Long-term and large-scale analyses of nest predation patterns in Australian songbirds and a global comparison of nest predation rates

Vladimír Remeš, Beata Matysioková and Andrew Cockburn

V. Remeš (vladimir.remes@upol.cz) and B. Matysioková, Laboratory of Ornithology, Dept of Zoology, Faculty of Science, Palacky Univ., CZ-77146 Olomouc, Czech Republic. – A. Cockburn, Div. of Evolution, Ecology and Genetics, Research School of Biology, Australian National Univ., ACT 0200 Canberra, Australia.

Juvenile mortality is one of crucial drivers of life-history evolution, and predation is the main cause of nest loss in birds. Thus, understanding how nest predation and failure vary in nature is important for understanding life history evolution and, moreover, for effective conservation. We used published data and unpublished records to study factors influencing nest predation and total failure in 138 populations of 90 species of Australian songbirds. Daily predation (average 2.0% d^{-1}) and failure rates (2.9%) increased from temperate regions to the tropics, over the last four decades, and were lowest in temperate south-western Australia. Predation and failure were higher in smaller species, and failure rates were lower in species with closed nests than in species with open nests. There was no effect of nest height or nest site (ground, shrub, canopy) or social organization on nest predation or failure rates. Nest predation caused on average 72% of total nest failure, similar to other tropical, subtropical, and temperate areas. Our study spanning from the tropics to temperate regions and using > 10 000 nests confirmed that tropical birds faced higher nest failure rates. We identified an increase in nest depredation rates in the last four decades in Australia, suggesting that a large-scale ecological phenomenon must be responsible. It may include increases in predator abundances and/or ranges, possibly connected with human-caused habitat change. A global comparison of nest failure rates confirmed that predation is the main source of nest mortality in songbirds worldwide. We discuss implications of our results for the evolution of reproductive strategies and for the conservation of Australian birds.

Juvenile mortality is one of crucial drivers of the evolution and plasticity of life-history traits (Stearns 1992). Thus, identification of robust predictors of juvenile mortality across a broad range of species is critical for better understanding of variation in life-history and behavioural traits (Bennett and Owens 2002, Lima 2009, Martin and Briskie 2009). For example, nest predation is the main source of nest failure in most birds (Ricklefs 1969, Martin 1993, Thompson 2007, Remeš et al. 2012) and has been identified as an important correlate of a suite of life-history traits across species (Martin 1995, Remeš and Martin 2002). Additionally, population growth of especially shorter-lived species (e.g. songbirds as opposed to long-lived seabirds) is particularly sensitive to reproductive failure (Sæther and Bakke 2000). Thus, effective conservation efforts require robust estimates of species vulnerability to nest depredation as a potential limit on population growth rates.

Many nest predation studies have been conducted on northern temperate songbirds (reviewed by Ricklefs 1969, Thompson 2007) including detailed studies of nest predators using video cameras (reviewed by Weidinger 2008). These studies identified several consistent correlates of nest predation, including nest type (Nice 1957, Lack 1968, Martin and Li 1992, Wesołowski and Tomiałojć 2005), nest height/vegetation layer (Martin 1993), habitat (Tewksbury et al. 2006), elevation (Boyle 2008), and geography (Thompson 2007). However, these studies have been conducted on limited samples of species and many of them in the context of habitat fragmentation and alteration of landscape structure. Moreover, how their results apply in tropical, subtropical, and southern hemisphere birds with their distinctive life histories is not clear (Martin 1996, Stutchbury and Morton 2001). Although nest predation studies of tropical and southern hemisphere birds have a long tradition (Marchant 1960, Oniki 1979, Skutch 1985), they are certainly much less numerous. The only correlate of nest predation that has been studied to some extent in these birds is nest type, with some studies reporting lower nest predation in cavity compared to open nesters (Oniki 1979, Skutch 1985, Auer et al. 2007, Brawn et al. 2011, Remeš et al. 2012), while others reported no difference (Lloyd 2004) or mixed results (Robinson et al. 2000).

For a major advance in identifying predictors of nest predation and failure in tropical and southern hemisphere

birds, we need studies on a broad and varied sample of species on a large number of nests (Remeš et al. 2012). Australian songbirds provide a unique opportunity to achieve these aims, because local avifauna is diverse and comparatively well studied. Moreover, Australian songbirds are phylogenetically distinct from well-studied European and North American species (Ericson et al. 2003) with typically slow life history more similar to that of tropical species than to northern temperate species living at corresponding latitudes (Woinarski 1985). Additionally, studies show that predators might significantly hamper reproductive success of native songbirds in Australia (Olsen et al. 2006). Consequently, identification of populations and species that are particularly vulnerable to nest predation might help in their conservation.

In this study we accumulated detailed data on nest predation and total nest failure in Australian songbirds based on published studies. Subsequently, we asked which of the traits identified previously to correlate with nest predation risk in northern temperate birds are important in Australian songbirds. Specifically, we tested whether geography (latitude and longitude), time (year when the study was conducted), allometry (adult body mass), nest attributes (nest height and type) or sociality predict nest mortality rates. This approach also provides assessment of the determinants of species vulnerability to nest predation that could be used in conservation. We provide comparisons with other published large-scale datasets elsewhere in the world to advance our general understanding of similarities and differences in nest predation patterns on a global scale.

Methods

Data collection

We collected data for this study from the literature. We focused on intensive field studies of single or several species and avoided published accounts based on Australian Nest Record Scheme. We started with Handbook of Australian, New Zealand, and Antarctic Birds (HANZAB) Vol. 5, 6, and 7 (Higgins et al. 2001, 2006, Higgins and Peter 2002). Here, we located all studies dealing with nest failure and predation and obtained the primary source. To find articles that were published after HANZAB had been published, we also surveyed all the articles between 2000 and 2008 in Australian Bird Watcher, Australian Field Ornithology, Austral Ecology, Australian Journal of Zoology, Australian Zoologist, Canberra Bird Notes, Corella, Emu, New Zealand Journal of Ecoogy, New Zealand Journal of Zoology, Notornis, Pacific Conservation Biology, South Australian Ornithologist, Sunbird, VOGR Notes, Western Australian Naturalist, and Wildlife Research.

We also comprehensively searched databases unrestricted by the year of publication. We searched by the scientific name of each species in Web of Science (available since 1945) and Zoological Record Plus (since 1978). We went through the titles and abstracts and obtained primary articles dealing with breeding biology. We left out articles describing captive birds, e.g. many studies of the zebra finch *Taeniopygia guttata*. We also searched on the web pages of Emu, Notornis, New Zealand Journal of Zoology, and New Zealand Journal of Ecology, i.e. all volumes of these journals. We used the scientific name of the species, and separately the above-mentioned search terms concerning breeding biology. Subsequently, we searched the text of the articles to locate information on nest failure and predation. All these searches were done from October 2008 to January 2009.

From the resulting articles we extracted where possible: the number of nests failed, number of nests destroyed by predators, number of nests studied, and when and where the study was done. An obvious constraint on the data is that it is not always possible to assign a particular nest loss to predation without direct evidence obtained by videotaping. Here we relied on two approaches to identify nest losses caused by predators. First, if the author(s) explicitly stated how many nests predators took, we accepted this claim. Second, if nests lost to predators were not explicitly enumerated, we assigned a loss to nest predation if the total clutch or brood disappeared suddenly without other obvious reasons (e.g. storm or human interference). We did not include partial losses unless losses were reported as total number of eggs or nestling lost instead of the number of nests affected. In such cases, there was no way of teasing apart partial and total losses. We calculated the number of nests studied as the number of eggs divided by clutch size reported for that particular study. Because this method includes partial predation, total loss will be slightly overestimated in these populations (n = 4).

We transformed the proportion of failed nests and nests lost to predators to daily failure (DFR) and daily predation rates (DPR). We used the method of Ricklefs (1969), but for validation we also calculated daily failure rates by an approach based on the Mayfield nest survival model (Mayfield 1975) suggested by Beintema (1996). The method of Ricklefs (1969) gives DPR $= -[\ln(1-\text{PR})]/\text{T}$, where PR is nest predation intensity (i.e. the fraction of nests destroyed by predators out of the nests found) and T is the length of the nest cycle. The method of Beintema (1996) gives DPR $= 1-(1-\text{PR})^{1/\text{T}}$. If T equals the total length of the nest cycle (NC), both methods give identical results, but at the same time assume that all nests are found before or on the day the first egg is laid. The method of Beintema (1996) allows varying T. If we set for example T $= 0.5 \times$ NC, we assume that nests were found on average in the middle of the nest cycle. By varying T, we can explicitly formulate our assumption about the part of the nest cycle at which the nests were on average found. We varied T as equal to NC, $0.75 \times$ NC, and $0.5 \times$ NC to show how absolute values of DPR depend on these assumptions. Estimates produced by all the above-mentioned approaches were highly correlated (r = 1.0, n = 137) and we provide average values across species in Table 1. However, we used only values obtained by the method of Ricklefs (1969), which are identical to those provided by the method of Beintema (1996) when T = NC, in all statistical analyses. Consequently, the reader should be aware that relationships of DPR and DFR to predictors are more reliable and robust than estimates of the absolute values (e.g. the intercept in the models), which are contingent on the selection of

Table 1. Descriptive characteristics of nest failure data in Australian songbirds.

	Mean	SD	Median	Range	n studies
No. of studied nests	75.7	101.7	38.5	5–656	138
Length of the study (yr)	3.1	3.5	2.0	1–22	129
Nests that failed (%)	57.5	19.8	57.8	8.3–100	131
Nests destroyed by predators (%)	43.8	22.9	43.1	0–100	138
Failed nests that failed due to predation (proportion)	0.72	0.24	0.77	0–1	131
Daily predation rate (d^{-1}), T = NC[a]	0.020	0.015	0.017	0–0.074	137
Daily predation rate (d^{-1}), T = 0.75 × NC[b]	0.026	0.020	0.022	0–0.097	137
Daily predation rate (d^{-1}), T = 0.5 × NC[c]	0.039	0.029	0.033	0–0.142	137
Daily failure rate (d^{-1}), T = NC	0.029	0.017	0.026	0.002–0.077	130

[a]Assuming nests were found before or on the day the first egg is laid.
[b]Assuming nests were found on average in the first quarter of the nest cycle (NC).
[c]Assuming nests were found on average in the middle of the nest cycle.

T when calculating daily rates. For all the estimates of daily rates, the length of the nest cycle was calculated as the sum of incubation period, nestling period, and clutch size. This is correct in species that lay eggs daily. In species that lay in intervals of two days, we added one day for the first egg and two days for every subsequent egg (n = 17 species). It should be noted that none of these methods estimates true daily rates that can be obtained only by applying the Mayfield method (Mayfield 1975) on original data sets, and these are obviously not available when working with literature data. Similarly, estimates of standard errors of DPR and DFR are not available.

For each species in our database, we obtained its nest type (open vs closed, which included domed and cavity nests), nest height (in meters), nest location (ground, shrub, and canopy), adult body mass (in grams) (Higgins et al. 2001, 2006, Higgins and Peter 2002), and social organization (pair, cooperative, and female-only breeding; Cockburn 2006). We assigned every study to one of the following three geographic regions: south-western (SW), south-eastern (SE), and tropical northern Australia (TN; Supplementary material, Fig. S1). We also estimated how common every species is in Australia by recording the percentage of squares that it occupied in the most recent mapping of all Australian birds (The New Atlas of Australian Birds; Barrett et al. 2003). To put our data from Australia into perspective, we compared them with published large-scale datasets elsewhere in the world.

Data analysis

We modelled DPR and DFR in linear mixed models (LMM) fit in the Mixed procedure of SAS 9.2. In these analyses, one estimate of DPR or DFR for a set of nests reported in a literature source was always treated as one data point (i.e. population estimate). To allow more statistical influence to population estimates with larger number of nests studied, we weighted the analyses by sample size. To check the robustness of our analyses, we also repeated them while weighting by the square root of sample size. This weighting scheme still gives more strength to population estimates with larger sample of nests but at the same time downweights the effect of population estimates with extremely large sample sizes. The results were quantitatively very similar and qualitatively unchanged.

Species might be similar to each other due to shared history, thus violating the assumption of non-independence in standard statistical tests. To account for potential phylogenetic effects, we thus initially included taxonomic family, genus (nested within family), and species (nested within genus) as random factors. Moreover, sometimes several studies were conducted at the same place, again potentially introducing non-independence among these data points. Thus, to account for potential site effects, we also initially included study site as a random factor (there were 91 different study sites). We tested for the significance of these random effects by likelihood-ratio tests as suggested by West et al. (2007). These tests suggested that taxonomy should be retained in the models (LR statistic = 20.6, DF = 1, p < 0.001), whereas study site could be dropped (LR statistic = 0.8, DF = 1, p = 0.186). Thus, we present results of the models with taxonomy retained but with study site removed.

Data non-independence might further stem from spatial proximity of study sites. In spatially structured data, nearby locations might be more similar than locations farther apart due to spatial autocorrelation (Fortin and Dale 2005). We adopted two approaches to deal with potential spatial autocorrelation in our data. First, we were interested in broad-scale geographical trends. We thus included latitude and longitude as linear explanatory variables into our statistical models in order to look for consistent increases or decreases in rates of nest failure both along an east–west and a north–south axis. This technique is known as a trend surface analysis. However, although it is well suited to model broad-scale trends in data, small-scale spatial autocorrelation in residuals might go unnoticed (Perez et al. 2010). Ignoring this potential small-scale autocorrelation could lead to biased parameter estimates and inflated type I error rates (Beale et al. 2010). Thus, second, we tested for potential remaining autocorrelation in residuals from trend surface analyses. We calculated semivariograms and spatial correlograms using Moran's I (Fortin and Dale 2005). Both these techniques agreed on the absence of small-scale autocorrelation in residuals from trend surface analyses (Supplementary material Appendix 1). Thus, we fit LMM with a trend surface component (i.e. including latitude and longitude) but with spatially uncorrelated error term (using variance components matrix).

To summarize what has been said so far about data modelling, we fit models weighted by sample size, with taxonomy

as a random effect (family, genus, and species), but with spatially uncorrelated error term. The main components of interest of our models were fixed effects. We fit the models with fixed effects that we considered potentially important based on past studies (Introduction). These predictors were: adult body mass (g), nest height (m), nest type (open, closed), social organization (pair, cooperative, female-only breeding), latitude (°S), longitude (°E), and the year of study. To test further for geographic effects, we also tested the effect of a broad geographic region (SW, SE, and TN Australia; Supplementary material, Fig. S1) as a categorical variable instead of latitude and longitude. All tests were two-tailed. We checked residuals for any deviations from normality, equal variance, and linearity. Residuals always conformed to all these requirements. To conform to the normal distribution, body mass and nest height were $\log_{10}$ transformed, while DPR and DFR were square root transformed. Denominator degrees of freedom were estimated by the Satterthwaite method. Besides tests of significance we always report parameter estimates for use in potential future meta-analyses and for judging biological significance of our results. Currently, there is an ongoing debate over the application of classical frequentist versus information-theoretic approaches to data analysis (Stephens et al. 2005). Both these methods have their advantages and disadvantages (Lukacs et al. 2007, Stephens et al. 2007) and thus we also provide results of an information-theoretic modelling based on AIC (Supplementary material Appendix 2).

Results

In total, we located 138 population estimates of nest predation (n = 10 453 nests) in 90 species of Australian songbirds belonging to 58 genera and 25 families. Families represented by the highest number of studies were Meliphagidae (22 studies), Maluridae (20), Petroicidae (20), and Pardalotidae (19), whereas there were seven families with only one study each. Our sample of species thus included members of most of 34 songbird families living in Australia (73.5%). It represented 27.9% of 323 breeding species of Australian songbirds (taxonomy based on Simpson and Day 2004).

The number of nests studied varied considerably among studies (Table 1) but did not change with the year when the study was published (r = 0.11, p = 0.21, n = 130). When assessed by the midpoint of the study period the earliest study was conducted in 1963 and number of studies per year increased steadily until the present (Supplementary material, Fig. S2). Only two studies were conducted on introduced species. Nest failure, nest predation, daily failure and daily predation rates, and proportion of losses caused by predators varied considerably among studies (Table 1).

Environmental predictors and covariates

Both DPR and DFR were lower for larger birds, for birds nesting further from the equator (Fig. 1), and in western sites, but were higher in more recent years (Table 2; Fig. 2).
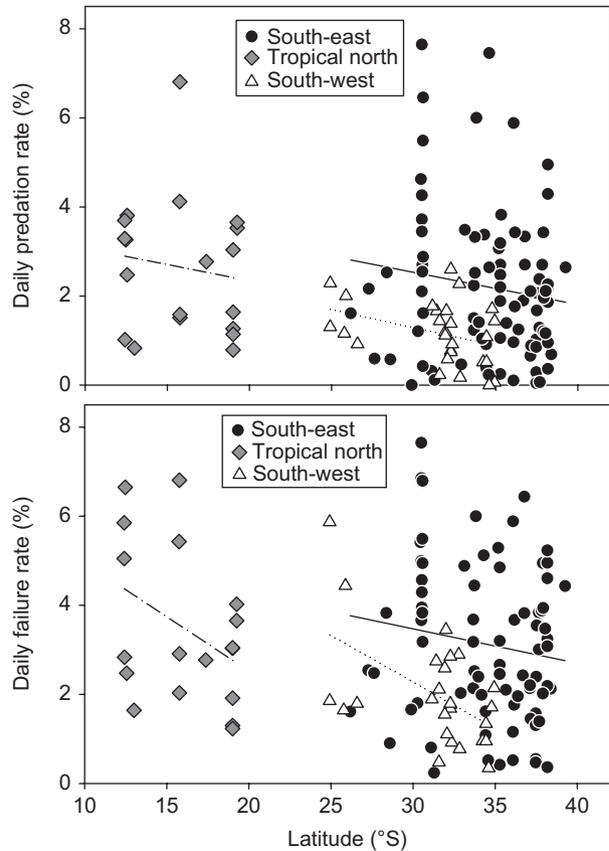

Figure 1. Daily nest predation and failure rates across latitude depicted separately for south-western (dotted line), tropical northern (hatched line) and south-eastern Australia (full line). For the sake of convenience raw data are shown and the fitted lines are simple least squares regression lines.

Species nesting in closed nests were less prone to nest failure (Table 2, LS means [95% confidence interval] of daily nest failure: open nests 3.23 [2.58–3.94] % d^{-1}, closed nests 2.33 [1.76–2.98] % d^{-1}). Both DPR and DFR were lower in south-western (SW) Australia than in south-eastern (SE) and tropical northern (TN) Australia (Fig. 3). These regional differences were significant even when controlling for other factors, of course except latitude and longitude (DPR: $F_{2,111.0} = 11.2$, p < 0.001; DFR: $F_{2,105.0} = 12.2$, p < 0.001). The differences among these three regions were responsible for the east-west trend, but not for the latitudinal or time trends that remained significant even when the variable representing the regions was put into the model (Supplementary material, Table S3a). Both latitudinal and time trends were homogeneous across the three regions as evidenced by non-significant interactions of the region with either latitude or year (Supplementary material, Table S3b; Fig. 1). To make sure that the time trend was not an artefact of species sampling in relation to their taxonomic affiliation or the extent of geographical distributions, we performed two additional analyses. First, we tested whether the year of study differs systematically among families and found no effect of taxonomy ($F_{25,102} = 1.2$, p = 0.232). Second, we tested whether there is an association between the commonness

Table 2. Models relating daily predation and failure rates to environmental factors and covariates. P-values of statistically significant factors are highlighted in bold. Reference levels of categorical variables are given in round brackets. Transformation function of a particular variable, if any, is given in square brackets.

Response	Daily predation rate [Sqrt]				Daily failure rate [Sqrt]			
Fixed effects	DF	F	p	Estimate (SE)	DF	F	p	Estimate (SE)
Intercept				−1.63 (0.66)				−0.97 (0.60)
Body mass [Log₁₀]	1,50.1	11.2	**0.002**	−0.053 (0.016)	1,49.4	32.5	**<0.001**	−0.073 (0.013)
Nest height[a] [Log₁₀]	1,72.5	0.1	0.708	−0.0087 (0.023)	1,69.8	0.01	0.766	−0.0058 (0.019)
Nest type (Open)	1,55.1	1.0	0.324	Closed: −0.014 (0.014)	1,46.4	5.9	**0.019**	Closed: −0.027 (0.011)
Social organization (Pair)	2,62.9	0.2	0.842	Cooperative: −0.0072 (0.012) Female-only: −0.0011 (0.027)	2,57.2	0.7	0.492	Cooperative: −0.0014 (0.010) Female-only: 0.028 (0.024)
Latitude	1,105.0	6.1	**0.015**	−0.0017 (0.00069)	1,95.6	9.8	**0.002**	−0.0018 (0.00059)
Longitude	1,73.3	27.7	**<0.001**	0.0017 (0.00032)	1,68.0	29.9	**<0.001**	0.0016 (0.00029)
Year[b]	1,94.5	6.3	**0.014**	0.00083 (0.00033)	1,98.8	3.2	0.076	0.00054 (0.00030)
Random effects	Estimate	SE	% var.		Estimate	SE	% var.	
Family	0[c]		0		0[c]		0	
Genus	0.00081	0.00044	1.59		0.00037	0.00025	0.87	
Species	0.00050	0.00028	0.98		0.00033	0.00018	0.78	
Residual	0.0496	0.0089	97.43		0.0417	0.0071	98.35	
n	128				122			
				R² = 0.86				R² = 0.85

[a]The same results were obtained when nest height categories were used (ground, shrub, canopy).
[b]Year of study publication (to increase sample size). However, correlation with midpoint of the study period was very high: r = 0.93, p < 0.001, n = 128.
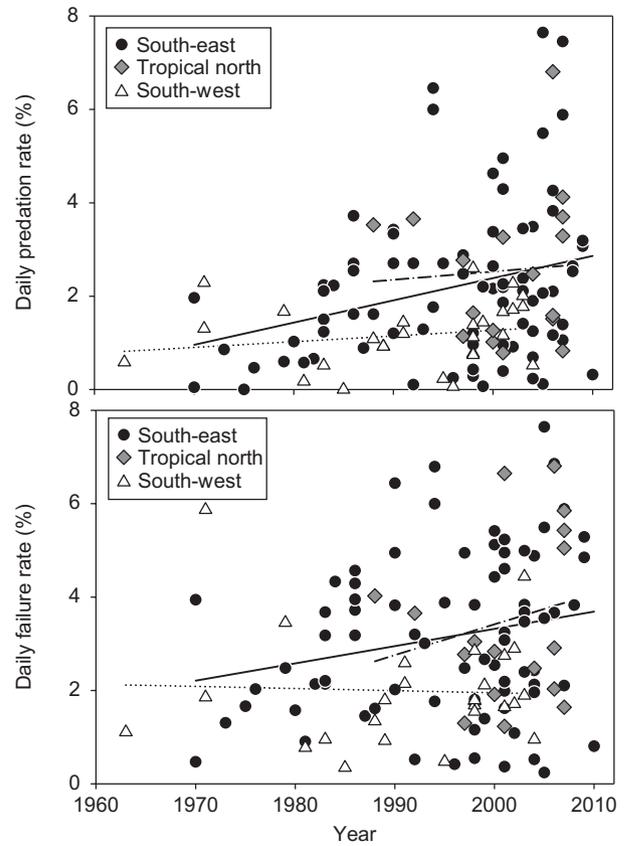[c]The estimate was zeroed by SAS.

Figure 2. Daily nest predation and failure rates across years depicted separately for south-western (dotted line), tropical northern (hatched line) and south-eastern Australia (full line). For the sake of convenience raw data are shown and the fitted lines are simple least squares regression lines.

of species (percentage of squares occupied in Australia) and the year of study and found none ($F_{1,126} < 0.1$, p = 0.936). Random effects of family, genus, and species accounted for little variance in all the analyses ranging between 0 and 1.6% (Table 2).

An information-theoretic approach based on AIC_c provided similar results highlighting the importance of geography (north-south and east-west trends), adult body
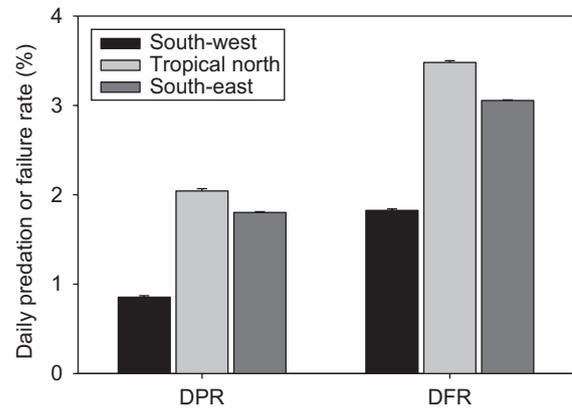

Figure 3. Least squares means (1 SE) for daily nest predation and failure rates for the three regions within Australia adjusted for other factors (Table 2) except latitude and longitude.

mass, and in case of daily predation rates, also year (Supplementary material Appendix 2). This convergence of different analytical approaches corroborates robustness of our conclusions.

Comparison with other regions

We compared the data reported in this study with multi-species studies or reviews based on substantial samples of species and nests for other regions. Overall, both nest failure and proportion of nest losses caused by predators in Australia were similar to other regions (Fig. 4).

Discussion

Nest predation and failure in Australian songbirds increased towards the equator, and were lowest in SW Australia. They were also higher in smaller birds. Nest predation rates increased in recent decades, whereas nest failure rates were lower in species with closed nests. In the following discussion we first address the necessary limits of our data, and then address explanations for the broad-scale patterns we have identified.

Although we assembled a large and very detailed dataset on nest failure and predation in Australian songbirds, there potentially remain problems with our data. As has been reported previously (Clarke 1997), the geographical distribution of studies is biased towards more populated areas. Most studies originated from SE and SW Australia with few studies coming from TN Australia and no studies from arid central Australia (Supplementary material, Fig. S1). Taxonomic coverage of families and species seemed reasonable. Most studies came from the last four decades and the frequency of study has increased over that time (Supplementary material, Fig. S2). While this is encouraging,

sample size of most of the studies is modest (median = 38.5 nests; Table 1) with no improvement over the years. Most studies also had short timespans (median = 2 yr). This certainly introduces substantial sampling variation into the data. There was high within-species variation as compared to among-species variation, which was reflected by low proportion of variation explained by taxonomy. However, despite this high variation our analyses revealed several robust predictors of nest failure and we discuss them in turn below.

Time

Daily nest predation rates increased over the last four decades (Fig. 2). This finding was not an artefact of the taxonomic composition of species or the extent of geographical distribution of species. At the same time, this finding was unlikely to be an artefact of methodology. We used only field studies focused on one or a few species and excluded data based on the Australian Nest Record Scheme. Moreover, all studies provided the proportion of nests failed and/or depredated and we transformed these values to DFR and DPR using the same formula, thus minimizing any potential methodological bias. We thus believe that the time trend we identified is real and think that at least two related explanations are possible. First, as nest predation studies have become commoner in recent decades (Supplementary material, Fig. S2) there might have been more studies in places that are fragmented or otherwise impacted by anthropogenic disturbance. Second, population increases of important nest predators might be the driver of this pattern. As an example that is best documented, pied currawongs *Strepera graculina* (ca 300 g bird) increased in abundance and colonised new areas during last decades. There was an increase of 62% in reporting rate between 1980s and 2000s across the range of this
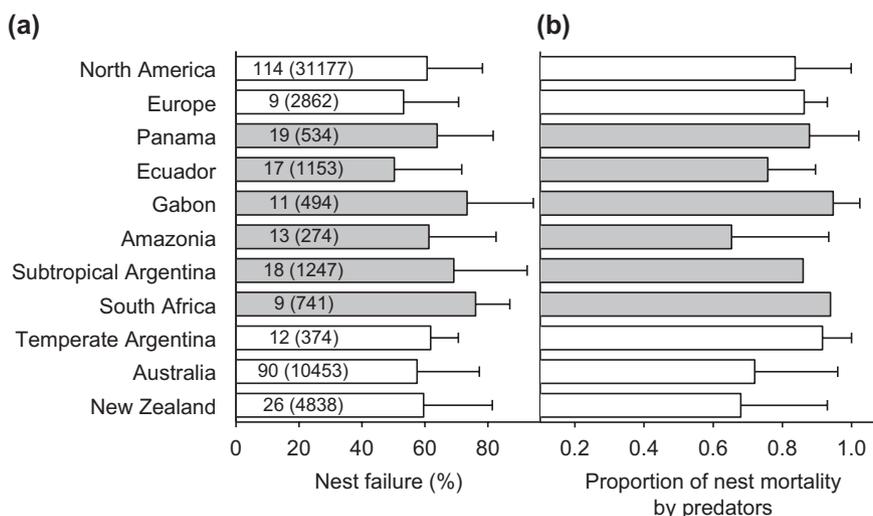

Figure 4. Comparison of nest failure and proportion of failure due to predators across regions. (a) Overall nest failure (1 SD) in Australia compared to temperate areas (white), and tropics and subtropics (grey). Figures within bars indicate number of species, with number of nests in brackets. (b) Proportion of nest failure caused by predators (1 SD; unknown for two studies). Localities are arrayed roughly from north to south (from top to bottom). Data come from following studies: North America (BBIRD 2003), Europe (Wesołowski and Tomiałojć 2005), Panama (Robinson et al. 2000), Ecuador (Marchant 1960), Gabon (Brosset and Érard 1986), Amazonia (Oniki 1979), subtropical Argentina (Auer et al. 2007), South Africa (Lloyd 2004), temperate Argentina (Mezquida and Marone 2001), and New Zealand (Remeš et al. 2012).

species (Barrett et al. 2003), which is usually ascribed to large-scale planting of exotic shrubs and trees with fleshy fruits on which pied currawongs depend during the non-breeding season (Wood 1998). The pied currawong has been identified as a significant nest predator by studies using both artificial nests (Major et al. 1996, Fulton and Ford 2001) and natural nests of woodland songbirds (Debus 2006). Pied currawongs live exclusively in eastern Australia, and thus cannot be solely responsible for the increase in nest predation, because it occurred also in SW and TN Australia (although less markedly so; Fig. 2) where this species does not live. However, they provide an illuminating example of how human-induced changes in landscape can contribute to population increases of important nest predators with potential detrimental consequences for native birds. Recent demonstration of a similar increase of nest predation rates over the last 50 yr in New Zealand suggests that this might be a more general phenomenon worth further attention in other regions (Remeš et al. 2012).

It has been recently estimated that about two-thirds of Australia's bird species are showing significant long-term declines (Olsen 2008), and nest predation has been implicated in many of these declines (Ford et al. 2009). However, increased nest predation does not automatically imply negative impacts on songbird populations (Ford et al. 2001). There are many other factors that may be causing declines of small birds, including insecticides, cats, increasingly fragmented vegetation, and spread of other abundant and aggressive native species such as noisy miner *Manorina melanocephala* (Major 2003). Moreover, birds might compensate higher nest losses by more frequent re-nesting, especially given long breeding seasons typical of Australian birds (Woinarski 1985). A clear demonstration of a causative effect of nest predation in songbird declines would have to involve predator removal and subsequent monitoring of songbird demography (Côté and Sutherland 1997, Holt et al. 2008). So far, only one study followed the effects of nest predator (pied currawong) exclusion on the breeding success of two woodland songbirds (eastern yellow robin *Eopsaltria australis* and scarlet robin *Petroica multicolor*), and nest survival increased strongly (Debus 2006). Moreover, there is growing evidence that low production of recruits caused by high nest predation might be responsible for long-term declines of some small songbirds (e.g. hooded robin *Melanodryas cucullata* (Ford et al. 2009)).

Geography

Avian life-history attributes usually vary across latitude (Cardillo 2002) and this variation has often been ascribed to nest predation rates being higher closer to the equator (Martin 1996). Indeed, nest predation and failure increased towards the equator in our sample of Australian passerines (Fig. 1), consistent with the traditional view. However, the causes of this pattern remain questionable. One possibility is changing diversity or composition of predator communities towards the equator. For instance, in North America the relative importance of snakes as predators increases towards the equator, in concert with their increasing diversity and abundance (Thompson 2007). However, Australian fauna underwent such dramatic changes caused by historically recent introductions and extinctions of many potential nest predators (Johnson 2006) that it is difficult to infer what the net effects on their populations were (Attiwill and Wilson 2006). Yet, even in highly perturbed Australian communities there are geographic gradients in the distribution of potential nest predators. European red foxes *Vulpes vulpes* are for example lacking from the tropical north (Menkhorst and Knight 2010). This is not to say that they are responsible for the nest predation gradient identified here, but to illustrate that predators with potentially strong interactions with other predatory and prey species (Johnson et al. 2007, Johnson and VanDerWal 2009) can be restricted in their distribution and this non-random distribution might contribute to geographic patterns in nest depredation rates.

Geographical patterns in our data were more complex than this north-south trend. Nest failure and predation were lower in SW Australia than in SE and TN Australia (Fig. 3). Again, different abundance and/or diversity of nest predators might be the clue. We know that biogeography (Thompson 2007), habitat type (Thompson and Burhans 2004), and habitat fragmentation (Robinson et al. 1995) all affect nest predation rates. However, effects of habitat fragmentation might be dependent on landscape context, being more profound in certain habitat types (Tewksbury et al. 2006) or geographic areas than in others (Cavitt and Martin 2002). One tentative explanation might be that nest predation is kept high by widespread (introduced) nest predators in SE and TN Australia, whereas in SW Australia the abundance of introduced mammalian predators has been restricted by large-scale poisoning with sodium monofluoroacetate, to which native mammals are resistant because of high levels of the toxin in native vegetation (Twigg 1991). However, until robust data on real nest predators are acquired, which requires substantial sampling effort (Weidinger 2008), no definite explanation for the geographic patterns can be offered.

Other factors

It has been repeatedly shown that nests in cavities are safer from predators and suffer from lower predation pressure, and that this is not just because cavity nesters are often studied in predator-proof artificial nest-boxes (Oniki 1979, Skutch 1985, Martin and Li 1992, Robinson et al. 2000, Wesołowski and Tomiałojć 2005, Auer et al. 2007, Brawn et al. 2011). Higher safety of cavities is also traditionally suggested as one of the main reasons for high nest success of typical primary cavity nesters, e.g. woodpeckers (Paclík et al. 2009). Our data only partly confirmed this pattern. There was no evidence that daily predation rates differed between nest types. However, daily failure rates were lower in closed nests as compared to open nests, although the support from the AIC-based approach was weak (Supplementary material Appendix 2). This overall weak effect of nest type is not surprising, as most Australian passerines with closed nests have a domed structure built from soft materials (e.g. typical for fairy-wrens, Maluridae) instead of being placed in tree cavities (only three species

in our sample had the nest situated in a site sheltered by a hard material). Moreover, although closed nests can be better defendable by a parent sitting on the nest as compared to open nests (Hansell 2000), parents might also adopt other compensatory behavioural strategies besides nest defence, e.g. watching for predators and luring them away from the nest, which can be equally effective in open nesters. Interactions between nest site, size and parental behaviour in determining nest survival are complex and require further attention (Weidinger 2002, 2004, Remeš 2005).

Large species suffered less from nest losses, which probably indicates that large species might be better able to defend their nest against predators. For example, nests of large and aggressive noisy friarbird *Philemon corniculatus* with a good view of surroundings were more successful than more hidden nests, suggesting that this species might be able to defend its nests against at least some nest predators (Ford 1999). However, this pattern is by no means general. Although Ricklefs (1969) also found lower daily nest failure rate in large-bodied species, his analysis included both songbirds and raptorial birds. The pattern would not have been apparent had he analysed only songbirds (Ricklefs 1969: Fig. 11). Similarly, there was no relationship between body mass and daily predation rates in North American (r = −0.05, p = 0.596, n = 129, data from Remeš 2006) or European songbirds (r = −0.03, p = 0.836, n = 62, data from Lyer 2008), whereas mixed results were reported in a previous analysis of Australian passerines (Poiani and Pagel 1997). An interesting twist on this problem is a finding of higher nest predation rates in larger species of woodpeckers (Paclík et al. 2009). This surprising pattern is probably caused by the fact that large species have large cavity entrance, which allows an access to a broader range of nest predators. Thus, the direction of the relationship between nest predation and body mass can differ across taxa, functional groups, and regions.

There was no relationship of nest predation and failure to nest height. This was true also when nest categories (ground, shrub, canopy) instead of nest height were used, which would allow for non-linear effects of nest height. Traditionally predation rates were linked to nest strata, at least in North America (Martin 1993), and thus our results show that relationships between nest predation and height might differ among continents or broad regions. Similarly, nest predation and failure did not differ between pair-breeding species, cooperative species and species with female-only care suggesting that the number of care-givers has no effect on the risk of nest destruction by predators or on the probability of nest failure. However, potential effect of social organization might have been occluded by the fact that observed nest predation intensity is a product of ambient predation risk and parental behaviour (Remeš 2005). Thus, if social organization with more care-givers evolved in response to increased nest predation risk (Poiani and Pagel 1997), their more effective antipredator defence might have decreased observed predation rates to the level typical of species with few care-givers. Consequently, in such a case we would have observed no relationship between social organization and predation rates even if there were a functional relationship.

Comparison with other regions

Nest failure rates and the contribution of predation to nest loss in Australia did not differ from the values reported for other regions (Fig. 4). There also seemed to be no clear-cut difference between temperate and tropical/subtropical regions. Results of some earlier, small-scale studies based on comparisons of phylogenetically and ecologically related species also questioned the paradigm of higher nest predation or failure in tropical/subtropical regions (Snow and Snow 1963, Martin et al. 2007). Although sampling issues might play a role, what seems to be a robust observation is that the magnitude of differences between sites within regions (i.e. within the temperate region, within the sub/tropics) are comparable to differences across regions (i.e. the temperate-sub/tropical comparison; Fig. 4). A factor that might have amplified within-region variation in nest predation rates is human disturbance. In North America, elevated rates of nest loss are usually found in altered landscapes (Thompson 2007). In contrast, nest predation rates in developed landscapes in Europe are usually lower than in relatively pristine conditions (Wesołowski and Tomiałojć 2005). Moreover, habitat or altitude (Boyle 2008) might contribute to within-region variation. Thus, when comparing temperate regions with tropical or southern temperate areas, it is imperative to control for potentially confounding variables such as landscape development, altitude or habitat.

It should be again noted, however, that we are comparing observed nest predation rates that are the outcome of the interaction between ambient predation risk and parental behaviour (Remeš 2005). Thus, there might still be higher predation risk in the tropics, but it might be compensated by small clutches and consequent low activity on the nests that makes them less conspicuous to visually oriented nest predators (Martin et al. 2000a). However, we must admit that the effect of parental activity on nest predation risk remains controversial (Martin et al. 2000b, Styrsky et al. 2005, Halupka and Greeney 2009), and latitudinal gradients in clutch size might be caused by other factors than nest predation (e.g. seasonality; McNamara et al. 2008, Griebeler et al. 2010). However, parental effects have not been robustly tested across latitudes and this hypothesis thus cannot be dismissed until proper, preferentially experimental, tests are performed.

Besides variation among sites, substantial variation in nest predation risk among species within sites often remains unexplained, besides usually significant effect of nest type (Auer et al. 2007, Brawn et al. 2011). It might prove more fruitful to search for population- and species-specific predictors of nest failure and predation risk rather than focus on broad-scale differences among distant geographical regions (Remeš et al. 2012). These distant geographic regions are often themselves highly heterogeneous in terms of life-history strategies of species, habitat types, and local predator communities. An approach focused on species-specific correlates of predation risk will be also more informative for revealing fine-scale life-history, physiological, and behavioural adaptations in individual species (Martin et al. 2000a), and human impact on breeding success (Remeš et al. 2012).

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Supplementary material (Appendix J5599 at <www.oikosoffice.lu.se/appendix>). Appendix 1–2.