they were sampled from forage or non-forage quadrats: *E. longiflora, S. media* and *P. annua* (p=0.001, p=0.029 and p=0.036, respectively). The abundance of the seeds of just one of these species, *P. annua*, was also affected by the same predictor. The presence of all three of these species was positively associated with forage quadrats, rather than non-forage quadrats.

Table G.i.: The effect of Forage (F) vs. Non-forage (NF) treatments on the presence or absence of seeding species

Species	Factor(s)	Positive association	p-value
Seeds in inflorescences			
Ehrharta longiflora	F/NF	Forage	0.001
Stellaria media	F/NF	Forage	0.029
Poa annua	F/NF	Forage	0.036
Festuca sp.	Area: F/NF	Forage (Rockleigh) Non-forage (Springton)	0.002
Seeds on soil surface			
Ehrharta longiflora	F/NF	Forage	0.001
Hypochaeris sp.	Area:Season: F/NF	Forage (Springton) Non-forage (Karinya) Forage (Summer, Autumn) Non-forage (Spring, Winter)	0.032

The presence or absence of each species producing seed in the understorey was modelled against sub-region (Rockleigh, Karinya and Springton), sampling period (spring 2014, summer 2015, autumn 2015 and winter 2015) and the Forage/Non-forage treatment ("F/NF"; quadrats where *S. guttata* foraged versus quadrats placed throughout their habitat) using multivariate generalised linear models (manyglms) with a binomial family and a "cloglog" link. Species that significantly responded to the F/NF factor or an interaction between F/NF and another factor are listed, along with the direction of their response ("Positive association") and their p-values. In the case of the three-way interaction, the positive association represented here has been simplified.

Table G.ii.: Model testing using Likelihood-Ratio-Test statistics for the effect of Season, Area, ‘Forage’ vs. ‘Non-forage’ quadrats and their interactions on the presence/absence of individual species of grass, forb, small shrub and sheoak seeds found a) in the standing crop and b) on the soil surface in 435 plots at nine sites in the eastern MLR during 2014–2015. P-values were calculated using 999 resampling iterations via the “PIT-trap” method.

Candidate model	Residual DF	DF diff.	Deviance	P-value
Seeds in inflorescences				
Null	433			
Area	431	2	853.1	0.001***
Season	428	3	1262.5	0.001***
F/NF	427	1	178.3	0.001***
Area:Season	421	6	177.4	0.001***
Area:F/NF	419	2	73.6	0.009**
Season:F/NF	416	3	92.0	0.001***
Area:Season:F/NF	410	6	41.7	0.001***
Seeds on soil surface				
Null	433			
Area	431	2	1350.5	0.001***
Season	428	3	2510.4	0.001***
F/NF	427	1	167.8	0.001***
Area:Season	421	6	304.3	0.001***
Area:F/NF	419	2	151.3	0.001***
Season:F/NF	416	3	161.9	0.001***
Area:Season:F/NF	410	6	89.1	0.001***

Explanatory variables in candidate models are: Area = study area, each with 3 sites (Rockleigh, Springton, Karinya), Season = period when seed sampling occurred (Oct – Nov 2014, Feb – Mar 2015, May – Jun 2015, Aug – Sep 2015), and F/NF = quadrats at which *S. guttata* were observed foraging (F) and quadrats placed elsewhere throughout study sites (NF). Colons separate factors and denote interactions in the candidate model set. All data from study areas Milang, Hartley and Monarto were removed from this analysis due to missing data at some levels of the interaction (*S. guttata* were not found foraging on every tracking day). Residual DF = Residual Degrees of Freedom; DF diff. = DFm^1 – DFm^2; Deviance = the log-likelihood ratio test statistic; P-value = significance of model at $\alpha = 0.05$. ‘*’ represents levels of significance

Appendix H: Sample quantifications for DNA barcoding

Appendix H.i.: Sample quantifications *x* used in the PCR master mix consisting of 6µL in total per PCR reaction, for DNA barcoding of plant material sampled from *Stagonopleura guttata* crops. The master mix contained 1µL volume of template DNA equating to *x* ng/µL, 0.6µL Buffer (10x Bioline (Australia) Pty Ltd), 0.12µL dNTP mix (2.5mM; Bioline (Australia) Pty Ltd), 0.24µL Mg2+ (MgSO4, 50 mM; Bioline (Australia) Pty Ltd), 0.3µL of Primer MIX (10nM), 0.03µL of Immolase (0.3 units per reaction; Bioline (Australia) Pty Ltd) and 3.71µL of DNase free water.

Sample Number	Sample Name	Concentration ng/ul
1	CoxFeb16_1	8.06
2	CoxFeb16_2	17.82
3	CoxFeb16_3	17.75
4	CoxFeb16_4	31.99
5	RBlowMar16_1	2.21
6	RBlowMar16_2	0.48
7	RBlowMar16_3	3.14
8	RBlowMar16_4	1.03
9	RBlowApr16_1	0.53
10	TroughApr16_1	0.8
11	TroughApr16_2	1.3
12	TroughApr16_3	5.7
13	TroughApr16_4	13.92
14	CoxFeb16_5	18.93
15	CoxFeb16_6	13.61
16	CoxFeb16_7	10.13
17	TalbMar16_1	0.27
18	RVBFeb16_1	0.19
19	RBLowMar16_5	1.69
20	TalbApr15_1	0.37
21	TalbApr15_2	0.02
22	TalbApr15_3	0.2
23	TalbApr15_4	0.06
24	TalbApr15_5	0.84
25	TalbApr15_6	0.73
26	TalbApr15_7	0.82
27	14/08/2014_1	0.87
28	14/08/2014_2	0.43
29	14/08/2014_3	0.36
30	SpriApr15_1	0.73
31	SpriApr15_2	0.54
32	SpriApr15_3	0.35
33	SpriApr15_4	0.61
34	SpriNov14_1	6.28
35	SpriNov14_2	7.23
36	SpriNov14_3	0.42
37	SpriNov14_4	0.85

38	SpriNov14_5	0.24
39	SpriNov14_6	0.48
40	PruNov14_1	2.15
41	PruNov14_2	0.59
42	PruNov14_3	0.68
43	PruNov14_4	1.03
44	PruNov14_5	1.51
45	PruNov14_6	14.95
46	PruNov14_7	2.26
47	PruNov14_8	4.95
48	PruNov14_9	0.82
49	PruNov14_10	1.07
50	PruNov14_11	0.18
51	PruNov14_12	0.33
52	PruNov14_13	2.86
53	PruNov14_14	1.3
54	PruNov14_15	0.45
55	PruNov14_16	21.57
56	WMNG_1	0.29
57	WMNG_2	0.12
58	WMNG_3	1.8
59	WMNG_4	1.33
60	WMNG_5	0.73
61	WMNG_6	0.64
62	WMNG_7	0.05

Appendix H.ii.: Primer sequences used for amplification of primary barcoding loci and PCR master mix contents and methodology.

The ITS2 loci was amplified using the primer (389-537bp): ITS2R (5'-ATGCGATACTTGGTGTGAAT-3') and ITS3R (5'- GACGCTTCTCCAGACTACAAT-3') (described in Chen *et al.* 2010). The *trn*L loci was amplified using the primer (456bp): *trn*L exon 1 (5’-CGAAATCGGTAGACGCTACG-3’) and *trn*L exon 2 (5’-GGGGATAGAGGGACTTGAAC-3’) (described in Taberlet *et al.* 2007). The PCR master mix consisted of a 6 µL total volume per reaction. Specifically, the master mix contained 1 µL volume of template DNA equating to *x* ng/µL (see above for sample quantifications *x*), 0.6 µL Buffer (10x Bioline Australia Pty Ltd), 0.12 µL dNTP mix (2.5 mM; Bioline Australia Pty Ltd), 0.24 µL Mg^{2+} ($MgSO_4$, 50 mM; Bioline (Australia) Pty Ltd), 0.3 µL of Primer MIX (10nM), 0.03 µL of Immolase (0.3 units per reaction; Bioline Australia Pty Ltd) and 3.71 µL of DNase free water. PCR reactions were run on a Veriti Thermal Cycler (Applied Biosystematics) for seven minutes at 95 °C, followed by 35 cycles of 1 minute treatments at: 94 °C, 55 °C and 72 °C, and a final extension period at 72 °C for 20 minutes.

Appendix I: Crop contents of *S. guttata*

Crop contents of 24 *S. guttata* individuals captured in mist-nets during August 2014–April 2016 at five sub-regions. Crop contents were determined using Genomic DNA from crop samples extracted and sequenced by AGRF. Consensus sequences were matched against sequences in the NCBI DNA databases and sorted according to Grade. Any species matches not occurring in the MLR were removed. 'Grade' = query coverage, 'Expect value' and identity value with weights 0.5, 0.25 and 0.25 respectively. The number of samples and individuals within which species were detected is displayed. Exotic species are denoted by '*'.

Season	**Area**	**Food Species**	**Grade (%)**	**# samples**	**# crops**
Winter - Aug '14	Monarto	*Galenia sp.**	84.5	1	1
		*Poa annua**	94.4 – 99.5	2	1
Spring - Nov '14	Springton	*Aristida behriana*	98.5	8	2
		Atriplex sp.	92.8 – 94.1	8	1
		*Avena fatua/sterilis/sativa**	99.7 – 100.0	3	2
		*Stellaria media**	98.9 – 99.0	2	2
Autumn - Apr '15	Rockleigh	*Chenopodium sp.*	98.2	1	1
		*Ehrharta calycina**	96.0 – 97.0	5	2
		*Eragrostis minor**	99.1 – 99.6	2	1
		*Lactuca serriola**	92.2	1	1
		*Panicum miliaceum**	98.6	2	1
		*Parapholis incurva**	96.9	1	1
		*Puccinellia sp.**	96.4 – 96.9	2	1
	Springton	*Arctotheca calendula**	98.9	1	2
		*Arctotheca calendula/populifolia**	99.0	1	1
		*Briza maxima**	99.8 – 100.0	2	1
Summer - Feb '16	Monarto	*Rytidosperma caespitosum*	98.5	1	1
	Hartley	*Arctotheca calendula**	99.9	1	1
		*Avena fatua/barbata**	99.4	1	1
		*Avena fatua/sativa**	95.3 – 97.5	2	1
		*Avena fatua/sativa/sterilis**	99.2 – 100.0	6	4
		*Avena sp.**	73.2	1	1
		*Cichorium sp.**	93.6	1	1
Autumn - Mar '16	Rockleigh	*Ehrharta calycina**	96.4 – 97.3	6	4
		*Ehrharta calycina**	97.3	1	1
- Apr '16	Karinya	*Aristida behriana*	97.3 – 98.4	3	1
- Apr '16		*Briza maxima**	98.9	1	1
Total				66	24

Appendix J: Food species—*S. guttata*—observations

Food species eaten by *S. guttata* as identified during independent foraging observations during September 2014–August 2016, at six sub-regions in the MLR. Introduced species are denoted by '*'.

Season	**Year**	**Area**	**Food Species**	**# observations**	**# DFTs foraging**
Spring	2014	Milang	*Rytidosperma sp.*	2	1
		Monarto	*Austrostipa drummondii*	1	1
			Austrostipa sp.	1	2
			Rytidosperma caespitosum	1	3
			Rytidosperma sp.	3	4
		Rockleigh	*Ehrharta calycina**	2	6
			Rytidosperma sp.	1	1
		Springton	*Austrostipa sp.*	1	1
			*Avena barbata**	3	6
			*Ehrharta calycina**	1	1
			Rytidosperma sp.	2	2
		Karinya	*Austrostipa sp.*	3	2
			Rytidosperma sp.	2	2
	2015	Hartley	*Avena sp.**	1	3
Summer	2015	Hartley	*Allocasuarina verticillata*	1	8
			*Eragrostis sp.**	2	2
		Monarto	*Allocasuarina verticillata*	2	1
			Austrostipa sp.	1	1
			Rytidosperma caespitosum	3	3
			Rytidosperma setaceum	2	3
			Setaria constricta	1	2
		Rockleigh	*Ehrharta calycina**	2	8
			*Ehrharta erecta**	1	8
	2016	Monarto	*Allocasuarina verticillata*	1	5
			*Ehrharta calycina**	1	2
			Rytidosperma caespitosum	1	2
		Rockleigh	*Austrostipa nodosa*	1	9
			Dysphania pumilio	1	4
			*Ehrharta calycina**	1	4
			*Galenia sp.**	2	6
			*Hordeum sp.**	1	1
			*Lagurus sp.**	2	1
		Springton	*Allocasuarina verticillata*	1	1
			Austrostipa sp.	2	2
			Setaria sp.	1	2
		Karinya	*Rytidosperma sp.*	1	4
Autumn	2015	Monarto	*Allocasuarina verticillata*	1	1
		Springton	*Allocasuarina verticillata*	1	3
			Aristida behriana	2	6
			Enneapogon nigricans	3	6
			Native forb	1	4
			Panicum sp.	1	3
			Rytidosperma racemosum var. racemosum	1	1
		Karinya	*Allocasuarina verticillata*	1	9
			*Briza maxima**	2	11
Winter	2015	Hartley	*Poa sp.**	1	1
		Rockleigh	*Allocasuarina verticillata*	2	2
			*Ehrharta calycina**	2	4
		Springton	*Briza maxima**	2	1
			*Casuarina glauca**	1	3
			Panicum sp.	1	1
		Karinya	*Austrostipa sp.*	1	13
			Rytidosperma sp.	1	13
	2016	Hartley	*Allocasuarina verticillata*	8	5
		Monarto	*Allocasuarina verticillata*	2	4
		Rockleigh	*Dysphania pumilio*	2	5

			Enchylaena tomentosa	1	2
		Springton	*Austrostipa sp.*	1	3
		Karinya	*Aristida sp.*	2	4

Appendix K: Food species *S. guttata*—crops

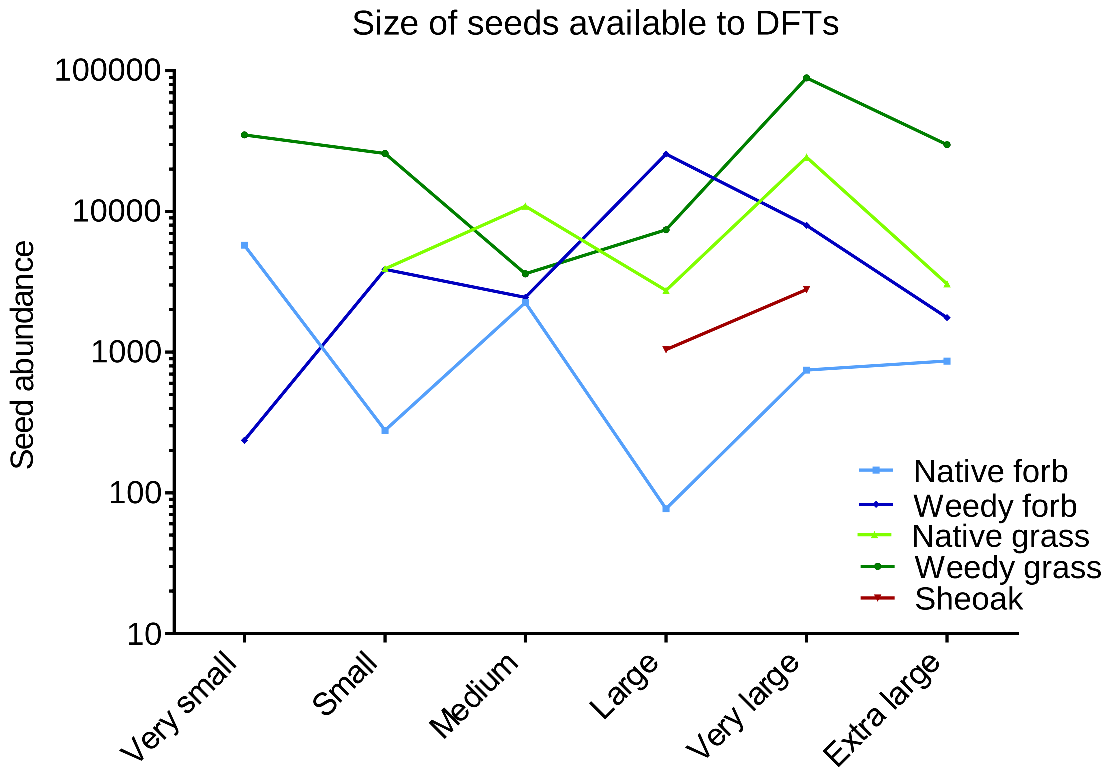
Food species identified in *S. guttata* crops or during foraging observations of flocks/individuals in different seasons over 24 months during Aug 2014–Aug 2016 in the southern MLR

Season	Food Species	# obs.	# crops (sampled)	# crops dominant	Grade (%)
Summer 2015 & 2016	*Allocasuarina verticillata*	5			
	Austrostipa nodosa	13			
	Austrostipa sp./Aristida sp.			1	
	*Arctotheca calendula**		1		99.9
	*Avena spp**		8	7	73.2 –
	*Cichorium sp.**		1		93.6
	Dysphania pumilio	1			
	*Ehrharta calycina**	4			
	*Ehrharta sp.**	1		1	
	*Eragrostis spp**	2			
	*Galenia spp**	2			
	*Hordeum sp.**	1			
	*Lagurus spp**	2			
	Rytidosperma caespitosum	4	1	1	98.5
	Rytidosperma setaceum	2			
	Rytidosperma sp.	1			
	Setaria constricta	1			
	Setaria sp.	1			
Autumn 2015	*Allocasuarina verticillata*	3			
	Aristida behriana	2			
	*Arctotheca calendula/populifolia**		3		98.9 – 99
	*Arctotheca spp./Galenia spp./Stellaria media**			8	
	Aristida behriana		1	1	97.3 –
	Austrostipa spp/Aristida spp			7	
	*Avena spp**			3	
	*Briza maxima**	2	2	2	99.8 –
	Chenopodium sp.		1		98.2
	*Ehrharta calycina**		7	6	96.0 –
	*Ehrharta spp**			21	
	Enneapogon nigricans	3			
	*Eragrostis minor**		1	1	99.1 –
	*Lactuca serriola**		1		92.2
	*Panicum miliaceum**		1	1	98.6
	Panicum sp.	1			
	*Parapholis incurva**		1		96.9
	*Poa spp./Eragrostis spp**			4	
	*Puccinellia sp.**		1		96.4 –
	Rytidosperma caespitosum		1		98.5
	Rytidosperma racemosum var. racemosum	1			
Winter 2014, 2015 & 2016	*Allocasuarina verticillata*	12			
	*Arctotheca spp./Galenia spp./Stellaria media**			1	
	Aristida spp	2			
	Austrostipa spp	2			
	*Avena sp. **			1	
	*Briza maxima**	2			
	*Casuarina glauca**	1			
	Dysphania pumilio	2			
	*Ehrharta calycina**	2			
	Enchylaena tomentosa	1			
	*Galenia sp.**		1		84.5
	Panicum sp.	1			
	*Poa annua**		1		94.4 –
	*Poa sp.**	1			
	Rytidosperma sp.	1			
Spring 2014 & 2015	*Aristida behriana*		2	2	97.5 –
	Atriplex sp.		1	1	92.8 –
	Austrostipa drummondii	1			
	Austrostipa spp	5			
	*Avena barbata**	3			
	*Avena spp**	1	2	2	99.7 –
	*Ehrharta calycina**	3			
	Rytidosperma caespitosum	1			

	Rytidosperma spp	10			
	*Stellaria media**		2	1	98.9 –

obs. = independent occasions when *S. guttata* were sighted eating a species. # crops (sampled) = number of crops (total *n*=24) from which seed species were sampled and genomic DNA was extracted. # crops dominant = crops where dominant spp. (or group of spp.) could be identified from photo by cross-referencing morphometrics with DNA barcoding. DNA sequences were matched against NCBI databases and sorted according to ‘Grade’. Species matches not occurring in the MLR were removed. ‘Grade’ = query coverage, ‘Expect value’ and identity value with weights 0.5, 0.25 and 0.25 respectively. Exotic species denoted with ‘*’.

Appendix L: Size of seeds available to *S. guttata*



Appendix L: Total number of seeds of each plant form and seed size category counted on the soil surface and on inflorescences in sampled plots where *S. guttata* foraged at 18 study sites in the eastern MLR between 2014–2016. Plant forms are: native forb (light blue), weedy forb (dark blue), native grass (light green), weedy grass (dark green), sheoak (maroon). Seed sizes based on average mass of 100 weighed seeds of each species sampled (x-axis). Seed abundance is presented on a logarithmic scale (y-axis).

Appendix M: Null Spatially-explicit Mark-resight model—Springton—determining the detection curve

Appendix M.i. Null Spatially-explicit Mark-resight model outputs for the Springton dataset. These models determined the appropriate detection curve; assuming a constant density of animals but with a different rate of detection with increasing distance from detectors.

Exponential Detection Curve

```
Model:              D~1 g0~1 sigma~1 pID~1
Fixed (real):       none
Detection fn:       exponential
Distribution:       poisson
N parameter:        4
Log likelihood:     -362.8733
AIC:                733.7467
AICc:               734.8895

Fitted (real) parameters evaluated at base levels of covariates
         link    estimate       SE.estimate    lcl            ucl
D        log     1.0861981      0.337118047    0.59948160     1.96807773
g0       logit   0.0229691      0.005879512    0.01387268     0.03780149
sigma    log     418.6725050    83.614531985   284.14333271   616.89522949
pID      logit   0.4583118      0.067925435    0.33106008     0.59124452
```

Half-normal Detection Curve

```
Model:              D~1 g0~1 sigma~1 pID~1
Fixed (real):       none
Detection fn:       halfnormal
Distribution:       poisson
N parameters:       4
Log likelihood:     -369.54
AIC:                747.08
AICc:               748.2228

Fitted (real) parameters evaluated at base levels of covariates
         link     estimate      SE.estimate    lcl            ucl
D        log     1.042012e+00   0.293818834    6.059445e-01   1.79189459
g0       logit   9.745372e-03   0.001886174    6.664687e-03   0.01422967
sigma    log     6.518822e+02   95.604932579   4.897739e+02   867.64612399
pID      logit   4.509327e-01   0.069594622    3.212964e-01   0.58759069
```

Hazard-rate Detection Curve

```
Model:              D~1 g0~1 sigma~1 z~1 pID~1
Fixed (real):       none
Detection fn:       hazard rate
Distribution:       poisson
N parameters:       5
Log likelihood:     -340.7955
AIC:                691.5909
AICc:               693.3556
```

```
Fitted (real) parameters evaluated at base levels of covariates
         link     estimate        SE.estimate      lcl             ucl
D        log      3.5452530       1.343798e+00     1.7289087       7.2697989
g0       logit    0.9999906       9.781773e-12     0.9999906       0.9999906
sigma    log      9.3261415       1.498178e+00     6.8207582       12.7517957
z        log      1.7183460       1.320020e-01     1.4784891       1.9971151
pID      logit    0.3493088       5.953342e-02     0.2431582       0.4728477
```

Appendix M.ii. Null Spatially-explicit Mark-resight model outputs for the Hartley dataset. These models determined the appropriate detection curve; assuming a constant density of animals but with a different rate of detection with increasing distance from detectors.

Exponential Detection Curve

```
Model:              D~1 g0~1 sigma~1 pID~1
Fixed (real):       none
Detection fn:       exponential
Distribution:       poisson
N parameters:       4
Log likelihood:     -1298.484
AIC:                2604.968
AICc:               2606.259

Fitted (real) parameters evaluated at base levels of covariates
         link     estimate        SE.estimate      lcl             ucl
D        log      1.602070e-03    2.825913e-04     1.136804e-03    2.257759e-03
g0       logit    6.719170e-01    7.277703e-02     5.174455e-01    7.963970e-01
sigma    log      1.468067e+03    1.789713e+02     1.157068e+03    1.862658e+03
pID      logit    8.415615e-02    1.376686e-02     6.081028e-02    1.153639e-01
```

Half-normal Detection Curve

```
Model:              D~1 g0~1 sigma~1 pID~1
Fixed (real):       none
Detection fn:       halfnormal
Distribution:       poisson
N parameters:       4
Log likelihood:     -1304.766
AIC:                2617.532
AICc:               2618.822

Fitted (real) parameters evaluated at base levels of covariates
         link     estimate        SE.estimate      lcl             ucl
D        log      1.610230e-03    2.791413e-04     1.149261e-03    2.256092e-03
g0       logit    3.804407e-01    3.694166e-02     3.111263e-01    4.549979e-01
sigma    log      1.836281e+03    1.620489e+02     1.545139e+03    2.182281e+03
pID      logit    9.115639e-02    1.493117e-02     6.581462e-02    1.249508e-01
```

Hazard-rate Detection Curve

```
Model:              D~1 g0~1 sigma~1 z~1 pID~1
Fixed (real):       none
Detection fn:       hazard rate
Distribution:       poisson
N parameters:       5
```

```
Log likelihood:     -1292.408
AIC:                2594.816
AICc:               2596.816
```

```
Fitted (real) parameters evaluated at base levels of covariates
         link     estimate        SE.estimate     lcl             ucl
D        log      1.428571e-03    2.455714e-04    1.022455e-03    1.995995e-03
g0       logit    1.000000e+00    7.469493e-15    1.000000e+00    1.000000e+00
sigma    log      3.241594e+02    5.557675e+01    2.322078e+02    4.525228e+02
z        log      1.049055e+00    1.190300e-01    8.404779e-01    1.309394e+00
pID      logit    7.324710e-02    1.166384e-02    5.342255e-02    9.965383e-02
```

Appendix M.iii. Null Spatially-explicit Mark-resight model outputs for the Rockleigh 2015 dataset. These models determined the appropriate detection curve; assuming a constant density of animals but with a different rate of detection with increasing distance from detectors.

Exponential Detection Curve

```
Model:              D~1 g0~1 sigma~1 pID~1
Fixed (real):       none
Detection fn:       exponential
Distribution:       poisson
N parameters:       4
Log likelihood:     -8456.711
AIC:                16921.42
AICc:               16922.05
```

```
Fitted (real) parameters evaluated at base levels of covariates
         link     estimate        SE.estimate     lcl             ucl
D        log      0.02897311      1.375307e-03    0.02640054      0.03179638
g0       logit    1.00000000      1.055853e-18    1.00000000      1.00000000
sigma    log      893.03082989    2.615659e+01    843.21897065    945.78524783
pID      logit    0.13516411      8.978447e-03    0.11851266      0.15374709
```

Half-normal Detection Curve

```
Model:              D~1 g0~1 sigma~1 pID~1
Fixed (real):       none
Detection fn:       halfnormal
Distribution:       poisson
N parameters:       4
Log likelihood:     -8506.994
AIC:                17021.99
AICc:               17022.61
```

```
Fitted (real) parameters evaluated at base levels of covariates
         link     estimate        SE.estimate     lcl             ucl
D        log      2.551594e-02    0.001044627     2.354929e-02    2.764683e-02
g0       logit    6.284267e-01    0.018241229     5.920300e-01    6.634224e-01
sigma    log      1.133824e+03    34.755441264    1.067725e+03    1.204014e+03
pID      logit    1.789675e-01    0.012694376     1.554230e-01    2.052119e-01
```

Hazard-rate Detection Curve

```
Model:            D~1 g0~1 sigma~1 z~1 pID~1
Fixed (real):     none
Detection fn:     hazard rate
Distribution:     poisson
N parameters:     5
Log likelihood:   -8432.908
AIC:              16875.82
AICc:             16876.77

Fitted (real) parameters evaluated at base levels of covariates
        link    estimate       SE.estimate    lcl            ucl
D       log     0.04194903     0.004152491    0.03456748     0.05090684
g0      logit   0.98222691     0.006757658    0.96279645     0.99159790
sigma   log     397.63935262   15.672936535   368.08855010   429.56254605
z       log     1.81161347     0.069695793    1.68008210     1.95344225
pID     logit   0.12891500     0.009645186    0.11116173     0.14902820
```

Appendix M.iv. Null Spatially-explicit Mark-resight model outputs for the Rockleigh 2016 dataset. These models determined the appropriate detection curve; assuming a constant density of animals but with a different rate of detection with increasing distance from detectors.

Exponential Detection Curve

```
Model:            D~1 g0~1 sigma~1 pID~1
Fixed (real):     none
Detection fn:     exponential
Distribution:     poisson
N parameters:     4
Log likelihood:   -3537.713
AIC:              7083.426
AICc:             7084.277

Fitted (real) parameters evaluated at base levels of covariates
        link    estimate       SE.estimate    lcl            ucl
D       log     3.608131e-03   2.233666e-04   3.196228e-03   4.073116e-03
g0      logit   8.794602e-01   7.562501e-02   6.431669e-01   9.672489e-01
sigma   log     2.106562e+03   2.150197e+02   1.725504e+03   2.571773e+03
pID     logit   2.102888e-02   2.150733e-03   1.720218e-02   2.568459e-02
```

Half-normal Detection Curve

```
Model:            D~1 g0~1 sigma~1 pID~1
Fixed (real):     none
Detection fn:     halfnormal
Distribution:     poisson
N parameters:     4
Log likelihood:   -3551.043
AIC:              7110.085
AICc:             7110.936

Fitted (real) parameters evaluated at base levels of covariates
        link    estimate       SE.estimate    lcl            ucl
D       log     3.536593e-03   2.221293e-04   3.127337e-03   3.999406e-03
```

g0	logit	5.886065e-01	3.857668e-02	5.114895e-01	6.616037e-01
sigma	log	2.394437e+03	1.523099e+02	2.114040e+03	2.712025e+03
pID	logit	2.079939e-02	2.107085e-03	1.704704e-02	2.535640e-02

Hazard-rate Detection Curve

Model: D~1 g0~1 sigma~1 z~1 pID~1
Fixed (real): none
Detection fn: hazard rate
Distribution: poisson
N parameters: 5
Log likelihood: -3524.365
AIC: 7058.729
AICc: 7060.033

Fitted (real) parameters evaluated at base levels of covariates

	link	estimate	SE.estimate	lcl	ucl
D	log	3.882758e-03	2.477163e-04	3.426806e-03	4.399375e-03
g0	logit	9.935415e-01	1.597773e-02	5.388236e-01	9.999506e-01
sigma	log	6.708891e+02	6.188923e+01	5.601368e+02	8.035399e+02
z	log	1.108551e+00	1.071844e-01	9.175835e-01	1.339263e+00
pID	logit	2.244770e-02	2.394840e-03	1.820360e-02	2.765343e-02

Appendix N: Null Spatially-explicit Mark-resight model—Springton—determining buffer size

Appendix N.i: Null Spatially-explicit Mark-resight model outputs for Springton, used to determine the appropriate buffer size. The best fit model (emboldened) was the one at which sigma stabilised. Density estimates showed little change between subsequent models.

Buffer = 4 x initial sigma

Fitted (real) parameters evaluated at base levels of covariates

	link	estimate	SE.estimate	lcl	ucl
D	log	0.39130171	0.076175433	0.26812991	0.57105538
g0	logit	0.01537559	0.003117168	0.01032267	0.02284482
sigma	log	459.19560487	52.486129510	367.299886	24 574.08295355
pID	logit	0.46406191	0.070007150	0.33276699	0.60053516

Buffer = 5 x initial sigma

Fitted (real) parameters evaluated at base levels of covariates

	link	estimate	SE.estimate	lcl	ucl
D	log	0.35904779	0.077581999	2.362225e-01	0.54573677
g0	logit	0.01450331	0.003013582	9.641261e-03	0.02176338
sigma	log	491.88963805	66.930343079	3.772049e+02	641.44292346
pID	logit	0.46447240	0.070243148	3.327350e-01	0.60136128

Buffer = 6 x initial sigma

Fitted (real) parameters evaluated at base levels of covariates

	link	estimate	SE.estimate	lcl	ucl
D	log	0.3459991	0.081216355	0.21975834	0.54475907
g0	logit	0.0141003	0.003053264	0.00921343	0.02152289
sigma	log	507.7357050	79.221455503	374.64805723	688.10058173
pID	logit	0.4646575	0.070341454	0.33273474	0.60171834

Buffer = 7 x initial sigma

Fitted (real) parameters evaluated at base levels of covariates

	link	estimate	SE.estimate	lcl	ucl
D	log	0.34286933	0.083231603	0.21451114	0.54803389
g0	logit	0.01399813	0.003096767	0.00906267	0.02156292
sigma	log	511.82994	591 84.375858482	371.31588552	705.51760305
pID	logit	0.46470297	0.070365591	0.33273466	0.60180597

Appendix N.ii: Null Spatially-explicit Mark-resight model outputs for the Hartley dataset. These models determined the appropriate buffer size; the buffer at which sigma stabilised and density estimates (‘estimate’) showed little change between subsequent models.

Buffer = 4 x initial sigma

Fitted (real) parameters evaluated at base levels of covariates

	link	estimate	SE.estimate	lcl	ucl
D	log	0.02191270	0.003192051	0.01649494	2.910994e-02
g0	logit	0.09136006	0.010307745	0.07306672	1.136717e-01
sigma	log	922.16253497	69.329256642	795.98209572	1.068345e+03
pID	logit	0.49332824	0.035313321	0.42468029	5.622287e-01

Buffer = 5 x initial sigma

```
Fitted (real) parameters evaluated at base levels of covariates
        link    estimate        SE.estimate     lcl             ucl
D       log     0.01934282      0.003315048     0.01385773      2.699899e-02
g0      logit   0.09099549      0.010120538     0.07300980      1.128724e-01
sigma   log     976.33344954    82.279781601    827.92436885    1.151346e+03
pID     logit   0.49472535      0.034910269     0.42682394      5.628219e-01
```

Buffer = 6 x initial sigma

```
Fitted (real) parameters evaluated at base levels of covariates
        link    estimate        SE.estimate     lcl             ucl
D       log     1.829336e-02    0.003491533     0.01262646      2.650365e-02
g0      logit   9.056314e-02    0.010050970     0.07269821      1.122866e-01
sigma   log     1.004439e+03    93.283188918    837.60884797    1.204497e+03
pID     logit   4.954900e-01    0.034754560     0.42787327      5.632721e-01
```

Buffer = 7 x initial sigma

```
Fitted (real) parameters evaluated at base levels of covariates
        link    estimate        SE.estimate     lcl             ucl
D       log     1.799646e-02    0.003595344     0.01221222      2.652037e-02
g0      logit   9.038626e-02    0.010040570     0.07254177      1.120898e-01
sigma   log     1.013353e+03    98.748880248    837.54630586    1.226062e+03
pID     logit   4.957367e-01    0.034716359     0.42818878      5.634406e-01
```

Appendix N.iii: Null Spatially-explicit Mark-resight model outputs for the Rockleigh 2015 dataset. These models determined the appropriate buffer size; the buffer at which sigma stabilised and density estimates (‘estimate’) showed little change between subsequent models.

Buffer = 4 x initial sigma

```
Fitted (real) parameters evaluated at base levels of covariates
        link    estimate        SE.estimate     lcl             ucl
D       log     0.16972083      0.0036050700    1.628008e-01    0.17693495
g0      logit   0.35405003      0.0007510601    3.525794e-01    0.35552346
sigma   log     388.58536258    0.8476755486    3.869275e+02    390.25033093
pID     logit   0.01046907      0.0016320471    7.709349e-03    0.01420254
```

Buffer = 5 x initial sigma

```
Fitted (real) parameters evaluated at base levels of covariates
        link    estimate        SE.estimate     lcl             ucl
D       log     0.1684044       0.004444930     1.599155e-01    0.1773440
g0      logit   0.3638165       0.006173631     3.518047e-01    0.3760006
sigma   log     386.3416178     1.636770329     3.831469e+02    389.5629701
pID     logit   0.0105146       0.001615507     7.777154e-03    0.0142018
```

Buffer = 6 x initial sigma

```
Fitted (real) parameters evaluated at base levels of covariates
        link    estimate        SE.estimate     lcl             ucl
D       log     0.1202698       0.003286409     0.11399918      0.1268854
g0      logit   0.3770339       0.002502017     0.37214280      0.3819502
sigma   log     465.1126322     4.616230183     456.15263803    474.2486234
pID     logit   0.0154333       0.001761105     0.01233585      0.0192933
```

Buffer = 7 x initial sigma

```
Fitted (real) parameters evaluated at base levels of covariates
          link     estimate        SE.estimate     lcl             ucl
D         log      0.1170151       0.001166804     0.11475049      0.11932445
g0        logit    0.3838651       NaN             NaN             NaN
sigma     log      468.6020549     NaN             NaN             NaN
pID       logit    0.0155825       0.001683808     0.01260418      0.01925088
```

Appendix N.iv: Null Spatially-explicit Mark-resight model outputs for the Rockleigh 2016 dataset. These models determined the appropriate buffer size; the buffer at which sigma stabilised and density estimates (‘estimate’) showed little change between subsequent models.

Buffer = 4 x initial sigma

```
Fitted (real) parameters evaluated at base levels of covariates
          link     estimate        SE.estimate     lcl             ucl
D          log     0.01859671      0.001047755     0.01665393      0.02076613
g0        logit    0.67617073      0.035303641     0.60353669      0.74120385
sigma     log      615.78473310    11.163078247    594.29136504    638.05543850
pID       logit    0.17074378      0.006602365     0.15818989      0.18407609
```

Buffer = 5 x initial sigma

```
Fitted (real) parameters evaluated at base levels of covariates
          link     estimate        SE.estimate     lcl             ucl
D         log      0.01340045      7.672079e-04    0.01197915      0.01499039
g0        logit    0.79120789      3.927964e-02    0.70395330      0.85793560
sigma     log      675.90706945    1.266747e+01    651.53185181    701.19421678
pID       logit    0.15872157      5.814810e-03    0.14765386      0.17045299
```

Buffer = 6 x initial sigma

```
Fitted (real) parameters evaluated at base levels of covariates
          link     estimate        SE.estimate     lcl             ucl
D         log      0.0100582       6.050598e-04    8.940498e-03    0.01131563
g0        logit    0.8878991       3.970570e-02    7.837407e-01    0.94538673
sigma     log      754.8381734     1.714389e+01    7.219778e+02    789.19416163
pID       logit    0.1549845       5.756716e-03    1.440338e-01    0.16660566
```

Buffer = 7 x initial sigma

```
Fitted (real) parameters evaluated at base levels of covariates
          link     estimate        SE.estimate     lcl             ucl
D         log      7.576463e-03    4.379339e-04    6.765602e-03    8.484506e-03
g0        logit    9.789678e-01    2.763403e-02    7.702877e-01    9.984546e-01
sigma     log      8.567528e+02    1.825183e+01    8.217203e+02    8.932788e+02
pID       logit    1.600846e-01    6.120733e-03    1.484488e-01    1.724477e-01
```

Appendix O: Seasonal density Spatially-explicit Mark-resight models—Springton sub-region—model outputs.

Appendix O.i.: Seasonal density Spatially-explicit Mark-resight models for the Springton sub-region; model outputs.

November–January, null model

Fitted (real) parameters evaluated at base levels of covariates

	link	estimate	SE.estimate	lcl	ucl
D	log	3.498325e-02	3.459178e-03	0.02883349	4.244467e-02
g0	logit	5.620453e-02	1.480268e-02	0.03331542	9.330160e-02
sigma	log	1.034000e+03	1.825319e+02	733.51542824	1.457578e+03
pID	logit	7.489085e-01	4.842232e-02	0.64292905	8.316685e-01

Appendix O.ii.: Seasonal density Spatially-explicit Mark-resight models for the Hartley sub-region; model outputs.

February–March, null model + B

Fitted (real) parameters evaluated at base levels of covariates

	link	estimate	SE.estimate	lcl	ucl
D	log	1.497437e-02	0.001727004	1.195372e-02	1.875833e-02
g0	logit	3.562292e-01	0.074797928	2.260016e-01	5.118704e-01
sigma	log	1.283547e+03	94.705533910	1.110943e+03	1.482968e+03
pID	logit	6.890708e-01	0.039686383	6.065255e-01	7.611195e-01

April–May, null model + B

Fitted (real) parameters evaluated at base levels of covariates

	link	estimate	SE.estimate	lcl	ucl
D	log	6.367619e-03	2.678454e-04	5.863923e-03	6.914582e-03
g0	logit	1.826277e-01	4.527334e-02	1.097713e-01	2.881860e-01
sigma	log	1.630211e+03	1.248554e+02	1.403289e+03	1.893830e+03
pID	logit	6.579818e-01	3.490031e-02	5.867037e-01	7.227757e-01

Appendix O.iii.: Seasonal density Spatially-explicit Mark-resight models for the Rockleigh sub-region for 2015; model outputs.

July–September, null model

Fitted (real) parameters evaluated at base levels of covariates

	link	estimate	SE.estimate	lcl	ucl
D	log	9.235991e-03	5.571175e-05	9.127442e-03	9.345831e-03
g0	logit	9.996443e-01	5.694348e-03	6.588839e-11	1.000000e+00
sigma	log	1.222166e+03	4.001787e+01	1.146215e+03	1.303148e+03
pID	logit	3.475682e-01	1.294649e-02	3.226447e-01	3.733558e-01

October–December, null model

Fitted (real) parameters evaluated at base levels of covariates

	link	estimate	SE.estimate	lcl	ucl
D	log	1.913946e-02	6.508758e-04	0.0179057	2.045823e-02
g0	logit	9.835998e-01	1.345382e-02	0.9212367	9.967589e-01

```
sigma    log      1.330177e+03    4.690690e+01    1241.3726768    1.425334e+03
pID      logit    2.414635e-01    6.622846e-03    0.2287218       2.546807e-01
```

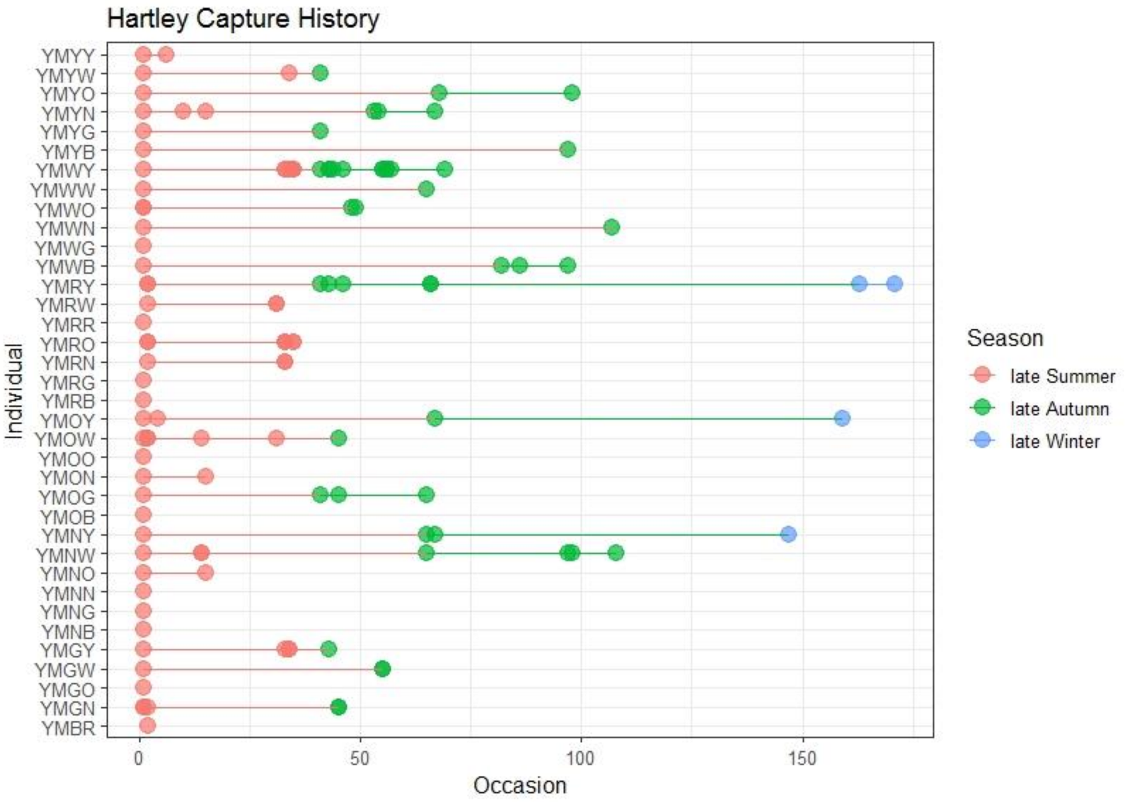
Appendix O.iv.: Seasonal density Spatially-explicit Mark-resight models for the Rockleigh sub-region for 2016; model outputs.

March–April, null model

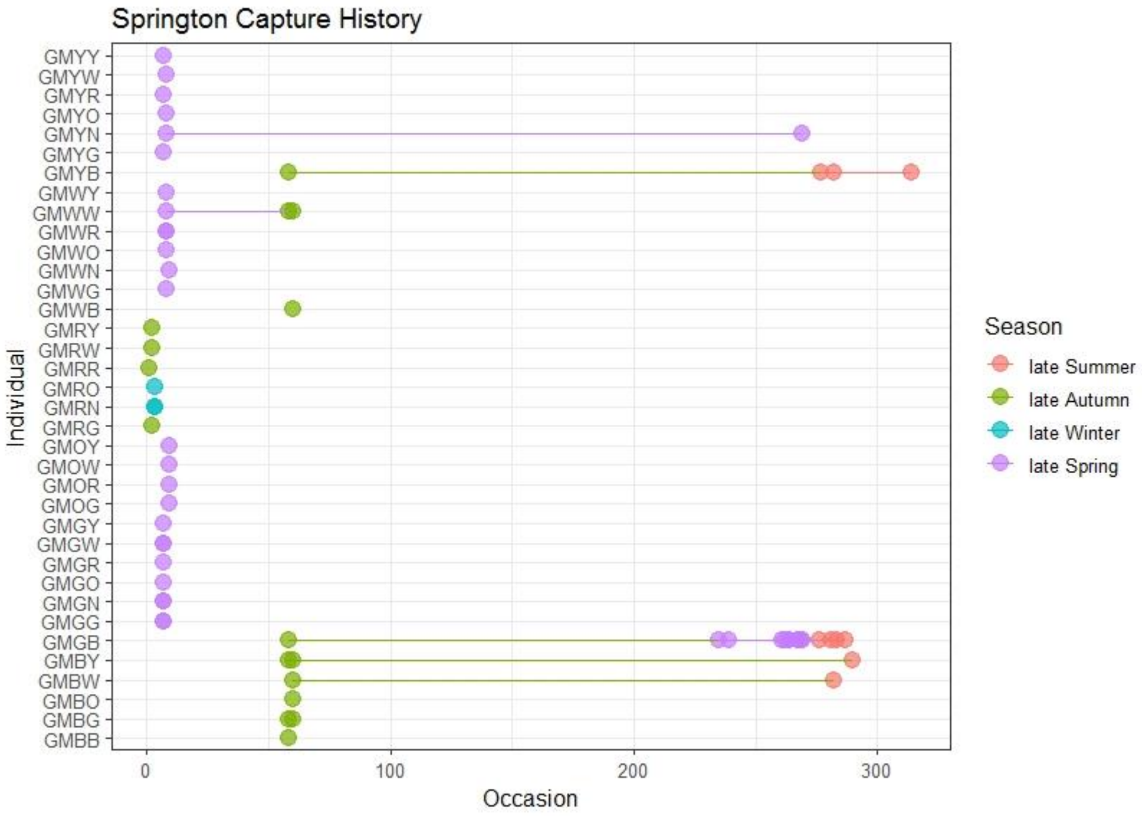
```
Fitted (real) parameters evaluated at base levels of covariates
         link     estimate        SE.estimate     lcl             ucl
D        log      0.03184567      4.125689e-04    0.03104726      0.03266461
g0       logit    0.99999994 7    .849856e-17     0.99999994      0.99999994
sigma    log      761.80645191    2.096645e+01    721.80901383    804.02025889
pID      logit    0.17901410      7.313631e-03    0.16512547      0.19379973
```

Appendix P: Capture histories of *S. guttata*—tagged

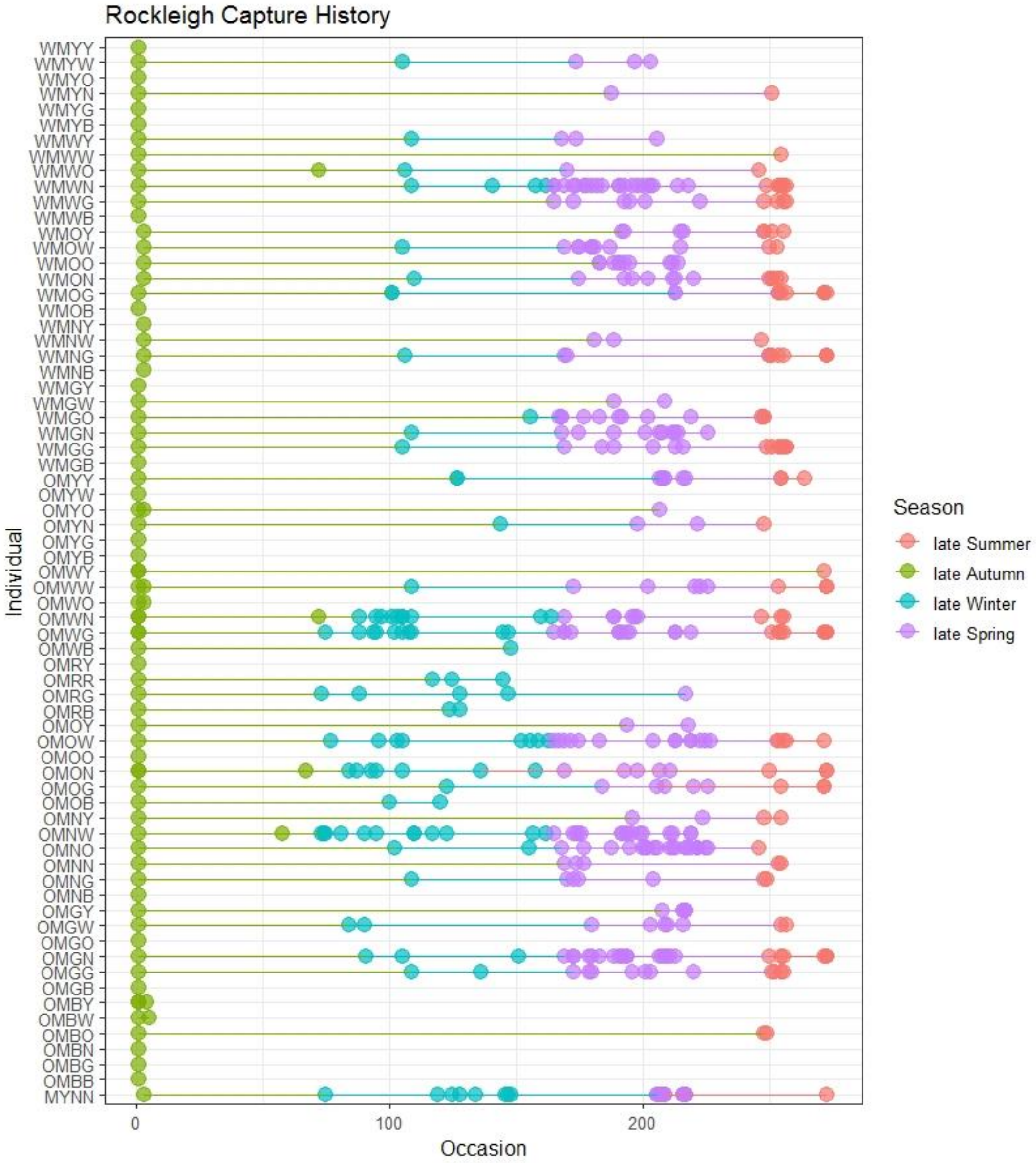
Appendix Pa: Capture histories of *S. guttata* individuals captured and tagged at Hartley in late summer (February) 2016 and re-sighted using motion sensor cameras within three study sites in this sub-region during consecutive seasons. Tagged individuals are represented on the *y*-axis and day number (“Occasion” when at least one camera was operating) is plotted on the *x*-axis. Occasions are not akin to consecutive days, as days when no cameras were operating were not included. Seasons are denoted by colours represented in the figure legend.



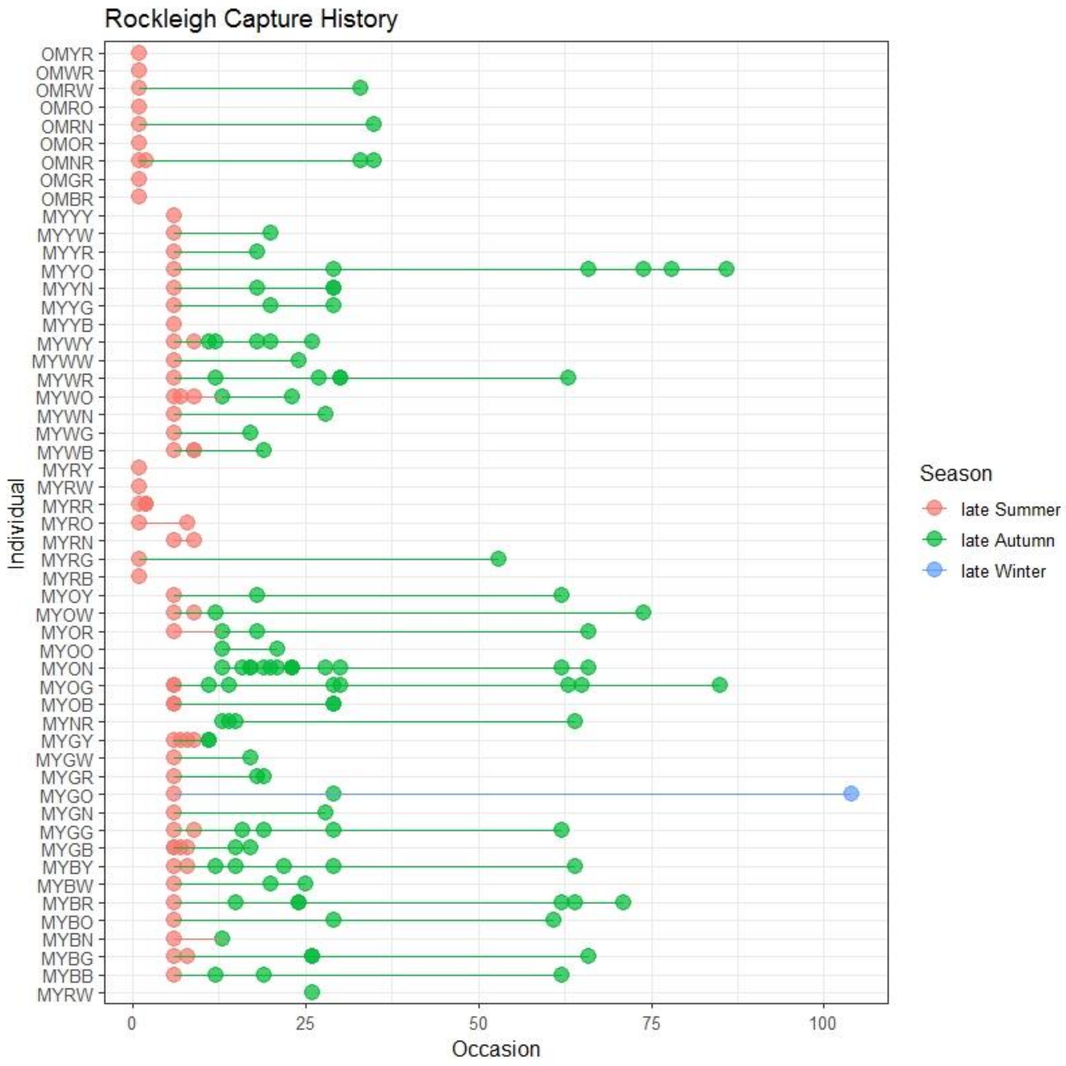
Appendix Pb: Capture histories of *S. guttata* individuals captured and tagged at Springton during late autumn, winter and spring 2014 and late autumn 2015, and re-sighted using motion sensor cameras within three study sites in this sub-region in consecutive seasons during 2015. Tagged individuals are represented on the *y*-axis and day number ('Occasion' when at least one camera was operating) is plotted on the *x*-axis. Occasions are not akin to consecutive days, as days when no cameras were operating are not included. Seasons are denoted by colours represented in the figure legend.



Appendix Pc: Capture histories of *S. guttata* individuals captured and tagged at Rockleigh during late autumn 2015 and re-sighted using motion sensor cameras within three study sites in this sub-region in consecutive seasons during 2015. Tagged individuals are represented on the *y*-axis and day number (‘Occasion’ when at least one camera was operating) is plotted on the *x*-axis. Occasions are not akin to consecutive days, as days when no cameras were operating are not included. Seasons are denoted by colours represented in the figure legend.



Appendix Pd: Capture histories of *S. guttata* individuals captured and tagged at Rockleigh in late summer 2016 and re-sighted using motion sensor cameras within three study sites in this sub-region in consecutive seasons during 2016. Tagged individuals are represented on the *y*-axis and day number ("Occasion" when at least one camera was operating) is plotted on the *x*-axis. Occasions are not akin to consecutive days, as days when no cameras were operating are not included. Seasons are denoted by colours represented in the figure legend.



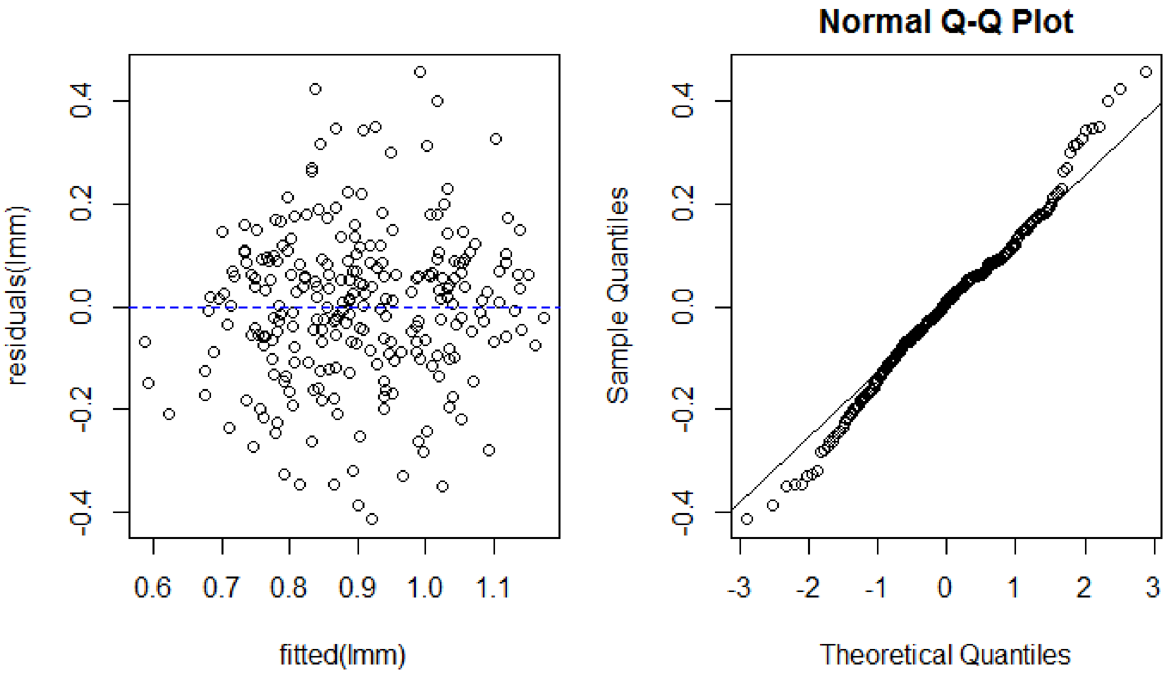
Appendix Q: Linear Mixed Models of energy intake

Appendix Q.i: Ranking of linear mixed models, using AICc model ranking procedures (Burnham and Anderson 2002), of the daily energy intake, standardised relative to the average daily requirements of a passerine of the same size (Nagy 1987), of *S. guttata* individuals at a supplement feeder at Monarto in the southern MLR 2014–2016.

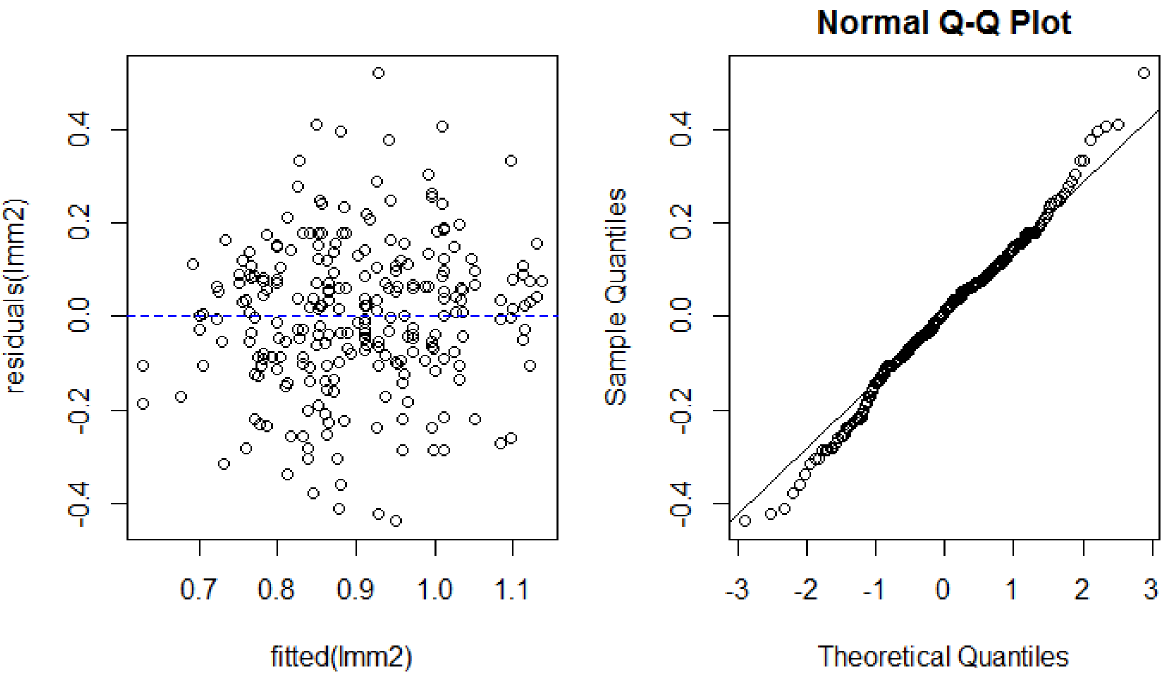
Candidate model	AICc	log(ʌ)	Dev.	χ^2	df	P-value
~ Season*Year	**-141.1**	**80.6**	**-161.1**			
~ Month*Year	-134.4	93.2	-186.4	25.3	16	0.065

The response variable is the amount of kJ obtained from supplement seed by individual *S. guttata* over the course of one day, divided by the standard amount of energy required by a passerine of their size, measured monthly for two years. This variable was cube-root transformed. Individual (bird ID) was included in the models as random factor. AICc = selection criterion for small sample sizes, log(ʌ) = the log likelihood of the model, Dev. = the model deviance, χ^2 = the chi-squared statistic, df = degrees of freedom. Candidate models with significant levels of empirical support are shown in bold.

Appendix Q.ii: Residuals against fitted values plot (left) and Normal Quantile-Quantile plot (right) of the linear mixed model of the effect of month and year on the energy intake by *S. guttata* from supplemented feed, standardised by expected daily requirements, at a site in Monarto, southern MLR between 2014 and 2016. Response variable was cube-root transformed.



Appendix Q.iii: Residuals against fitted values plot (left) and Normal Quantile-Quantile plot (right) of the linear mixed model of the effect of season and year on the energy intake by *S. guttata* from supplemented feed, standardised by expected daily requirements, at a site in Monarto, southern MLR between 2014 and 2016. Response variable was cube-root transformed.



References

Alexander P (1997) Kangaroo culling, harvesting and farming in South Australia: an ecological approach. *Australian Biologist* **10(1)**, 23-29.

Allen LR, Hume ID (1997) The importance of green seed in the nitrogen nutrition of the zebra finch *Taeniopygia guttata*. *Australian Journal of Ecology* **22(4)**, 412-418.

Altschul SF, Gish W, Miller W, Myers EW, Lipman DJ (1990) Basic local alignment search tool. *Journal of Molecular Biology* **215(3)**, 403-410.

Anders AD, Dearborn DC, Faaborg J, Thompson FR (1997) Juvenile survival in a population of neotropical migrant birds. *Conservation Biology* **11(3)**, 698-707.

Andersen AN (1987) Effects of seed predation by ants on seedling densities at a woodland site in SE Australia. *Oikos* **48(2)**, 171-174.

Ankor E (2005) Is seed availability a limiting factor for diamond firetails in the Monarto Region, South Australia? Honours thesis, unpub. (The University of Adelaide:Adelaide)

Antos MJ, Bennett A (2005) How important are different types of temperate woodlands for ground-foraging birds? *Wildlife Research* **32,** 557-572.

Antos MJ, Bennett A (2006) Foraging ecology of ground-feeding woodland birds in temperate woodlands of southern Australia. *Emu* **106**, 29-40.

Antos MJ, Bennett A, White JG (2008) Where exactly do ground-foraging woodland birds forage? Foraging sites and microhabitat selection in temperate woodlands of southern Australia. *Emu* **108**, 201-211.

Arredondo JT, Jones TA, Johnson DA (1998) Seedling Growth of Intermountain Perennial and Weedy Annual Grasses. *Journal of Range Management* **51(5)**, 584-589.

Ashmole NP (1963) The regulation of numbers of tropical oceanic birds. *Ibis* **103**, 458–473.

Attwood SJ, Park SE, Maron M, Collard SJ, Robinson D, Reardon-Smith KM, Cockfield G (2009) Declining birds in Australian agricultural landscapes may benefit from aspects of the European agri-environment model. *Biological Conservation* **142(10)**, 1981-1991.

Augustine B, Stewart F, Royle JA, Fisher J, Kelly M (2018) Spatial mark-resight for categorically marked populations with an application to genetic capture-recapture. bioRxiv, Cold Spring Harbor Laboratory. Available at <https://www.biorxiv.org/content/10.1101/299982v1.full>

Baker PJ, Bentley AJ, Ansell RJ, Harris S (2005) Impact of predation by domestic cats *Felis catus* in an urban area. *Mammal Review* **35(3- 4)**, 302-312.

Barratt DG (1997) Predation by house cats, *Felis catus* (L.), in Canberra, Australia. I. Prey composition and preference. *Wildlife Research* **24(3)**, 263-277.

Barrett G, Silcocks A, Barry S, Cunningham R, Poulter R (2003) 'The new atlas of Australian birds.' (Birds Australia:Country East Hawthorn, Victoria)

Barrett GW, Ford HA, Recher HF (1994) Conservation of woodland birds in a fragmented rural landscape. *Pacific Conservation Biology* **1**, 245-256.

Bates D, Machler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using {lme4}. *Journal of Statistical Software* **67(1)**, 1-48.

Bazzaz FA, Chiariello NR, Coley PD, Pitelka LF (1987) Allocating resources to reproduction and defense. *BioScience* **37(1)**, 58-67.

Beauchamp G (2005) Does group foraging promote efficient exploitation of resources? *Oikos* **111(2)**, 403-407.Benson JS, Redpath PA (1997) The nature of pre-European native vegetation in south-eastern Australia: critique of Ryan, D.G., Ryan, J.R. and Starr, B.J. (1995), The Australian landscape—observations of explorers and early settlers. *Cunninghamia* **5(2)**, 285-328.

Benton TG, Bryant DM, Cole L, Crick HQP (2002) Linking agricultural practice to insect and bird populations: a historical study over three decades. *Journal of Applied Ecology* **39(4)**, 673-687.

Bickford S, Gell P (2005) Holocene vegetation change, Aboriginal wetland use and the impact of European settlement on the Fleurieu Peninsula, South Australia. *The Holocene* **15(2)**, 200-215.

Bird P, Mutze G, Peacock D, Jennings S (2012) Damage caused by low-density exotic herbivore populations: the impact of introduced European rabbits on marsupial herbivores and *Allocasuarina* and *Bursaria* seedling survival in Australian coastal shrubland. *Biological Invasions* **14(3)**, 743-755.

Birdlife International (2019) Mapping of Australian bird species records. Electronic dataset, viewed January 2019, Available at: <birdata.birdlife.org.au>.

Blakers M, Davies SJJF, Reilly PN (1984) 'The atlas of Australian birds.' (Melbourne University Press: Melbourne)

Blendinger PG, Ojeda RA (2001) Seed supply as a limiting factor for granivorous bird assemblages in the Monte Desert, Argentina. *Austral Ecology* **26(4)**, 413-422.

Boag PT, Grant PR (1984) Darwin's finches (Geospiza) on Isla Daphne Major, Galapagos: breeding and feeding ecology in a climatically variable environment. *Ecological Monographs* **54(4)**, 463-489.

Boakes E, Mace G, McGowan P, Fuller R (2010) Extreme contagion in global habitat clearance. *Proceedings of the Royal Society B* **277**, 1081-1085.

Boutin S (1990) Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. *Canadian Journal of Zoology* **68(2)**, 203-220.

Boyle WA, Conway CJ, Bronstein JL (2011) Why do some, but not all, tropical birds migrate? A comparative study of diet breadth and fruit preference. *Evolutionary Ecology* **25(1)**, 219-236.

Bradshaw CJA (2012) Little left to lose: deforestation and forest degradation in Australia since European colonisation. *Journal of Plant Ecology* **5(1)**, 109-120.

Brown JH, Grover JJ, Davidson DW, Lieberman GA (1975) A preliminary study of seed predation in desert and montane habitats. *Ecology* **56(4)**, 987-992.

Bucher EH (1992) The causes of extinction of the passenger pigeon. *Current Ornithology* **9**, 1-36.

Buckingham DL, Bentley S, Dodd S, Peach WJ (2011) Seeded rygrass swards allow granivorous birds to winter in agriculturally improved grassland landscapes. *Agriculture, Ecosystems and Environment* **142(3)**, 256-265.

Burbidge AA, Manly BFJ (2002) Mammal extinctions on Australian islands: causes and conservation implications. *Journal of Biogeography* **29(4)**, 465-473.

Burbidge AA, McKenzie NL (1989) Patterns in the modern decline of western Australia's vertebrate fauna: causes and conservation implications. *Biological Conservation* **50(1)**, 143-198.

Bureau of Meteorology (2019) Long-term climate data. Electronic dataset, Commonwealth of Australia, viewed 12 Nov 2018, Available at: <http://www.bom.gov.au>.

Burnham KP, Anderson DR (2002) 'Model selection and multi-model inference: a practical information-theoretic approach.' 2 edn. (Springer: New York)

Calenge C (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* **197**, 516-519.

Calizza E, Costantini ML, Careddu G, Rossi L (2017) Effect of habitat degradation on competition, carrying capacity, and species assesmblage stability. *Ecology and Evolution* **7**:5784–5796.

Camín SR, Cueto VR, Lopez de Casenave J, Marone L (2015) Exploring food preferences and the limits of feeding flexibility of seed-eating desert birds. *Emu - Austral Ornithology* **115(3)**, 261-269.

Cannon A (1999) The significance of private gardens for bird conservation. *Bird Conservation International* **9(4)**, 287-297.

Cannon A (2000) 'Garden birdwatch handbook.' (British Trust for Ornithology:Thetford, United Kingdom)

Carpenter G (2012) 'A survey of the diamond firetail *Stagonopleura guttata* in the Mount Lofty Ranges, summer 2012.' (Department of Environment, Water and Natural Resources:Adelaide)

Caswell H (2000) Prospective and retrospective perturbation analyses: their roles in conservation biology. *Ecology* **81(3)**, 619-627.

Catterall CP, Green RJ, Jones DN (1991) Habitat use by birds across a forest-suburb interface in Brisbane: implications for corridors. *Nature Conservation* **2**, 247-258.

Ceballos G, Ehrlich PR, Barnosky AD, Garcia A, Pringle RM, Palmer TM (2015) Accelerated modern human-induced species losses: entering the sixth mass extinction. *Science Advances* **1**:e1400253.

Chaplin SB (1974) Daily energetics of the black-capped chickadee, *Parus atricapillus*, in winter. *Journal of Comparative Physiology* **89(4)**, 321-330.

Chen S, Yao H, Han J, Liu C, Song J, Shi L, Zhu Y, Ma X, Gao T, Pang X, Luo K, Li Y, Li X, Jia X, Lin Y Leon C (2010) Validation of the ITS2 region as a novel DNA barcode for identifying medicinal plant species. *PLoS ONE* **5(1)**.

Christian CE (2001) Consequences of a biological invasion reveal the importance of mutualism for plant communities. *Nature* **413(6856)**, 635-9.

Clark CW, Mangel M (1986) The evolutionary advantages of group foraging. *Theoretical Population Biology* **30(1)**, 45-75.

Clark DA (1982) Foraging behavior of a vertebrate omnivore (*Rattus rattus*): meal structure, sampling, and diet breadth. *Ecology* **63(3)**, 763-772.

Clarke MF, Oldland JM (2007) Penetration of remnant edges by noisy miners (*Manorina melanocephala*) and implications for habitat restoration. *Wildlife Research* **34(4)**, 253-261.

Clout MN (1989) Foraging behaviour of Glossy Black-Cockatoos. Australian Wildlife Research **16**:467–473.

Clutton-Brock TH (1988) 'Reproductive success: studies of individual variation in contrasting breeding systems.' (The University of Chicago Press: Chicago and London)

Cole I, Lunt ID (2005) Restoring Kangaroo Grass (*Themeda triandra*) to grassland and woodland understoreys: a review of establishment requirements and restoration exercises in south-east Australia. *Ecological management & restoration* **6(1)**, 28-33.

Collins BG, Newland C, Briffa P (1984) Nectar utilization and pollination by Australian honeyeaters and insects visiting *Calothamnus quadrifidus* (Myrtaceae). *Australian Journal of Ecology* **9(4)**, 353-365.

Colombelli-Négrel D, Kleindorfer, S (2009) Nest height, nest concealment, and predator type predict nest predation in superb fairy-wrens (*Malurus cyaneus*). *Ecological Research* **24(4)**, 921-928.

Conn PB, Kendall WL, Samuel MD (2004) A general model for the analysis of mark-resight, mark-recapture, and band-recovery data under tag loss. *Biometrics* **60(4)**, 900-909.

Cooke BD (1988) The effects of rabbit grazing on regeneration of sheoaks, *Allocasuarina verticillata* and saltwater ti-trees, *Melaleuca halmaturorum*, in the Coorong National Park, South Australia. *Australian Journal of Ecology* **13(1)**, 11-20.

Cooney SJN, Watson DM (2005) Diamond Firetails (*Stagonopleura guttata*) preferentially nest in mistletoe. *Emu* **105**, 317-322.

Corbin JD, D'Antonio CM (2004) Competition between native perennial and exotic annual grasses: implications for an historical invasion. *Ecology* **85(5)**, 1273-1283.

Crossman ND, Bryan BA, Cooke DA (2011) An invasive plant and climate change threat index for weed risk management: integrating habitat distribution pattern and dispersal process. *Ecological Indicators* **11(1)**, 183-198.

Crowder A (1991) Acidification, metals and macrophytes. *Environmental Pollution* **71(2)**, 171-203.

Crowhurst CL, Zanollo V, Griggio M, Robertson J, Kleindorfer S (2012). White flank spots signal feeding dominance in female diamond firetails, *Stagonopleura guttata*. *Ethology* **118**(1): 63–75.

Crowley G, Garnett S (1999) Seeds of the annual grasses *Schizachyrium* spp. as a food resource for tropical granivorous birds. *Australian Journal of Ecology* **24(3)**, 208-220.

Crowley GM, Garnett ST (2001a) Food value and tree selection by glossy black-cockatoos *Calyptorhynchus lathami*. *Austral Ecology* **26(1)**, 116-126.

Crowley GM, Garnett ST (2001b) Growth, seed production and effect of defoliation in an early flowering perennial grass, *Alloteropsis semialata* (Poaceae), on Cape York Peninsula, Australia. *Australian Journal of Botany* **49(6)**, 735-743.

D'Amore A, Kirby E, McNicholas M (2009) Invasive species shifts ontogenetic resource partitioning and microhabitat use of a threatened native amphibian. *Aquatic Conservation: Marine and Freshwater* Ecosystems **19(5)**, 534-541.

D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* **23(1)**, 63-87.

Davidson DW, Brown JH and Inouye RS (1980) Competition and the structure of granivore communities. *BioScience* **30(4)**, 233 – 238.

Davies R J-P (1997) 'Weed management in temperate native grasslands and box grassy woodlands in South Australia.' (Black Hill Flora Centre:Botanic Gardens of Adelaide, Adelaide)

Davies, R.J-P. (1999) 'Temperate eucalypt woodlands in Australia: biology, conservation, management and restoration.' (Eds Hobbs RJ, Yates CJ)(Surrey Beatty and Sons:Chipping Norton, NSW)

Deagle BE, Gales NJ, Evans K, Jarman SN, Robinson S, Trebilco R, Hindell MA (2007) Studying seabird diet through genetic analysis of faeces: A case study on macaroni penguins (*Eudyptes chrysolophus*). *PLoS One* **2(9)**.

Department for Environment and Heritage (2010) 'Informing biodiversity conservation for the Adelaide and Mount Lofty Ranges region, South Australia. Priorities, strategies and targets.' (Government of South Australia: Adelaide)

Department for Environment and Water (2018) 2019 quota report for commercial kangaroo harvest in South Australia. Department for Environment and Water, Adelaide. Available at https://www.environment.sa.gov.au/topics/plants-and-animals/Abundant_species/kangaroo-conservation-and-management/quotas-harvest-data

Didham RK, Tylianakis JM, Gemmell NJ, Rand TA, Ewers RM (2007) Interactive effects of habitat modification and species invasion on native species decline. *Trends in Ecology & Evolution* **22(9),** 489-496.

Dimond WJ (2001) 'The effect of a translocation on a source population using North Island robins as a case study.' (Massey University:Palmerston North, New Zealand)DiTomaso JM (2000) Invasive weeds in rangelands: species, impacts, and management. *Weed Science* **48(2)**, 255-265.

Dong Y, Zhu Y-G, Smith FA, Wang Y, Chen B (2008) Arbuscular mycorrhiza enhanced arsenic resistance of both white clover (*Trifolium repens* Linn.) and ryegrass (*Lolium perenne* L.) plants in an arsenic-contaminated soil. *Environmental Pollution* **155(1)**, 174-181.

Donovan TM, Jones PW, Annand EM, Thompson III FR (1997) Variation in local-scale edge effects: mechanisms and landscape context. *Ecology* **78(7)**, 2064-2075.

Doran J, Hall N (1983) Notes on fifteen Australian casuarina species. (Eds SJ Midgley, JW Turnbull, RD Johnson) pp. 19-52 (CSIRO:Canberra)

Dorrough J, Ash J, McIntyre S (2004) Plant responses to livestock grazing frequency in an Australian temperate grassland. *Ecography* **27(6)**, 798-810.

Dorrough J, Moxham C, Turner V, Sutter G (2006) Soil phosphorus and tree cover modify the effects of livestock grazing on plant species richness in Australian grassy woodland. *Biological Conservation* **130(3)**, 394-405.

Dostine PL, Franklin DC (2002) A comparison of the diet of three finch species in the Yinberrie Hills area, Northern Territory. *Emu - Austral Ornithology* **102(2)**, 159-164.

Dostine PL, Johnson GC, Franklin DC, Zhang Y, Hempel C (2001) Seasonal use of savanna landscapes by the Gouldian finch, *Erythrura gouldiae*, in the Yinberrie Hills area, Northern Territory. *Wildlife Research* **28(4)**, 445-458.

Driscoll DA (2017). Disturbance maintains native and exotic plant species richness in invaded grassy woodlands. *Journal of Vegetation Science* **28**:573–584.

Dunn PK and Smyth GK (2005) Series evaluation of Tweedie exponential dispersion model densities. *Statistics and Computing* **15(4)**, 267–280.

Efford MG (2018). secr: spatially explicit capture-recapture models. R package version 3.1.6. Available at <https://CRAN.R-project.org/>.

Efford MG, Fewster RM (2013) Estimating population size by spatially explicit capture–recapture. *Oikos* **122(6)**, 918-928.

Efford MG, Hunter CM (2017) Spatial capture-mark-resight estimation of animal population density. *Biometrics* **74(2)**, 411-420.

Ehmke G, Cunningham R, O'Connor J, Garnett S, Lau J, Herman K (Eds) (2014) The state of Australia's birds 2015: headline trends for terrestrial birds.(BirdLife Australia:Melbourne)

Er KBH, Wong TH, Tidemann CR (1998) An analysis of the occurrence of terrestrial bird species in the lowland yellow box-Blakely's red gum woodland remnants of the Australian Capital Territory. *Australian Bird Watcher* **17**, 370-382.

Fahrig L (2017). Ecological responses to habitat fragmentation *per se*. Annual Review of Ecology, Evolution, and Systematics **48**: 1–23.

Fahrig L, Arroyo-Rodríguez V, Bennett JR, Boucher-Lalonde V, Cazetta E, Currie DJ, Eigenbrod F, Ford AT, Harrison SP, Jaeger JA and Koper N (2019). Is habitat fragmentation bad for biodiversity? *Biological Conservation* **230**: 179–186.

Feinsinger P, Swarm LA (1982) Seasonal variation in food supply, and the hummingbird *Amazilia tobaci* on Trinidad and Tobago. *Ecology* **63(5)**, 1574-1587.

Finnie JW, Windsor PA, Kessell AE (2011) Neurological diseases of ruminant livestock in Australia. II: toxic disorders and nutritional deficiencies. *Australian Veterinary Journal* **89(7)**, 247-253.

Fischer J, Lindenmayer DB (2007) Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography* **16(3)**, 265-280.

Fisher DO, Blomberg SP, Ian PFO (2003) Extrinsic versus intrinsic factors in the decline and extinction of Australian Marsupials. *Proceedings: Biological Sciences* **270(1526)**, 1801-1808.

Fisher JL, Loneragan WA, Dixon K, Veneklaas EJ (2009) Soil seed bank compositional change constrains biodiversity in an invaded species-rich woodland. *Biological Conservation* **142(2)**, 256-269.

Fletcher Jr RJ, Didham RK, Banks-Leite C, Barlow J, Ewers RM, Rosindell J, Holt RD, Gonzalez A, Pardini R, Damschen EI, Melo FP (2018). Is habitat fragmentation good for biodiversity? *Biological conservation* **226**: 9–15.

Foley JA, DeFries R, Asner GP, Barford C, Bonan G, Carpenter SR, Chapin FS, Coe MT, Daily GC, Gibbs HK, Helkowski JH, Holloway T, Howard EA, Kucharik CJ, Monfreda C, Patz JA, Prentice IC, Ramankutty N, Snyder, PK (2005) Global consequences of land use. *Science* **309(5734)**, 570-574.

Fonturbel FE, Candia AB, Malebran J, Salazar DA, Gonzalez-Browne C, Medel R (2015) Meta-analysis of anthropogenic habitat disturbance effects on animal-mediated seed dispersal. *Global Change Biology* **21**:3951–3960.

Ford HA (1985) Density of birds in eucalypt woodland near Armidale, north-eastern New South Wales. *Corella* **9**, 78-107.

Ford HA (2011) The causes of decline of birds of eucalypt woodlands: advances in our knowledge over the last 10 years. *Emu* **111(1)**, 1-9.

Ford HA, Barrett GW, Saunders DA, Recher HF (2001) Why have birds in the woodlands of southern Australia declined? *Biological Conservation* **97**, 71-88.

Ford HA, Bell H (1981) Density of birds in eucalypt woodland affected to varying degrees by dieback. *Emu* **81(4)**, 202-208.

Ford HA, Bridges L, Noske S (1985) Density of birds in eucalypt woodland near Armidale, north-eastern New South Wales. *Corella* **9(4)**, 78-107.

Ford HA, Davis WE, Debus S, Ley A, Recher H, Williams B (1993) Foraging and aggressive behaviour of the regent honeyeater *Xanthomyza phrygia* in northern New South Wales. *Emu - Austral Ornithology* **93(4)**, 277-281.

Ford HA, Howe R (1980) The future of birds in the Mount Lofty Ranges. *South Australian Ornithologist* **28**, 85-89.

Forshaw JM, Shephard M, Pridham A (2012) ‘Grassfinches in Australia.’ (CSIRO Publishing: Collingwood, Australia)

Frank CL (1988) The influence of moisture content on seed selection by kangaroo rats. *Journal of Mammology* **69(2)**, 353-357.

Franklin DC, Menkhorst PW, Robinson JL (1989) Ecology of the regent honeyeater *Xanthomyza phrygia*. *Emu - Austral Ornithology* **89(3)**, 140-154.

Franklin DC, Whitehead PJ, Pardon G, Matthews J, McMahon P, McIntyre D (2005) Geographic patterns and correlates of the decline of granivorous birds in northern Australia. *Wildlife Research* **32(5)**, 399-408.

Fretwell SD (1972) 'Populations in a seasonal environment.' (Princeton University Press: Princeton, New Jersey)

Garnett S, Crowley G (1994) Wet-season feeding by four species of granivorous birds in the Northern Territory. *Australian Bird Watcher* **15(7)**, 306-309.

Garnett S, Crowley G (1995a) ‘Ecology and conservation of the golden-shouldered parrot.’ (Department of the Environment, Sports and Territories:Canberra and Queensland Department of Environment and Heritage:Brisbane)

Garnett S, Crowley G (1995b) Feeding ecology of hooded parrots *Psephotus dissimilis* during the early wet season. *Emu* **95(1)**, 54-61.

Garnett S, Crowley G (2000) ‘The action plan for Australian birds 2000.’ Environment Australia and Birds Australia: Canberra, ACT. Available at: https://www.environment.gov.au/node/34417.

Garnett S, Franklin D (2014) 'Climate Change Adaptation Plan for Australian Birds.' (CSIRO Publishing:Collingwood, Victoria)

Garnett S, Szabo J, Dutson G (2011) ‘The action plan for Australian birds 2010.’ (CSIRO Publishing: Collingwood, Victoria)

Garnier E (1992) Growth analysis of congeneric annual and perennial grass species. *Journal of Ecology* **80(4)**, 665-675.

George WG (1974) Domestic cats as predators and factors in winter shortages of raptor prey. *The Wilson Bulletin* **86(4)**, 384-396.

Geoscience Australia (2017) Vegetation - pre-European settlement (1788). Electronic dataset, west Murraylands and southern Mount Lofty Ranges pre-European settlement vegetation mapping project, national mapping division: viewed 13 Nov 2018. Available at < https://data.gov.au/dataset/vegetation-pre-european-settlement-1788>.

Geyle HM, Woinarski JCZ, Baker GB, Dickman CR, Dutson G, Fisher DO, Ford H, Holdsworth M, Jones ME, Kutt A, Legge S, Leiper I, Loyn R, Murphy BP, Menkhorst P, Reside AE, Ritchie EG, Roberts FE, Tingley R, Garnett ST (2018) Quantifying extinction risk and forecasting the number of impending Australian bird and mammal extinctions. *Pacific Conservation Biology* **24(2)**, 157–167.

Gibbs J (2001) ‘Grass identification manual - for everyone : a pictorial guide to recognition of native and exotic grasses in the northern and southern Lofty botanical regions of South Australia.’ (University of South Australia: Mawson Lakes, Adelaide)

Gibson-Roy P, Moore G, Delpratt J (2010) Testing methods for reducing weed loads in preparation for reconstructing species-rich native grassland by direct seeding. E*cological management and restoration* **11(2)** 135-139.

Gill AM, Woinarski JCZ, York A (1999) Australia's biodiversity - responses to fire: plants, birds and invertebrates. Biodiversity Technical Paper No 1, Department of Environment and Heritage, Commonwealth of Australia, Canberra.

Greenberg R (2003) The role of neophobia and neophilia in the development of innovative behavior of birds. In 'Animal Innovation.' (Eds SN Reader, KN Laland) pp. 175–196. (Oxford University Press: New York)

Grice AC, Barchia I (1992) Does grazing reduce survival of indigenous perennial grasses of the semi-arid woodlands of western New South Wales? *Australian Journal of Ecology* **17(2)**, 195-205.

Groves RH (1986) Invasion of Mediterranean ecosystems by weeds. In 'Resilience in Mediterranean-type ecosystems.' (Eds B Dell, AJM Hopkins, BB Lamont) pp. 129-145. (Springer Netherlands: Dordrecht).

Grubb TC, Cimprich DA (1990) Supplementary Food Improves the Nutritional Condition of Wintering Woodland Birds: Evidence from Ptilochronology. *Ornis Scandinavica (Scandinavian Journal of Ornithology)* **21(4)**, 277-281.

Gurevitch J, Padilla DK (2004) Are invasive species a major cause of extinctions? *Trends in Ecology & Evolution* **19(9)**, 470-474.

Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, Lovejoy TE, Sexton JO, Austin MP, Collins CD, Cook WM (2015). Habitat fragmentation and its lasting impact on Earth’s ecosystems. *Science advances* **1(2)**: p.e1500052.

Heinrichs JA, Bender DJ, Schumaker NH (2016). Habitat degradation and loss as key drivers of regional population extinction. *Ecological Modelling* **335(10)**: 64–73.

Herrera CM (1998) Long-term dynamics of mediterranean frugivorousbirds and fleshy fruits: a 12-year study. *Ecological Monographs* **68(4)**, 511-538.

Higgins PJ, Peter JM, Cowling SJ (2006) ‘Handbook of Australian, New Zealand and Antarctic birds. Volume 7: Boatbill to Starlings.’ (Oxford University Press: Melbourne)

Hobbs RJ (2001) Synergisms among habitat fragmentation, livestock grazing, and biotic invasions in southwestern Australia. *Conservation Biology* **15(6)**, 1522-1528.

Hofreiter M, Betancourt JL, Sbriller AP, Markgraf V, McDonald HG (2017) Phylogeny, diet, and habitat of an extinct ground sloth from Cuchillo Curá, Neuquén Province, southwest Argentina. *Quaternary Research* **59(3)**, 364-378.

Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. *Biometrical Journal* **50(3)**, 346--363.

Houdet JRA (2003) Factors influencing Poaceae seed availability for the Diamond Firetail (*Stagonopleura guttata*). Honours Thesis, unpub. (University of Adelaide: Adelaide)

Houston DC, Donnan D, Jones PJ (1995) The source of the nutrients required for egg production in zebra finches *Poephila guttata*. *Journal of Zoology* **235(3)**, 469-483.

Howe FP, Knight RL, McEwen LC, George TL (2000) Diet switching and food delivery by shrubsteppe passerines in response to an experimental reduction in food. *Western North American Naturalist* **60(2)**, 139-154.

Hueneke K (1976) ‘Aspects of the autoecology and secondary succession of *Casuarina stricta* on Canberra's hills.’ (Australian National University:Canberra)

Hulme P, Benkman C (2002) Granivory. In 'Plant animal interactions: an evolutionary approach.' (Eds CM Herrera, O Pellmyr) pp. 132-154 (Wiley-Blackwell:Oxford)

Immelmann K (1982) ‘Australian finches in bush and aviary.’ (Angus & Robertson Publishers:Australia)

Intergovernmental Platform on Biodiversity and Ecosystem Services (2019) Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. (Eds S Díaz, J Settele, ES Brondizio, HT Ngo, M Guèze, J Agard, A Arneth, P Balvanera, KA Brauman, SHM Butchart, KMA Chan, LA Garibaldi, K Ichii, J Liu, SM Subramanian, GF Midgley, P Miloslavich, Z Molnár, D Obura, A Pfaff, S Polasky, A Purvis, J Razzaque, B Reyers, R Roy Chowdhury, YJ Shin, IJ Visseren-Hamakers, KJ Willis, CN Zayas) (IPBES secretariat:Bonn, Germany)

Jessop JP, Dashorst GRM, James FM (2006) ‘Grasses of South Australia: an illustrated guide to the native and naturalised species.’ (The Board of Botanic Gardens of Adelaide and State Herbarium: South Australia)

Jones D (2011) An appetite for connection: why we need to understand the effect and value of feeding wild birds. *Emu* **-** *Austral Ornithology* **111(2)**, 1-7.

Joseph L (1982) The glossy black-cockatoo in the south Mount Lofty Ranges. *South Australian Ornithologist* **30**, 202-204.

Joseph L (1985) Seed-eating birds of southern Australia. In 'The dynamic partnership, birds and plants in southern Australia.' (Eds HA Ford and DC) pp. 85-93. (South Australian Government Printer: Adelaide)

Jost L (2006) Entropy and diversity. *Oikos* **113(2)**, 363-375.

Källander H (1981) The effects of provision of food in winter on a population of the great tit *Parus major* and the blue tit *P. caeruleus*. *Ornis Scandinavica (Scandinavian Journal of Ornithology)* **12(3)**, 244-248.

Kattan GH, Alvarez-Lopez H, Giraldo M (1994) Forest fragmentation and bird extinctions: San Antonio eighty years later. *Conservation Biology* **8(1)**, 138-146.

Kearns CA, Inouye DW, Waser NM (1998) Endangered mutualism: the conservation of plant-pollinator interactions. *Annual Review of Ecology and Systematics* **29**, 83-112.

Kendall WL (1999) Robustness of closed capture-recapture methods to violations of the closure assumption. *Ecology* **80(8)**, 2517-2525.

Kennedy PL, Dewey SR (2001) Effects of supplemental food on parental-care strategies and juvenile survival of northern goshawks. *The Auk: Ornithological Advances* **118(2)**, 352-365.

Kennedy SJ, Overs AE (2001) Foraging ecology and habitat use of the swift parrot on the south-western slopes of New South Wales. *Corella* **25**, 68-74.

Kissling LM, Garton EO (2006) Estimating detection probability and density from point-count surveys: a combination of distance and double-observer sampling. *The Auk* **123(3)**, 735-752.

Kitaysky AS, Wingfield JC, Piatt JF (1999) Dynamics of food availability, body condition and physiological stress response in breeding black-legged kittiwakes. *Functional Ecology* **13(5)**, 577-584.

Kordjazi Z, Frusher S, Buxton C, Gardner C, Bird T (2016) The influence of mark-recapture sampling effort on estimates of rock lobster survival. *Plos one* **11(3)**, e0151683.

Krebs JR (1971) Territory and breeding density in the great tit, *Parus Major* L. *Ecology* **52(1)**, 2-22.

Kriticos D, Crossman ND, Ota N, Scott J (2010) 'Climate change and invasive plants in South Australia.' (CSIRO Climate Adaptation Flagship:Canberra)

Laake JL (2013) RMark: An R interface for analysis of capture-recapture data with MARK. Alaska Fisheries Science Centre, National Marine Fisheries Service: 7600 Sand Point Way NE, Seattle WA 98115. Unpublished.

Lack D (1954) 'The natural regulation of animal numbers.' (Clarendon Press: Oxford)

Lack D (1966) 'Population studies of birds.' (Oxford University Press:Oxford)

Lambeck RJ (1995). 'The minimum resource requirements of a honeyeater community in a fragmented landscape.' (Curtin University of Technology, School of Environmental Biology: Canberra, Australia)

Lambert S, Kleindorfer S (2006) Nest concealment but not human visitation predicts predation of new holland honeyeater nests. *Emu - Austral Ornithology* **106(1)**, 63-68.

Laurance WF (2002) Hyperdynamism in fragmented habitats. *Journal of Vegetation Science* **13(4)**, 595-602.

Laut P, Heyligers PC, Keig G, Löffler E, Margules C, Scott RM, Sullivan ME (1977) 'Environments of South Australia Province 3 Mt. Lofty Block.' (Commonwealth Scientific and Industrial Research Organisation:Canberra, Australia)

Law BS (1994) Banksia nectar and pollen: dietary items affecting the abundance of the common blossom bat, *Syconycteris australis*, in southeastern Australia. *Australian Journal of Ecology* **19(4)**, 425-434.Leck CF (1972) Seasonal changes in feeding pressures of fruit-and nectar-eating birds in Panam. *The Condor* **74(1)**, 54-60.

Lee ATK, Wright D, Barnard P (2017) Hot bird drinking patterns: drivers of water visitation in a fynbos bird community. *African Journal of Ecology* **55(4)**, 541-553.

Lehikoinen E (1987) Seasonality of the daily weight cycle in wintering Passerines and its consequences. *Ornis Scandinavica (Scandinavian Journal of Ornithology)* **18(3)**, 216-226.

Lenth RV (2016) Least-squares means: The R package 'lsmeans'. *Journal of Statistical Software* **69(1)**, 1-33.

Levey DJ (1988) Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. *Ecological Monographs* **58(4)**, 251-269.

Levey DJ, Stiles FG (1992) Evolutionary precursors of long-distance migration: resource availability and movement patterns in neotropical landbirds. *The American Naturalist* **140(3)**, 447-476.

Lima SL (1986) Predation risk and unpredictable feeding conditions: determinants of body mass in birds. *Ecology* **67(2)**, 377-385.

Lindenmayer D, Bennett A, Hobbs R (2010) 'Temperate woodland conservation and management.' (CSIRO Publishing: Collingwood, Victoria)

Lindholm A, Gauthier G, Desrochers A (1994) Effects of hatch date and food supply on gosling growth in Arctic-nesting greater snow geese. *The Condor: Ornithological Applications* **96(4)**, 898-908.

Litzow MA, Piatt JF (2003) Variance in prey abundance influences time budgets of breeding seabirds: evidence from pigeon guillemots *Cepphus columba*. *Journal of Avian Biology* **34(1)**, 54-64.

Longmore N (1978) Avifauna of the Rockhampton area, Queensland. *Sunbird: Journal of the Queensland Ornithological Society, The* **9(3/4)**, 25-33.

Lord EAR (1956) The birds of the Murphy's creek district, southern Queensland. *Emu* **56(2)**, 100-128.

Lynn JC, Chambers CL, Rosenstock SS (2006) Use of wildlife water developments by birds in southwest Arizona during migration. *Wildlife Society Bulletin* **34(3)**, 592-601.

MacArthur RH, Pianka ER (1966) On optimal use of a patchy environment. *The American Naturalist* **100(916)**, 603-609.

Macherey-Nagel (2014) Genomic DNA from plant: user manual. Macherey-Nagel GmbH & Co. KG, Rev. 09 2019 Available at https://www.mn-net.com/Portals/8/attachments/Redakteure_Bio/Protocols/Genomic%20DNA/UM_gDNAPlant_NSPlantII.pdf

Magrach A, Laurance W, Larrinaga AR, Santamaria L (2014) Meta-Analysis of the effects of forest fragmentation on interspecific interactions. *Conservation Biology* **28(5)**, 1342-1348.

Magrath RD (1991) Nestling weight and juvenile survival in the blackbird, *Turdus merula*. *Journal of Animal Ecology* **60(1)**, 335-351.

Manly B, McDonald L, Thomas D, McDonald T, Erickson W (2004) 'Resource selection by animals: statistical design and analysis for field studies.' (Kluwer Academic Publishers: Dordrecht)

Marcon E, Hérault B (2015) Decomposing phylodiversity. *Methods in Ecology and Evolution* **6(3)**, 333-339.

Marcon E, Hérault B, Baraloto C, Lang G (2012) The decomposition of Shannon's entropy and a confidence interval for beta diversity. *Oikos* **121(4)**, 516-522.

Marcon E, Scotti I, Hérault B, Rossi V, Lang G (2014) Generalization of the partitioning of Shannon Diversity. *PLoS One* **9(3)**. doi.org/10.1371/journal.pone.0090289

Maron M, Kennedy S (2007) Roads, fire and aggressive competitors: determinants of bird distribution in subtropical production forests. *Forest Ecology and Management* **240(1)**, 24-31.

Maron M, Lill A (2005) The influence of livestock grazing and weed invasion on habitat use by birds in grassy woodland remnants. *Biological Conservation* **124(4)**, 439-450.

Marone L, Olmedo M., Valdes DY, Zarco A, de Casenave JL, Pol RG (2017) Diet switching of seed-eating birds wintering in grazed habitats of the central Monte Desert, Argentina. *The Condor: Ornithological Applications*, **119(4)**, 673–682.

Marshall AJ (1932) In search of a ‘lost’ bird. *Emu* **32(2)**, 99-103.

Martin T, Possingham HP (2005) Predicting the impact of livestock grazing on birds using foraging height data. *Journal of Applied Ecology* **42(2)**, 400-408.

Martin TE (1987) Food as a limit on breeding birds: a life-history perspective. *Annual Review of Ecology and Systematics* **18**, 453-487.

Martínez-Abraín A, Tavecchia G, Regan HM, Jiménez J, Surroca M, Oro D (2012) Effects of wind farms and food scarcity on a large scavenging bird species following an epidemic of bovine spongiform encephalopathy. *Journal of Applied Ecology* **49(1)**, 109-117.

Martinson HM, Fagan WF (2014) Trophic disruption: a meta-analysis of how habitat fragmentation affects resource consumption in terrestrial arthropod systems. *Ecology Letters* **17(9)**, 1178-1189.

Matthew D, Johnson MD, Christa M, Horn CM (2008) Effects of rotational grazing on rodents and raptors in a coastal grassland. *Western North American Naturalist* **68(4)**, 444–452.

McCleery RH, Perrins CM (1985) Territory size, reproductive success and population dynamics in the great tit, *Parus major*. In 'Behavioural ecology: ecological consequences of adaptive behaviour. ' (Eds RM Sibly and RH Smith) pp. 353-374. (Blackwell Scientific Publications: Oxford)

McClintock BT, White GC (2009) A less field-intensive robust design for estimating demographic parameters with mark–resight data. *Ecology* **90(2)**, 313-320.

McClintock BT, White GC, Antolin MF, Tripp DW (2009) Estimating abundance using mark–resight when sampling is with replacement or the number of marked individuals is unknown. *Biometrics* **65(1)**, 237–246.

McCormick MI and Lonnstedt OM (2016) Disrupted learning: habitat degradation impairs crucial antipredator responses in naïve prey. *Proc. Royal Society B* **283**:20160441.

McFarland DC (1986) Seasonal changes in the abundance and body condition of honeyeaters (Meliphagidae) in response to inflorescence and nectar availability in the New England National Park, New South Wales. *Australian Journal of Ecology* **11(4)**, 331-340.

McGrath K (2015) AGRF Sanger sequencing: sample preparation guide(GSEQDOC00166). v1.8 edn. The Australian Genome Research Facility. Available at https://www.agrf.org.au/docs/sanger-sequencing-sample-preparation-guide.pdf

McGregor R, Whittingham MJ, Cresswell W (2007) Survival rates of tropical birds in Nigeria, West Africa. *Ibis* **149**, 615–618.

McGuire A, Kleindorfer S (2007) Nesting success and apparent nest-adornment in diamond firetails (*Stagonopleura guttata*). *Emu* **107**, 44-51.

McKenzie NL, Burbidge AA (2002) Mammals. Australian terrestrial biodiversity assessment 2002. (Eds P Sattler, C Creighton) pp. 84-96. (National Land and Water Resources Audit: Canberra)

McKenzie NL, Burbidge AA, Baynes A, Brereton RN, Dickman CR, Gordon G, Gibson LA, Menkhorst PW, AC, Williams MR, Woinarski JCZ (2007) Analysis of factors implicated in the recent decline of Australia's mammal fauna. *Journal of Biogeography* **34(4)**, 597-611.

Meijer T, Rozman J, Schulte M, Stach-Dreesmann C (1996) New findings in body mass regulation in zebra finches (*Taeniopygia guttata*) in response to photoperiod and temperature. *Journal of Zoology* **240(4)**, 717-734.

Merigot H, Paton D (2018) Strategic revegetation: applying eucalypt flowering phenologies to rebuild landscapes for nectarivorous birds. In ‘Restore, Regenerate, Revegetate Conference Proceedings, A Conference on Restoring Ecological processes, Ecosystems and landscapes in a Changing World 5-9 February 2017.’ (Ed.) pp 59–60. (University of New England:Armidale, New South Wales)

Milenkaya O, Legge S, Walters JR (2011) Breeding biology and life-history traits of an Australasian tropical granivore, the crimson finch (*Neochmia phaeton*). *Emu* **111(4)**, 312–320.

Monks DP, Sadatasilan K and Moot DJ (2009) Cardinal temperatures and thermal time requirements for germination of annual and perennial temperate pasture species. *Agronomy New Zealand* **39**, 95–109.

Montserrat V, Espinar JL, Hejda M, Hulme PE, Vojtěch J, Maron JL, Pergl J, Schaffner U, Sun Y, Pysek P (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters* **14(7)**, 702-708.

Moore RM (1965) 'Ecological effects of grazing on grasslands in south-eastern Australia.' Proceedings of the 9th International Grassland Congress, Sao Paulo, Brazil, 1964. pp 5.

Morton SR (1990) The impact of European settlement on the vertebrate animals of arid Australia: a conceptual model. *Proceedings of the Ecological Society of Australia* **16**, 210-213.

Mott JJ (1972) Germination studies on some annual species from an arid region of Western Australia. *Journal of Ecology* **60(2)**, 293-304.

Mott JJ, Andrew MH (1985) The effect of fire on the population dynamics of native grasses in tropical savannas of north-west Australia. In 'Ecology of the wet-dry tropics: proceedings of a joint symposium with the Australian Mammal Society'. (Eds MG Ridpath, LK Corbett) pp. 231-239. (Ecological Society of Australia: Darwin).

Murray BR, Dickman CR (1994) Food preferences and seed selection in two species of Australian desert rodent. *Wildlife Research* **21(6)**, 647-655.

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858.

Nagy KA (1987) Field metabolic rate and food requirement scaling in mammals and birds. *Ecological Monographs* **57(2)**, 111-128.

Newton I (1980) The role of food in limiting bird numbers. *Ardea* **68(1)**, 11-30.

Norbury G, Norbury D, Hacker R (1993) Impact of red kangaroos on the pasture layer in the Western Australian Arid Zone. *The Rangeland Journal* **15(1)**, 12-23.

Northeast PJ (2014) Defining habitat use by declining woodland birds to inform restoration programs. PhD thesis (University of Adelaide:Adelaide)

O'Brien, CS, Waddell RB, Rosenstock SS, Rabe MJ (2006) Wildlife use of water catchments in southwestern Arizona. *Wildlife Society Bulletin* **34(3)**, 582-591.

O'Connor TG, Pickett GA (1992) The influence of grazing on seed production and seed banks of some African savanna grasslands. *Journal of Applied Ecology* **29(1)**, 247-260.

O'Gorman B (1980) A breeding study of the Diamond Firetail. *Australian Aviculture* **34**, 13-19.

Oksanen JB, F, Friendly M, *et al.* (2016) vegan: Community Ecology Package. (R package version 2.4-0). Available at https://cran.r-project.org.

Olssen L, Barbosa H, Bhadwal S, Cowie A, Delusca K, Flores-Renteria D, Hermans K, Jobbagy E, Kurz W, Li D, Sonwa DJ, Stringer L (2019) Climate change and land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems. Intergovernmental Panel on Climate Change. Available at https://report.ipcc.ch/srccl/pdf/FullReport-1.pdf

Palminteri S, Powell GVN, Peres CA (2016) Determinants of spatial behavior of a tropical forest seed predator: the roles of optimal foraging, dietary diversification, and home range defense. *American Journal of Primatology* **78(5)**, 523-533.

Paton DC (1980) The importance of manna, honeydew and lerp in the diets of honeyeaters. *Emu – Austral Ornithology* **80(4)**, 213-226.

Paton DC (2010) Restoring woodlands in the Mount Lofty Ranges region. In ‘The state of Australia’s birds 2009: restoring woodland habitat for birds.’ *Supplement to Wingspan* **20(1),** 2-4.

Paton DC, Prescott AM, Davies RJ-P, Heard LM (1999) Temperate eucalypt woodlands in Australia: biology, conservation, management and restoration. In ‘The distribution, status and threats to temperate woodlands in South Australia.’ (Eds R Hobbs, CJ Yates) pp. 57-85. (Surrey Beatty & Sons Pty Limited: Australia)

Paton DC, Rogers DJ, Harris W (2004) Birdscaping the environment : restoring the woodland systems of the Mt. Lofty region, South Australia. In ‘Conservation of Australia's forest fauna.’ 2nd edn. (Ed. D Lunney) pp. 331-358. (Royal Zoological Society of New South Wales: Mosman, New South Wales)

Paton DC, Sinclair RG, Carpenter G (1994) A second bird atlas of the Adelaide region. Part 1: Changes in the distribution of birds: 1974-75 vs 1984-85. *South Australian Ornithologist* **31(7)**, 151-193.

Perdeck AC, Visser ME, Balen JHV (2000) Great tit *Parus major* survival and the beech-crop cycle. *Ardea* **88(1)**, 99-106.

Pollock KH (1982) A capture-recapture design robust to unequal probability of capture. *The Journal of Wildlife Management* **46(3)**, 752-757.

Price MV (1983) Laboratory studies of seed size and seed species selection by heteromyid rodents. *Oecologia* **60(2)**, 259-263.

Prior LD, McCaw WL, Grierson PF, Murphy BP, Bowman DMJS (2011) Population structures of the widespread Australian conifer *Callitris columellaris* are a bio-indicator of continental environmental change. *Forest Ecology and Management* **262(2)**, 252-262.

Prober SM, Thiele KR (2005) Restoring Australia's temperate grasslands and grassy woodlands: integrating function and diversity. *Ecological Management & Restoration* **6(1)**, 16-27.

Prober SM, Thiele KR, Koen TB (2004) Spring burns control exotic annual grasses in a temperate grassy woodland. *Ecological Management & Restoration* **5(2)**, 131-134.

Pulliam HR (1983) Ecological community theory and the coexistence of sparrows. *Ecology* **64(1)**, 45-52.

Pulliam HR (1988) Sources, sinks, and population regulation. *The American Naturalist* **132(5)**, 652-661.

Pulliam HR, Enders F (1971) The feeding ecology of five sympatric finch species. *Ecology* **52(4)**, 557-566.

R Core Team (2016) R: A language and environment for statistical computing. (R Foundation for Statistical Computing: Vienna).

Rahel S, Beth G, Parsons AW, Stocking JJ, McClintock BT, Simons TR, Pollock KH, O’Connell AF (2013) A spatial mark–resight model augmented with telemetry data. *Ecology* **94(3)**, 553-559.

Read JL (1987) The ecology of firetail finches. Honours thesis (University of Adelaide:Adelaide)

Read JL (1994) The diet of three species of firetail finches in temperate South Australia. *Emu – Austral Ornithology* **94**, 1-8.

Reed DH, O’Grady JJ, Brook BW, Ballou JD, Frankham R (2003) Estimates of minimum viable population sizes for vertebrates and factors influencing those estimates. Biological Conservation **113(1)**, 23–34.

Rees JD, Kingsford RT, Letnic M (2017) In the absence of an apex predator, irruptive herbivores suppress grass seed production: implications for small granivores. *Biological Conservation*. **213(1)**, 13–8.

Recher H (1999) The state of Australia's avifauna: a personal opinion and prediction for the new millennium. *Australian Zoologist* **31(1)**, 11-27.

Recher HF, Davis JWE, Calver MC (2002) Comparative foraging ecology of five species of ground-pouncing birds in Western Australian woodlands with comments on species decline. *Ornithological Science* **1(1)**, 29-40.

Reid JRW (1999) Threatened and declining birds in the New South Wales wheat-sheep belt: I. diagnosis, characteristics and management. Consultancy report to New South Wales National Parks and Wildlife Service, CSIRO Wildlife and Ecology, Canberra.

Renton K (2001) Lilac-crowned parrot diet and food resource availability: resource tracking by a parrot seed predator. *The Condor* **103(1)**, 62-69.

Reynolds SA, Corbin JD, D'Antonio CM (2001) The effects of litter and temperature on the germination of native and exotic grasses in a coastal Calinornia grassland. *California Botanical Society* **48(4)**, 230-235.

Robinson D (1994) Research plan for threatened woodland birds of southeastern Australia. Technical report series, Arthur Rylah Institute for Environmental Research, no. 133, Department of Conservation and Natural Resources, Victoria.

Robinson D, Triall BJ (1996) Conserving woodland birds in the wheat and sheep belts of southern Australia. *Supplement to Wingspan* **6(2)**, Conservation Statement Number 10, Royal Australasian Ornithologists Union, Hawthorn East, Victoria.

Rockwell SM, Bocetti CI, Marra PP (2012) Carry-over effects of winter climate on spring arrival date and reproductive success in an endangered migratory bird, Kirtland's warbler *Setophaga kirtlandii*. *The Auk* **129(4)**, 744-752.

Rogers DJ (2011) ‘A landscape assessment for the Southern Mount Lofty Ranges landscape.’ (Department of Environment and Natural Resources:South Australia).

Rotenberry JT (1980) Dietary relationships among shrubsteppe passerine birds: competition or opportunism in a variable environment. *Ecological Monographs* **50(1)**, 93-110.

Rubega M, Inouye C (1994) Prey switching in red-necked phalaropes *Phalaropus lobatus*: feeding limitations, the functional response and water management at Mono Lake, California, USA. *Biological Conservation* **70(3)**, 205-210.

Rutz C, Bijlsma RG (2006) Food-limitation in a generalist predator. *Proceedings: Biological Sciences* **273(1597)**, 2069-2076.

Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH (2000) Global biodiversity scenarios for the year 2100. *Science* **287(5459)**, 1770-1774.

Sánchez R, Blendinger PG (2014) Trophic ecology of the ringed warbling-finch (*Poospiza torquata*) in neotropical semi-arid scrublands. *Emu - Austral Ornithology* **114(3)**, 229-233.

Saunders D, Brereton R, Tzaros C, Holdsworth M, Price R (2007) Conservation of the swift parrot *Lathamus discolor* - management lessons for a threatened migratory species. *Pacific conservation biology* **(13)** 111-19.

Saunders DA (1989) Changes in the avifauna of a region, district and remnant as a result of fragmentation of native vegetation: the wheatbelt of Western Australia. A case study. *Biological Conservation* **50(1)**, 99-135.

Schluter D (1981) Does the theory of optimal diets apply in complex environments? *The American Naturalist* **118(1)**, 139-147.

Schluter D (1982) Seed and patch selection by Galapagos ground finches: relation to foraging efficiency and food supply. *Ecology* **63(4)**, 1106-1120.

Schluter D (1988) The evolution of finch communities on islands and continents: Kenya vs. Galapagos. *Ecological Monographs* **58(4)**, 229-249.

Schopfer M (1989) Feeding ecology of five sympatric species of grassfinches in south-eastern Australia. Phd thesis (La Trobe University: Bundoora, Victoria)

Shipley LA, Forbey JS, Moore BD (2009) Revisiting the dietary niche: when is a mammalian herbivore a specialist? *Integrative and Comparative Biology* **49(3)**, 274-290.

Shirtliffe SJ, Entz MH, Van Acker RC (2000) *Avena fatua* development and seed shatter as related to thermal time. *Weed Science* **48(5)**, 555-560.

Siriwardena GM, Stevens DK, Anderson GQA, Vickery JA, Calbrade NA, Dodd S (2007) The effect of supplementary winter seed food on breeding populations of farmland birds: evidence from two large-scale experiments. *Journal of Applied Ecology* **44(5)**, 920-932.

Skórka P, Lenda M, Tryjanowski P (2010) Invasive alien goldenrods negatively affect grassland bird communities in eastern Europe. *Biological Conservation* **143(4)**, 856-861.

Smith AP, Quin DG (1996) Patterns and causes of extinction and decline in Australian conilurine rodents. *Biological Conservation* **77(2)**, 243-267.

Smith JNM, Montgomerie RD, Taitt MJ, Yom-Tov Y (1980) A winter feeding experiment on an island song sparrow population. *Oecologia* **47(2)**, 164-170.

Smith MA, Bell DT, Loneragan WA (1999) Comparative seed germination ecology of *Austrostipa compressa* and *Ehrharta calycina* (Poaceae) in a Western Australian banksia woodland. *Australian Journal of Ecology* **24(1)**, 35-42.

Sollmann R, Gardner B, Chandler RB, Shindle DB, Onorato DP, Royle JA, O'Connell AF (2013) Using multiple data sources provides density estimates for endangered Florida panther. *Journal of Applied Ecology* **50(4)**, 961-968.

Specht RL (1972) ‘The vegetation of South Australia.’ (Government Printer: Adelaide).

State Herbarium of South Australia (2007) eFloraSA: Electronic flora of South Australia. 2018, viewed Oct 2018 (Department of Environment, Water and Natural Resources: South Australia), <http://www.flora.sa.gov.au/>.

Stork NE (2010) Re-assessing current extinction rates. *Biodiversity and Conservation* **19**, 357–371.

Strong AM, Sherry TW (2000) Habitat-specific effects of food abundance on the condition of ovenbirds wintering in Jamaica. *Journal of Animal Ecology* **69(5)**, 883-895.

Stowe M, Bugnyar T, Heinrich B, Kotrschal K (2006) Effects of group size on approach to novel objects in ravens (Corvus corax). *Ethology* **112**, 1079–1088.

Studds CE, Marra PP (2011) Rainfall-induced changes in food availability modify the spring departure programme of a migratory bird. *Proceedings of the Royal Society B: Biological Sciences* **(278)**, 3437–344.

Swihart RK, Gehring TM, Kolozsvary MB, Nupp TE (2003) Responses of ‘resistant’ vertebrates to habitat loss and fragmentation: the importance of niche breadth and range boundaries. *Diversity and Distributions* **9(1)**, 1-18.

Swihart RK, Slade NA (1985) Testing for independence of observations in animal movements. *Ecology* **66(4)**, 1176–1184.

Szabo JK, Khwaja N, Garnett ST, Butchart SHM (2012) Global patterns and drivers of avian extinctions at the species and subspecies level. *Plos One* **7(10)**, doi.org/10.1371/journal.pone.0047080.

Szabo JK, Vesk PA, Baxter PWJ, Possingham HP (2011) Paying the extinction debt: woodland birds in the Mount Lofty Ranges, South Australia. *Emu - Austral Ornithology* **111(1)**, 59-70.

Taberlet P, Coissac E, Pompanon F, Gielly L, Miquel C, Valentini A, Vermat T, Corthier G, Brochmann C, Willerslev E. (2007) Power and limitations of the chloroplast trn L (UAA) intron for plant DNA barcoding. Nucleic Acids Research **35(3)**, e14.

Tan DC, Flematti GR, Ghisalberti EL, Sivasithamparam K, Barbetti MJ (2011a) Toxigenicity of enniatins from Western Australian *Fusarium* species to brine shrimp (*Artemia franciscana*). *Toxicon* **57(5)**, 817-825.

Tan DC, Flematti GR, Ghisalberti EL, Sivasithamparam K, Chakraborty S, Obanor F, Barbetti MJ (2011b) Mycotoxins produced by *Fusarium* species associated with annual legume pastures and 'sheep feed refusal disorders' in Western Australia. *Mycotoxin Research* **27(2)**, 123-135.

Thompson DB, Brown JH, Spencer WD (1991) Indirect facilitation of granivorous birds by desert rodents: experimental evidence from foraging patterns. *Ecology* **72(3)**, 852-863.

Thompson WL (2004) 'Sampling rare or elusive species.' (Island Press:Washington)Tidemann SC (1993) Management of a threatened species: the Gouldian Finch example. In 'Birds and their Habitats: Status and Conservation in Queensland.' (Ed. CP Catterall, K Hulsman, D Muir, A Taplin) pp. 123–131 (Queensland Ornithological Society:St Lucia, Queensland).

Tidemann SC (1996) Causes of the decline of the Gouldian finch *Erythrura gouldiae*. Bird Conservation International **6**:49–61.

Tilman D, Clark M, Williams DR, Kimmel K, Polasky S, Packer C (2017) Future threats to biodiversity and pathways to their prevention. *Nature* **546(7656)**, 73-81.

Tilman D, Fargione J, Wolff B, D'Antonio C, Dobson A, Howarth R, Schindler D, Schlesinger WH, Simberloff D, Swackhamer D (2001) Forecasting agriculturally driven global environmental change. *Science* **292(5515)**, 281-284.

Tinbergen JM, Van Balen JH, Van Eck HM (1985) Density dependent survival in an isolated great tit population: Kluijvers data reanalysed. *Ardea* **73(1)**, 38 – 48.

Todd LD, Poulin RG, Wellicome TI, Brigham RM (2003) Post-fledging survival of burrowing owls in Saskatchewan. *The Journal of Wildlife Management* **67(3)**, 512-519.

Todd MK, Felton A, Garnett ST (2003) Morphological and dietary differences between common and uncommon subspecies of crimson finch, *Neochmia phaeton*, and star finch, *Neochmia ruficauda*, in northern Australia. *Emu - Austral Ornithology* **103(2)**, 141-148.

Tom-Tov Y, McCleery R, Purchase D (1992) The survival rate of Australian passerines. *Ibis* **134(4)**, 374–379.

Torssell BWR, McKeon GM (1976) Germination effects on pasture composition in a dry monsoonal climate. *Journal of Applied Ecology* **13(2)**, 593-603.

Traveset A, Riera N (2005) Disruption of a plant-lizard seed dispersal system and its ecological effects on a threatened endemic plant in the Balearic Islands. *Conservation Biology* **19(2)**, 421-431.

Tylianakis JM, Didham RK, Bascompte J, Wardle DA (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters* **11(12)**, 1351-1363.

Valeix M, Fritz H, Matsika R, Matsvimbo F, Madzikanda H (2007) The role of water abundance, thermoregulation, perceived predation risk and interference competition in water access by African herbivores. *African Journal of Ecology* **46**: 402–410.

Valentini A, Miquel C, Nawaz MA, E Bellemain, E Coissac, F Pompanon, L Gielly, C Cruaud, G Nascetti, P Wincker, JE Swenson, P Taberlet (2009) New perspectives in diet analysis based on DNA barcoding and parallel pyrosequencing: the *trn*L approach. *Molecular Ecology Resources* **9**, 51-60.

Van Doorn A, Woinarski JCZ, Werner PA (2015) Livestock grazing affects habitat quality and persistence of the threatened Purple-crowned Fairy-wren *Malurus coronatus* in the Victoria River District, Northern Territory, Australia. *Emu – Austral Ornithology* **115(4)**:302–308.

Van Katwyk KE (2014) 'Empirical validation of closed population abundance estimates and spatially explicit density estimates using a censused population of North American red squirrels.' (University of Alberta:Alberta, USA)

Vickery JA, Tallowin JR, Feber RE, Asteraki EJ, Atkinson PW, Fuller RJ, Brown VK (2001) The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. *Journal of Applied Ecology* **38(3)**, 647-664.

Vie JC, Hilton-Taylor C, Stuart SN (Eds) (2009) 'Wildlife in a changing world: an analysis of the 2008 IUCN red list of threatened species.' (IUCN:Gland, Switzerland)

Villard M-A, Trzcinski MK, Merriam G (1999) Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. *Conservation Biology* **13(4)**, 774-783.

Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of Earth's ecosystems. *Science* **277(5325)**, 494-499.

Wang Y, Naumann U, Wright S, Warton DI (2012) mvabund - an R package for model-based analysis of multivariate data. *Methods in Ecology & Evolution* **3**, 471-474.

Ward JM, Kennedy PL (1996) Effects of supplemental food on size and survival of juvenile northern goshawks. *The Auk: Ornithological Advances* **113(1)**, 200-208.

Warton DI, Thibaut L, Wang YA (2017) The PIT-trap-A "model-free" bootstrap procedure for inference about regression models with discrete, multivariate responses. *PLoS one* **12(7)**, e0181790.

Waters C, Whalley W, Huxtable C (2001) 'Grassed up: guidelines for revegetating with Australian native grasses.' (NSW Agriculture: Orange, NSW)

Watson A, Moss R (1970) Dominance, spacing behaviour and aggression in relation to population limitation in vertebrates. In 'Animal populations in relation to their feed resources.' (Ed. A Watson) pp. 167-218. (Blackwell Scientific Publications: Oxford)

Watson DM (2011) A productivity-based explanation for woodland bird declines: poorer soils yield less food. *Emu - Austral Ornithology* **111(1)**, 10-18.

Watson J, Watson A, Paull D, Freudenberger D (2002) Woodland fragmentation is causing the decline of species and functional groups of birds in southeastern Australia. *Pacific Conservation Biology* **8(4)**, 261-270.

Weathers WW, Sullivan KA (1989) Juvenile foraging proficiency, parental effort, and avian reproductive success. *Ecological Monographs* **59(3)**, 223-246.

Westfall PH, Young SS (1989) Value adjustments for multiple tests in multivariate binomial models. *Journal of the American Statistical Association* **84(407)**, 780-786.

Whalley RDB, Price JN, Macdonald MJ, Berney PJ (2011) Drivers of change in the social-ecological systems of the Gwydir Wetlands and Macquarie Marshes in northern New South Wales, Australia. *The Rangeland Journal* **33(2)**, 109-119.

White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study* **46(sup1)**, S120-S139.

White TCR (1976) Weather, food and plagues of locusts. *Oecologia* **22(2)**, 119-134.

White TCR (1978) The importance of a relative shortage of food in animal ecology. *Oecologia* **33(1)**, 71-86.

White TCR (2008) The role of food, weather and climate in limiting the abundance of animals. *Biological Review* **(83)** 227-248.

Wickham H (2009) ‘ggplot2: elegant graphics for data analysis.’ (Springer-Verlag:New York)

Wiggins N, Mcarthur C, Davies N (2006) Diet switching in a generalist mammalian folivore: fundamental to maximising intake. *Oecologia* **147(4)**, 650-7.

Wilbur SR, Carrier WD, Borneman JC (1974) Supplemental feeding program for California condors. *The Journal of Wildlife Management* **38(2)**, 343-346.

Wilcove DS, Rothstein D, Dubow J, Phillips A, Losos E (1998) Quantifying threats to imperiled species in the United States. *Bioscience* **48(8)**, 607-615.

Williams BK, Nichols JD, Conroy MJ (2002) 'Analysis and management of animal populations: modeling, estimation and decision making.' (Academic Press, an Imprint of Elsevier: USA)

Williams TD, Cooch EG, Jefferies RL, Cooke F (1993) Environmental degradation, food limitation and reproductive output: juvenile survival in lesser snow geese. *Journal of Animal Ecology* **62(4)**, 766-777.

Willson MF, Harmeson JC (1973) Seed preferences and digestive efficiency of cardinals and song sparrows. *The Condor* **75(2)**, 225-234.

Wilson A, Bignall J (2009) ‘Regional recovery plan for threatened species and ecological communities of Adelaide and the Mount Lofty Ranges, South Australia.’ (Department for Environment and Heritage:South Australia)

Wilson AHR, Leach JA (1928) Bird notes from Yarraberb. *Emu* **28(2)**, 121-128.

Wilson JD, Morris AJ, Arroyo BE, Clark SC, Bradbury RB (1999) A review of the abundance and diversity of invertebrate and plant foods of granivorous birds in northern Europe in relation to agricultural change. *Agriculture, Ecosystems & Environment* **75(1)**, 13-30.

Woinarski JCZ, Braithwaite RW (1990) Conservation foci for Australian birds and mammals. *Search* **21(2)**, 65-68.

Wunderle JM (1991) Age-specific foraging proficiency in birds. *Current Ornithology* **8**, 273-324.

Yates CJ, Hobbs RJ (1997) Temperate eucalypt woodlands: a review of their status, processes threatening their persistence and techniques for restoration. *Australian Journal of Botany* **45**, 949-973.

Yeoh H-H, Watson L (1981) Systematic variation in amino acid compositions of grass caryopses. *Phytochemistry* **20(5)**, 1041-1051.

Yom-Tov Y (1974) The effect of food and predation on breeding density and success, clutch size and laying date of the crow (*Corvus corone* L.). *Journal of Animal Ecology* **43(2)**, 479-498.

Yom-Tov Y, McCleery R, Purchase D (1992) The survival rate of passerines. 1992. *Ibis* **(134)** 374-379.Yu L, Chivas AR, Garcia A, Hu J (2011) Decline of the Macquarie Marshes ecosystem, Australia, since European arrival recorded by organic geochemical proxies in sediments. American Geophysical Union, Fall Meeting 2011.

Zanette L, Doyle P, Tremont SM (2000) Food shortage in small fragments: evidence from an area-sensitive passerine. *Ecology* **81(6)**, 1654-1666.

Zanette L, Smith JNM, Oort Hv, Clinchy M (2003) Synergistic effects of food and predators on annual reproductive success in song sparrows. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **270(1517)**, 799-803.

Zann R, Straw B (1983) A non-destructive method to determine the diet of seed-eating birds. *Emu* **84**, 40-41.

Zann R, Straw B (1984) Feeding ecology and breeding of zebra finches in farmland in Northern Victoria. *Wildlife Research* **11(3)**, 533-552.

Zann RA (1994) Reproduction in a zebra finch colony in south-eastern Australia: the significance of monogamy, precocial breeding and multiple broods in a highly mobile species. *Emu - Austral Ornithology* **94(4)**, 285-299.

Zanollo V, Griggio M, Myers SA, Robertson J, Stangoulis J, Guild G, Kleindorfer S (2013). Maternal investment in the Diamond Firetail: Female spot number predicts egg volume and yolk lutein. *Acta Ornithologica* **48(2)**: 253–261.

Zanollo V, Griggio M, Robertson J, Kleindorfer S (2012). The number and coloration of white flank spots predict the strength of a cutaneous immune response in female diamond firetails, Stagonopleura guttata. Journal of Ornithology **153(4)**: 1233–1244.

Zhang Y (2013) Likelihood-based and Bayesian methods for tweedie compound Poisson linear mixed models. *Statistics and Computing* **23**, 743-757.

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) 'Mixed effects models and extensions in ecology with R.' (Springer: New york).