

Brevia

IUCN Red List protects avian genetic diversity

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Low genetic diversity may be associated with an increase in species' extinction risk (Spielman et al. 2004, Frankham 2005). Still, global conservation assessments do not consider relevant genetic-based estimates for evaluating species threat status. Rather, they rely primarily on changes in population abundance and range size, with the inherent assumption that intra-specific genetic variability is tightly correlated with population size and range area (Frankham 1996). If this assumption was universally true, species considered to be at high risk, because of small range sizes and/or low abundances, should have lower levels of genetic diversity than low-risk species and vice-versa. However, contradictory evidence, for birds and mammals (Reed 2010), suggests that omitting genetic diversity from threat classification criteria could potentially lead to under- or over-estimating the actual extinction risk of species.

Here, we investigate whether bird species considered at risk of extinction, by widely used threat assessment criteria (IUCN 2021), have less intra-specific nucleotide diversity than non-threatened bird species (Supporting information). To accomplish this aim, we established differences in intra-specific nucleotide diversity for threatened (Vulnerable – VU, Endangered – EN and Critically Endangered – CR) vs non-threatened bird species (Least Concern – LC and Near Threatened – NT) by compiling 28 403 publicly available avian mitochondrial DNA (mtDNA) sequences from GenBank. We calculated cytochrome-b (cyt-b) nucleotide diversity for 1036 species (approximately 10% of all bird species), with an average number of sequences per species being 27 ± 44 (Supporting information). The average sequence length (base-pairs) across species was 887 ± 201 . Using phylANOVAs, to control for phylogenetic signal (Freckleton et al. 2002), corrected for varying sample sizes between groups, we show that threatened species have significantly lower cyt-b nucleotide diversity ($p < 0.05$, in 953 out of the 1000 phylANOVA repetitions; mean $p = 0.010 \pm 0.025$) than non-threatened species (Fig. 1a; Supporting information), with medium to large effect size in 97.2% of repetitions ($\omega^2 > 0.06$). The mean effect size was 0.16 ± 0.05 (Supporting information).

Our results reveal that current threat assessment criteria indirectly prioritize species with low levels of cyt-b nucleotide diversity, which can be at greater risk of extinction by virtue of low genetic diversity (Frankham 2005) (Fig. 1c). For example, the African houbara (*Chlamydotis undulata*, VU) is among the birds with the lowest



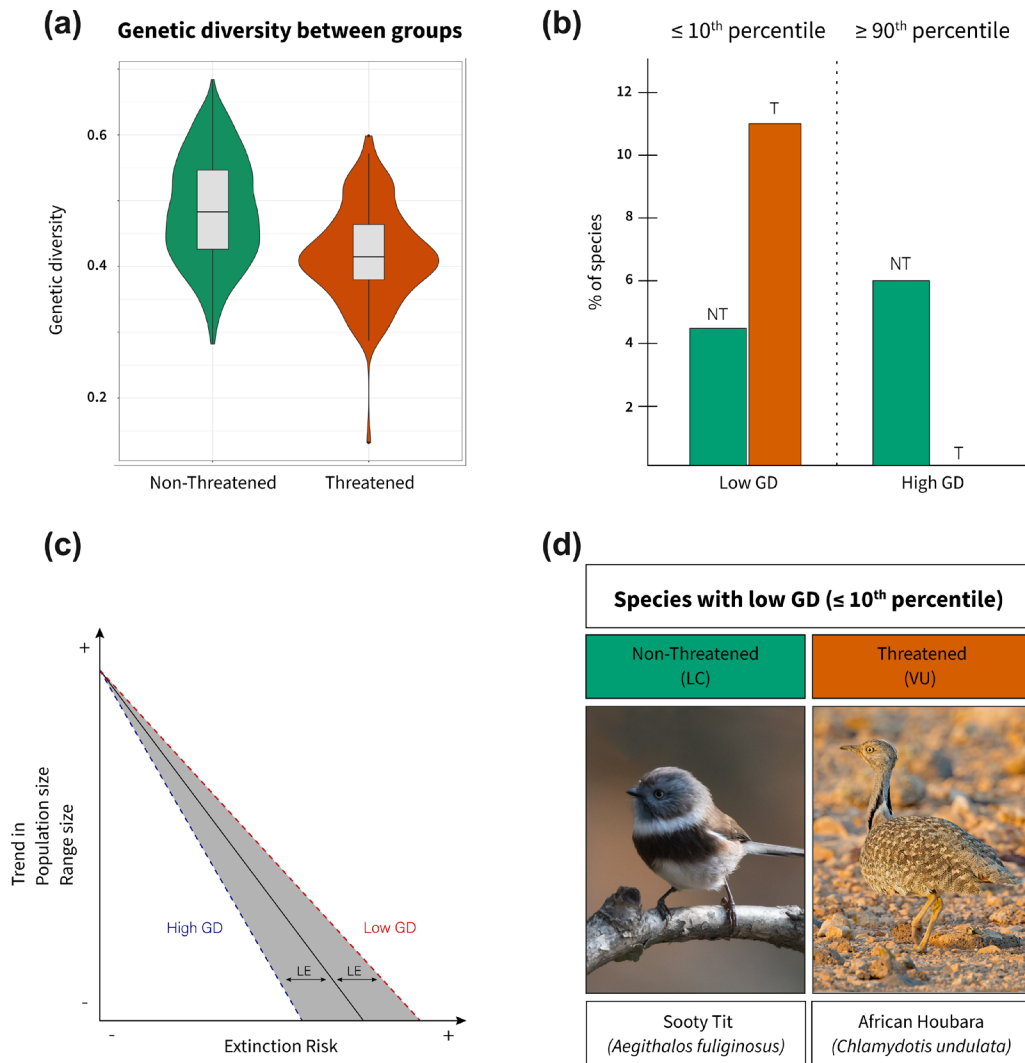


Figure 1. Genetic diversity in threatened and non-threatened bird species. (a) Threatened species have significantly lower intra-specific cytb nucleotide diversity than non-threatened species. (b) Percentage of threatened (T) and non-threatened (NT) species with the lowest ($\leq 10^{\text{th}}$ percentile) and highest ($\geq 90^{\text{th}}$ percentile) values of cytb nucleotide diversity. (c) Conceptual figure showing a species experiencing declines (negative trend) in range size and/or population abundance through time, enhancing its extinction risk. Due to low or high genetic diversity (GD; low or high GD), the same species might be of greater (red dashed line) or lesser (blue dashed line) extinction risk, respectively, potentially producing a mismatch between the evaluated extinction risk (black solid line) and the actual extinction risk (latent extinction risk, LE). (d) Examples of a non-threatened (sooty tit; *Aegithalos fuliginosus*; photo credits: Tim Melling) and a threatened bird species (African houbara; *Chlamydotis undulata*) with some of the lowest levels of cytb nucleotide diversity ($\leq 10^{\text{th}}$ percentile).

cytb nucleotide diversity in our data set ($\leq 10^{\text{th}}$ percentile: $GD \leq 0.0015$; Fig. 1d), and its persistence is affected by inbreeding and/or genetic drift (Korrida et al. 2012). Moreover, the millerbird (*Acrocephalus familiaris*, CR) and the inaccessible finch (*Nesospiza acunhae*, VU) are both range-restricted small-island endemics with limited cytb nucleotide diversity ($\leq 10^{\text{th}}$ percentile; Supporting information), making them particularly vulnerable to rapid environmental changes from introduced predators and extreme climatic events (Vincenzi et al. 2017). Although mtDNA has been shown, under some circumstances, to be of limited use for inferring population size (Bazin et al. 2006,

Nabholz et al. 2009), the low levels of nucleotide diversity in threatened species of birds suggest a correlation, direct or indirect, between cytb nucleotide diversity and small population or range size. For species that have not experienced large range contractions and population declines in recent times (non-threatened species), we found that cytb nucleotide diversity was generally high ($\geq 90^{\text{th}}$ percentile: $GD \geq 0.0302$). Higher levels of genetic diversity might, through the process of local adaptation, aid species' resilience to rapid environmental changes (DeWoody et al. 2021) and reverse or slow species' decline (Fig. 1c). However, in some instances, non-threatened species can harbour low genetic

diversity, most probably due to recent or past bottlenecks (Weber et al. 2000).

Four per cent of all non-threatened birds analysed had low levels of *cyt-b* nucleotide diversity (\leq 10th percentile; Fig. 1b). For example, the sooty tit (*Aegithalos fuliginosus*, LC; Fig. 1d) is the non-threatened species with the lowest *cyt-b* nucleotide diversity in our data set (Supporting information). Despite having a restricted range, the sooty tit is considered as 'Least Concern', due to a population that is suspected to be stable (IUCN 2021). Low nucleotide diversity for the sooty tit signals that extinction risk for the species might be higher than its IUCN threat status indicates, encouraging further assessments of its conservation status using census and genomic techniques. Low genetic diversity in non-threatened species can result from recent or past dramatic demographic events, after which levels of intra-specific genetic diversity remain temporally low, while the overall population size increases (Weber et al. 2000). For these species, whole-genome studies will help reveal the role of genetic diversity in long-term species survival.

While our results could be contingent on the length of sequences, sample size, and geographic and taxonomic biases associated with genetic sequences in public repositories such as GenBank, we found no correlation between nucleotide diversity and average sequence length or number of sequences (Supporting information). Furthermore, we found a low phylogenetic signal ($\lambda=0.56$, $p < 0.001$), and the *phylANOVAs* confirm the independence of the data in relation to the evolutionary history of the species (Supporting information). Indeed, there is a significant difference between the *F*-statistics calculated on the actual data and the *F*-statistics calculated with simulated data (null hypothesis; Supporting information). Lastly, our results do not reflect geographic biases in our dataset, which covers ~57% of all avian families and all zoogeographic realms (Supporting information). Despite existing challenges with using mitochondrial data and single genetic markers (Carling and Brumfield 2007), including the real possibility that genetic diversity calculated using mtDNA might not reflect genome-wide diversity or the diversity of specific functionally relevant parts of the genome, the relationship between conservation status and genetic diversity, explored in this paper, concords with long-standing expectations from the literature (DeWoody et al. 2021), including findings from meta-analyses across smaller subsets of taxa (Spielman et al. 2004, Willoughby et al. 2015) using nuclear DNA (allozymes, microsatellites, minisatellites), and other mtDNA genes (Petit-Marty et al. 2021).

Species-level conservation criteria capture low levels of intra-specific nucleotide variability in species of greatest concern. Nonetheless, low levels of nucleotide diversity are present in a small proportion of non-threatened birds, causing them, in theory, to be more vulnerable to rapidly changing environmental conditions than their conservation status, alone, indicates (Frankham 2005). As genomic techniques get cheaper, the inclusion of whole-genome data in relevant measures of genetic diversity is a likely near-term prospect for conservation. Future research should aim to integrate large-scale field-work campaigns with strategic sequencing of

contemporary and historical specimens from biological collections, in order to unravel eco-evolutionary determinants of increased extinction risk.

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Author contributions

Elisabetta Canteri: conceptualization (equal); data curation (equal); formal analysis (lead); writing - original draft (equal); writing - review and edit (equal). **Damien A. Fordham:** conceptualization (equal); funding acquisition (equal); supervision (equal); writing - review and edit (equal). **Sen Li:** investigation (lead); software (lead); writing - review and edit (equal). **Peter A. Hosner:** data curation (equal); writing - review and edit (equal). **Carsten Rahbek:** funding acquisition (equal); writing - review and edit (equal). **David Nogues-Bravo:** funding acquisition (equal); conceptualization (equal); supervision (lead); writing - original draft (equal); writing - review and edit (equal).

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Data availability statement

Data are available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.pzgm5bcn6>> (Canteri et al. 2021).

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