



The evolution of clutch size in Australian songbirds in relation to climate, predation, and nestling development

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ABSTRACT

The study of clutch size has been a productive approach to gaining better understanding of life-history evolution, especially in Northern Hemisphere birds. Factors driving life-history evolution in Southern Hemisphere species are less well understood. Moreover, studies often focus on single hypotheses for clutch size evolution and rarely test several hypotheses simultaneously. This severely limits more general conclusions of life-history evolution. We assembled an extensive dataset on 313 species (*ca.*98%) of Australian songbirds (Passeriformes) and tested three hypotheses for the evolution of clutch size in birds: (1) resource availability and their seasonality (Lack's and Ashmole's hypotheses), (2) nestling mortality (age-specific mortality and Skutch's hypotheses), and (3) fledgling developmental gradient (Martin's hypothesis). The mean clutch size of Australian songbirds was 2.69 eggs and increased in higher latitudes. Clutch size was positively related to the length of the nestling period and in species with short nestling periods offspring left the nest with lower body mass, consistent with Martin's hypothesis. In contrast to many Northern Hemisphere studies we did not detect any direct effect of the productivity of environment, its seasonality or nest predation rate. Our work provides one of only a handful of comprehensive tests of clutch size evolution in Southern Hemisphere birds. Its findings stress the importance of breaking the Northern temperate bias of life-history studies.

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Introduction

Patterns in clutch size variation among birds have been well documented, yet the mechanisms generating these patterns on both interspecific and intraspecific levels are still not fully understood. First, Lack (1947, 1948) and Ashmole (1963) stressed the importance of resource availability for optimal clutch size. Lack (1947, 1948) proposed that available resources determine how many offspring parents are able to rear: more resources per capita allow for larger clutch size. Ashmole (1963) later suggested that per-capita food availability during the breeding season is driven by the interaction between population density (which is regulated during the winter months), resource availability, and its seasonality. In areas with high seasonality of resources and low-resource winter periods, high over-winter mortality of individuals reduces population density. This results in high availability of food per capita in the following breeding season. Birds can then have larger clutches because they are able to nourish more offspring. Clutch size is thus predicted

to increase with increasing seasonality of resources. Several studies have confirmed this prediction both across and within species (Ricklefs 1980; Koenig 1984; Yom-Tov 1994; Dunn *et al.* 2000; Yom-Tov and Geffen 2002; Jetz *et al.* 2008; Hořák *et al.* 2015; partial support in Evans *et al.* 2005; Samaš *et al.* 2013). Moreover, its logic was backed by modelling studies (McNamara *et al.* 2008; Griebeler *et al.* 2010). However, Ashmole's mechanism is certainly not the only process affecting clutch size evolution in birds, because there is usually substantial residual variation in clutch size across species and space after accounting for seasonality (Ricklefs 1980; Jetz *et al.* 2008). Moreover, it does not account for migrants, which are not exposed to harsh winter conditions, immigrate to highly seasonal areas, and exploit local resources during the breeding season, even though their mortality rates might increase during the migration. Most importantly, Ashmole's hypothesis has been tested simultaneously with other hypotheses to judge its relative importance in explaining clutch size variation across species only a few times (Hořák *et al.* 2011; Samaš *et al.* 2013).

Second, according to Skutch (1949), larger broods are more likely to be depredated than smaller ones, because nests with more offspring attract the attention of predators more than nests with fewer offspring due to more frequent feeding visits by parents. Parents are thus selected to decrease their food delivery rates. Although they can partly compensate by delivering larger food items, lower delivery rates result in the reduction of clutch size (Martin *et al.* 2000), because parents are not able to nourish many offspring. Low food delivery rates under high nest predation were documented by Martin *et al.* (2000, 2011), suggesting that this mechanism might at least partially explain clutch size variation among species. Predictions of Skutch's hypothesis are in accordance with the age-specific mortality hypothesis, whereby under high nest predation rate it should be advantageous to decrease clutch size and thus save energy for easier re-nesting in the case of clutch or brood loss (Ricklefs 1968; Stearns 1976; Martin 1995). On the other hand, when mortality is high in adults (e.g. due to predation or starvation in the lean season), it is better to invest more energy (and thus increase clutch size) in the current reproductive attempt (Williams 1966; Sæther 1988; Martin 1995; Ghalambor and Martin 2001; but see Lloyd *et al.* 2014). These two hypotheses (i.e. age-specific mortalities) were suggested to explain increasing clutch size with latitude, because nest predation and adult survival rates are probably higher in the tropics than in the temperate zone (Skutch 1949; Slagsvold 1982; Yom-Tov *et al.* 1992; Martin *et al.* 2000; Ghalambor and Martin 2001). However, geographic gradients in nest predation rates seem to differ between regions (Martin 1996; Martin *et al.* 2000; Remeš *et al.* 2012a) and differences in adult survival between temperate and tropical regions can be sometimes weak or absent (e.g. Karr *et al.* 1990). Thus, it remains to be demonstrated how well age-specific mortalities predict clutch size in different parts of the world, especially when tested simultaneously with other relevant hypotheses.

Third, Martin (2014) proposed a new hypothesis that follows the basic idea of nest predation being the main driver of clutch size evolution, but with additional mechanisms. According to this hypothesis, higher nest predation risk leads to shortened nestling periods to avoid nest depredation and nestlings consequently fledge with underdeveloped wing feathers (Cheng and Martin 2012) and low body mass (Remeš and Martin 2002; Remeš and Matysioková 2016). Wing length and body mass at fledging vary between species and this gradient sets the amount of energy that must be spent on every offspring after fledging.

More energy is needed for less developed fledglings as they are less agile, more dispersed, it takes them longer to develop self-feeding, and they have higher mortality rates (Martin 2014; Remeš and Matysioková 2016). The mortality rate of offspring, together with the daily energy expenditure of parents for the whole brood, then determines clutch size. This hypothesis predicts larger clutch sizes in species with longer nestling periods for a given adult body mass. Martin (2014, 2015) found support for his hypothesis in songbirds from North America, Malaysia, and Venezuela, but it now needs to be tested on additional datasets and on species from other parts of the world, preferably together with other relevant hypotheses.

Most studies concerning the evolution and geographic variation of clutch size and life histories in general were conducted on species inhabiting the Northern Hemisphere. Comparatively little is known about birds from the tropics and the Southern Hemisphere (Martin 1996, 2004, 2015). However, these species are distinct by their generally slow life histories, including longer breeding seasons and smaller clutches compared to birds from the same Northern latitudes (Cody 1966; Wyndham 1986; Martin *et al.* 2000; Jetz *et al.* 2008; Freeman and Mason 2014), and the latitudinal gradient of clutch size on the Southern Hemisphere is weak (Yom-Tov *et al.* 1994; Young 1994; Jetz *et al.* 2008). Australia represents a unique study system with highly endemic and diverse avifauna (Holt *et al.* 2013). Climatic and environmental conditions vary substantially both across latitude and from inland to coast, which makes this area ideal for studying life-history hypotheses based on such pronounced differences. Most of the continent is arid while productive environments with high precipitation are distributed along the northern, eastern, and southern coasts, creating somewhat unusual spatial pattern of climatic variability. Moreover, Australian avifauna is quite well studied compared to other Southern Hemisphere birds and provides a great opportunity for studying life histories of resident species of birds in the Southern Hemisphere.

In this study we put together a large dataset of several intrinsic and extrinsic traits obtained from the literature and test simultaneously for the first time all the hypotheses described above on Australian songbirds. We test the effects of (1) resource availability (Lack's and Ashmole's hypotheses), (2) the rate of nest predation (age-specific mortality and Skutch's hypotheses), and (3) the length of the nestling period and relative fledging mass and wing length (indirect test of the new Martin's hypothesis). Our study thus

contributes to the understanding of the relative strengths of competing hypotheses for clutch size evolution in Australian songbirds, and more generally of the evolution of life histories in Southern Hemisphere birds.

Methods

Species-level data

Our species-level dataset consisted of 11 intrinsic and 2 extrinsic traits of Australian songbirds (Passeriformes) obtained from the literature. Altogether, we covered 313 species out of 318 species of songbirds (i.e. ca.98%) listed in our main data and taxonomy source, the ‘Handbook of Australian, New Zealand and Antarctic Birds’ (HANZAB; Higgins *et al.* 2001, 2006; Higgins and Peter 2002). Here we searched for the following data for each species: average clutch size (number of eggs; mean of completed clutches), nest type (open vs. closed nests, the latter including both cavities and domed nests), nestling period duration (number of days from hatching to leaving the nest), length of breeding season (months when the species breeds), migration strategy (sedentary species vs. migrants, which also included partial migrants and nomadic species), mean body mass of adults (grams), and type of foraging behaviour (foraging in air or elsewhere; as aerial foragers we considered species catching flying insects both by constant flying and from a perch). We obtained daily nest predation rates (DPR) from Remeš *et al.* (2012a) supplemented with additional literature (Supplement S1), and annual adult survival, relative wing length (wing length at fledging divided by wing length of adults) and relative body mass (body mass at fledging divided by body mass of adults) from the primary literature (Supplements S2 and S3).

Since HANZAB sometimes gives multiple values for individual species, we always calculated arithmetic means of all available values for a given species. To see whether these multiple values of our response variable were consistent, we calculated repeatability of clutch size, which proved to be high (ICC = 0.8, CI = 0.75–0.84, $n = 313$). For this calculation, we used the ‘ICCest’ function from the ‘ICC’ package in R (R Core Team 2015) which estimates the Interclass Correlation Coefficient using variance components from a one-way ANOVA (Wolak *et al.* 2012).

To estimate environmental productivity for each species in our dataset, we needed information on the geographic ranges of all species. Data on the

geographic ranges of Australian birds were provided by BirdLife International and NatureServe (2011) as GIS shapefiles. We wanted to use only breeding ranges where the species are currently present. We thus adjusted range polygons according to their coding of species’ presence (1 – extant, 2 – probably extant, 3 – possibly extant, 4 – possibly extinct, 5 – extinct, 6 – presence uncertain) and season (1 – resident, 2 – breeding season, 3 – non-breeding season, 4 – passage, 5 – seasonal occurrence uncertain) to keep only polygons with codes 1, 2, and 3 for species’ presence (extant) and 1 and 2 for season (breeding area).

Using these breeding ranges, we estimated the environmental productivity for each species. As a proxy of environmental productivity, we used the Normalised Difference Vegetation Index (NDVI) available from the Australian Government’s Bureau of Meteorology (2015). We used the Monthly NDVI Average for Australia dataset with mean monthly values of the NDVI for the years 2008–2014 to calculate the maximum breeding season NDVI and NDVI seasonality in the breeding range of each species. To do that, we first rasterised ranges in Australia and Tasmania to fit the $0.05 \times 0.05^\circ$ geographic (longitude \times latitude) resolution of the NDVI data. Then we calculated mean monthly NDVI values for all cells within the geographic range of every species. Finally, we calculated two values for every species: (i) maximum breeding season NDVI as the value of the month with the highest NDVI out of species’ breeding months, and (ii) NDVI seasonality as a difference between maximum breeding season NDVI and the month with the minimum value of the NDVI.

Assemblage-level data

For mapping the spatial variation in clutch size, we needed to convert species data into assemblage-level data. To obtain these assemblage-level data, we started with creating a grid across Australia and Tasmania and chose the resolution of $1 \times 1^\circ$ (longitude \times latitude) as the smallest size of the cell that leads to unbiased results when using coarse range data (Hurlbert and Jetz 2007). We then removed cells containing islands (except Tasmania) and those with less than 50% of mainland in Quantum GIS v1.8 (QGIS Development Team 2014). The final grid consisted of 686 cells. We used this grid to obtain assemblage-level data on clutch size. We used breeding ranges (see above) to generate presence–absence data for all species in each cell of our grid. Species present in each grid cell composed the local assemblage. We obtained values of clutch size in each cell as the mean of the clutch size in all species present in that cell (i.e. assemblage means).

Statistical analyses

An assemblage-level spatial model was fitted to describe effects of latitude and longitude on clutch size. The model consisted of one dependent variable (clutch size) and two predictors (latitude and longitude) with their interaction. We first fitted the simple linear model with centred and scaled geographical position of grid cells ($n = 686$) as statistical units. However, geographical data often show spatial autocorrelation that might negatively affect analyses, so we tested for spatial autocorrelation in the residuals of the regression model using Moran's I (Moran 1950). The data points were spatially non-independent, so we fitted new regression analysis using a simultaneous autoregressive error model (SAR_{err}), which accounts for spatial autocorrelation (Kissling and Carl 2008).

For the phylogenetic analyses, we used species-level data and set up a priori models with their respective predictor variables (Table 1). Each model consisted of focal predictors stemming from the particular hypothesis and covariates that were previously shown to correlate with clutch size, including nest type (species nesting in a closed nest are expected to have larger clutches than species nesting in an open nest; Slagsvold 1982; Jetz *et al.* 2008), migration strategy (migrants tend to have smaller clutches than resident species; Yom-Tov and Geffen 2002; but see Jetz *et al.* 2008), body mass (larger species of passerines usually lay fewer eggs; Averill 1933), aerial foraging (aerial foragers can have smaller clutches than species with other foraging strategies; Martin 1995, 2014), and the length of the breeding season (as a surrogate for the number of broods per year; according to the principle of allocation, species with short breeding seasons should have time to rear only a few larger clutches, while species with long breeding seasons should have time to rear more clutches and allocate available resources among them; Cody 1966; Martin 1995).

There are other factors, which may influence the evolution of clutch size, such as cooperative breeding and diet. However, due to conflicting or lack of evidence that these variables do have effects on clutch size, we did not include them in our analyses (for more information see the Discussion).

The lack of available data for some species limited our dataset. We obtained data for all 313 species only on clutch size and the length of the breeding season. Across the traits, the mean number of species with available data was 217.3 (median = 283, $n = 13$ traits); the smallest number of species was available for relative wing length at fledging (19 species). For each analysis, data are needed for all traits used in that particular analysis and since different variables are missing in different species, this further reduces sample size. None of the analyses were therefore conducted on the full ($n = 313$) number of species. The sample size used in each analysis is shown in Table 1.

In the first model, we used two indices expressing per capita food availability, namely max NDVI as a surrogate of the maximum productivity during the breeding season and NDVI seasonality as a surrogate of how productivity varies across the year (Lack's and Ashmole's hypotheses). For this analysis we used only non-migratory species ($n = 224$), because Ashmole's predictions cannot be applied to migrants. DPR in the second model tests the nestling mortality hypothesis and the length of the nestling period in the third model tests Martin's hypothesis concerning relative development of nestlings. Martin (2014, 2015) used also adult survival, relative wing length and relative body mass at fledging, but because limited availability of data would dramatically reduce species sample ($n = 52$; adult survival), we fitted one model with nestling period only, and another model that included also adult survival. The reduction of sample would be even more pronounced in analyses with relative wing length ($n = 18$) and relative body mass ($n = 25$). We thus fitted two models (one for relative wing length and one for

Table 1. The three main hypotheses for the evolution of clutch size that we tested, together with associated statistical models

Hypothesis	No. of species	Response variable	Predictors
Lack and Ashmole (productivity)	224	Clutch size	Max NDVI, NDVI seasonality , nest type, body mass, aerial foraging, season length
Skutch (nest predation)	97	Clutch size	DPR , nest type, migration, body mass, aerial foraging, season length
Martin (development)	191	Clutch size	Nestling period , nest type, migration, body mass, aerial foraging, season length
Martin (adjusted for adult survival)	52	Clutch size	Nestling period, adult survival , nest type, migration, body mass, aerial foraging, season length
Martin (relative wing length)	18	Relative wing length	Nestling period , body mass
Martin (relative body mass)	25	Relative body mass	Nestling period , body mass
All three together	93	Clutch size	Max NDVI, NDVI seasonality, DPR, nestling period , nest type, migration, body mass, aerial foraging, season length

These models were tested in the phylogenetic context. Target variables of each hypothesis are in bold font, covariates in normal font.

relative body mass) with only the length of the nestling period and adult body mass as predictors (Table 1). Finally, we put all variables into one model and tested all hypotheses simultaneously (Table 1). To avoid further reduction of sample size we did not omit migrants from this joint analysis. Instead we accounted for them by adding interactions between max NDVI and migration and between NDVI seasonality and migration. However, because the interactions were not significant (Table S5), we excluded them from the final model.

All models were fitted using species-level phylogenetic analyses. We used the phylogenetic generalised least squares (PGLS) method using the ‘gls’ (package ‘nlme’ of R language; R Core Team 2015) function. We accounted for phylogenetic uncertainty by running PGLS models across 100 phylogenies obtained from birdtree.org (Jetz *et al.* 2012). We used both Hackett and Ericson constraint but the results were similar, so we present only the results obtained with Hackett constraint. As a correlation structure for PGLS models we used Pagel’s lambda, which is based on the Brownian motion model and optimally adjusts the analysis for phylogenetic autocorrelation in model residuals (Freckleton *et al.* 2002). We obtained R^2 values using the fast likelihood code of Freckleton (2012). There were 100 outcomes of every PGLS analysis (one for every phylogenetic tree), so we present the averages of parameters in the main text, but provide confidence intervals for the estimates in the Supplement. In every analysis we always transformed data to approach the normal distribution. Since the number and identity of species differed between analyses (see above), the type of transformation differed between analyses as well. Transformation used in a particular analysis is always clearly stated in a given table. After transformation we scaled the data so that their mean was zero and variance was one, and set statistical significance at $\alpha = 0.05$. All models were fitted in R v3.0.2 (R Core Team 2015).

Results

We collected data on the clutch size of 313 Australian species of songbirds, which ranged from 1 to 6 eggs (mean 2.69 ± 0.92 SD, $n = 313$; Figure 1). The mean clutch size of avian assemblages in grid cells ranged from 2.6 to 3.0 eggs (grand mean 2.86 ± 0.08 SD, $n = 686$ grid cells; Figure 2). Clutch size was smallest in assemblages in south-western Australia and north Queensland and largest in eastern and south-eastern Australia and in Tasmania (Figure 2). Interestingly, large clutch sizes in Tasmania are driven by introduced species, not by Tasmanian endemics (Figure S1). When testing the effect

of geography statistically, clutch size significantly increased with increasing latitude from the equator towards the south (SAR_{err} : Est = 0.54, SE = 0.23, $z = 2.39$, $p = 0.02$), but not with longitude (SAR_{err} : Est = -0.08 , SE = 0.29, $z = -0.26$, $p = 0.80$) and did not change with their interaction (SAR_{err} : Est = 0.28, SE = 0.20, $z = 1.41$, $p = 0.16$). The effect of latitude remained significant even when Tasmania was excluded from the analysis (SAR_{err} : Est = 0.68, SE = 0.25, $z = 2.65$, $p = 0.01$), confirming that the latitudinal trend was not driven by introduced species (with large clutches) being relatively important in assemblages on the species-depauperate island of Tasmania.

In phylogeny-based analyses conducted across species, clutch size was not correlated with either max annual NDVI or NDVI seasonality (Lack and Ashmole’s hypotheses; Figure 3; Table 2). Similarly, neither daily nest predation rate (DPR; Skutch’s hypothesis) nor nestling period length predicted clutch size significantly (Martin’s hypothesis; Figure 3; Table 2). However, nestling period became statistically significant when DPR and both NDVI measures were accounted for in the most complete model testing all three main hypotheses (Figure 3; Table 2). Clutch size was then increasing with increasing length of the nest-

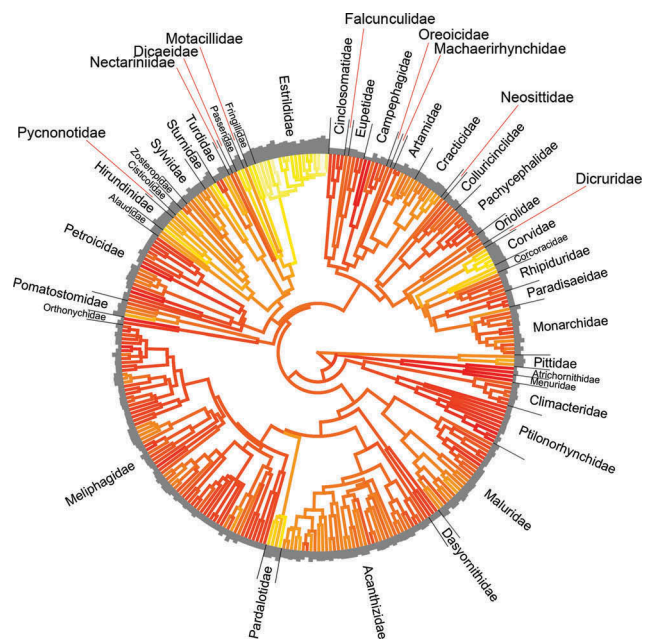


Figure 1. Clutch size in Australian songbirds depicted on a phylogenetic tree. Clutch size (number of eggs in a clutch) ranges from 1 to 6 eggs (columns) and is strongly linked to phylogeny (phylogenetic signal $\lambda \sim 0.95$; see Table 2). Dark shades represent small clutch size and light shades represent large clutch size, respectively. The depicted phylogeny is a Bayesian maximum clade credibility tree of 313 species based on 100 phylogenies, which we obtained from birdtree.org (Jetz *et al.* 2012).

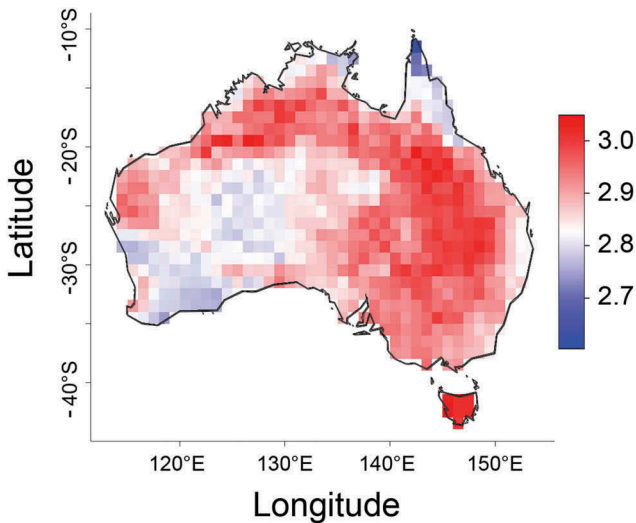


Figure 2. Geographic variation of clutch size in Australian songbirds. Mean clutch size (number of eggs in a clutch) of songbirds ($n = 313$) in Australia and Tasmania for assemblages within $1 \times 1^\circ$ grid cells ($n = 686$).

ling period. We did not include adult survival, relative wing length and relative body mass during fledging in our models, because their inclusion would lead to a substantial reduction in sample size. However, to evaluate Martin's (2014) finding that the effect of the nestling period was significant when statistically accounting for adult survival, we included adult survival into the model testing Martin's (2014) hypothesis. In this model, the effect of the nestling period remained statistically significant (Table S6). Moreover, we also tested whether relative body measurements at fledging correlated with the length of the nestling period, as assumed by Martin (2014). This relationship was significant only for relative body mass, where relative body mass increased with increasing length of the nestling period (Table S9), but not for relative wing length (Table S10).

Discussion

Clutch size in birds generally increases with latitude, from the tropics to temperate and arctic areas (Jetz *et al.* 2008). However, while this increase is strong in the Northern Hemisphere, it is generally weaker in the Southern Hemisphere (Yom-Tov *et al.* 1994; Jetz *et al.* 2008). This is partly caused by the absence of land in higher latitudes in the Southern Hemisphere and consequently lack of data. Although clutch size varied substantially across species (1–6 eggs; Figure 1), it did not vary as much spatially across the assemblages of species (assemblage averages ranged from 2.6 to 3.0 eggs; Figure 2). Despite this, we detected a significant increase in clutch size with latitude, which agrees with previous findings.

Productivity

Lack (1947, 1948) and Ashmole (1963) suggested that resource availability and its seasonality could affect the evolution of clutch size in birds. We did not find any statistically significant effect of the maximum environmental productivity during the breeding season (NDVI) or its seasonality on clutch size. We thus do not confirm findings of previous studies showing that clutch size increases with increasing environmental seasonality (Cody 1966; Jetz *et al.* 2008; Hořák *et al.* 2015) and, by implication, seasonality of resource availability (Ricklefs 1980). We offer two potential explanations for these conflicting results.

First, Australia is a climatically extraordinary continent with most of the interior area arid, while many coastal areas are dominated by humid forests. Moreover, climatic seasonality is not as profound in Australia (Figures S2 and S3) as in the Northern Hemisphere (Greenwood and Wing 1995) and resource availability thus probably does not change so

Table 2. Results of phylogenetic generalised least squares models of clutch size in relation to productivity (Lack's and Ashmole's hypotheses), predation (nest predation hypothesis), length of the nestling period (Martin's hypothesis), and all three hypotheses tested together

Response: Sqrt Clutch size	Productivity (adj. $R^2 = -0.004$, $\lambda = 0.93$)			Nest predation (adj. $R^2 = 0.02$, $\lambda = 0.96$)			Development (adj. $R^2 = 0.05$, $\lambda = 0.95$)			All three together (adj. $R^2 = 0.06$, $\lambda = 0.97$)		
	Estimate \pm SE	F	P	Estimate \pm SE	F	P	Estimate \pm SE	F	P	Estimate \pm SE	F	P
Max NDVI	-0.01 ± 0.05	0.10	0.83	–	–	–	–	–	–	-0.07 ± 0.10	0.51	0.50
Sqrt NDVI seasonality	-0.06 ± 0.04	2.32	0.16	–	–	–	–	–	–	-0.01 ± 0.08	0.09	0.84
Sqrt DPR	–	–	–	-0.12 ± 0.07	2.88	0.10	–	–	–	-0.05 ± 0.07	0.51	0.50
Ln Nestling period	–	–	–	–	–	–	0.09 ± 0.08	1.31	0.28	0.32 ± 0.12	7.06	0.01
Migration (Sedentary)	–	–	–	0.02 ± 0.07	0.16	0.74	-0.07 ± 0.04	3.53	0.08	0.03 ± 0.08	0.19	0.71
Nest type (Open)	-0.07 ± 0.09	0.70	0.42	-0.14 ± 0.14	1.08	0.31	-0.08 ± 0.10	0.70	0.41	-0.01 ± 0.14	0.02	0.92
Ln Body mass	0.05 ± 0.08	0.44	0.55	-0.12 ± 0.12	0.93	0.36	0.06 ± 0.09	0.52	0.54	-0.28 ± 0.14	3.92	0.05
Aerial (Yes)	0.02 ± 0.04	0.51	0.50	0.12 ± 0.08	2.13	0.15	0.05 ± 0.04	1.43	0.28	0.09 ± 0.08	1.35	0.25
Season length	0.03 ± 0.04	0.54	0.51	-0.02 ± 0.07	0.17	0.75	0.02 ± 0.04	0.37	0.61	0.04 ± 0.07	0.40	0.55

Models were run on 100 phylogenies, and means of parameters and test statistics are presented. Levels of binary predictors for which the estimates are valid are listed in parentheses. Focal predictors of each hypothesis are in bold font. 'Sqrt' = square root transformed.

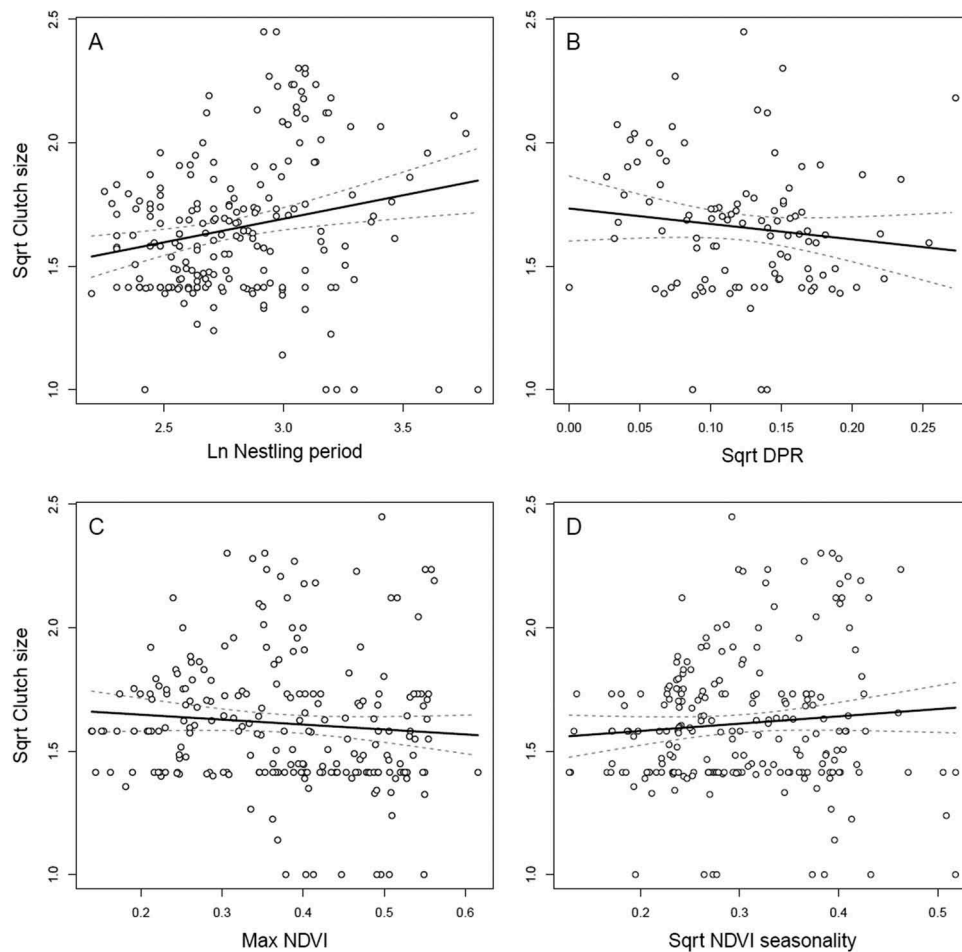


Figure 3. Relationships between clutch size (square root transformed) and focal predictors of the tested hypotheses: (A) nestling period ($n = 208$; ln transformed), (B) DPR ($n = 102$; square root transformed), (C) maximum breeding season NDVI ($n = 224$), and (D) NDVI seasonality ($n = 224$; square root transformed). Only the relationship of clutch size to nestling period was statistically significant in the phylogenetic analyses (A). Solid lines represent linear regression lines; dashed lines are 95% confidence intervals.

markedly throughout the year. However, the Australian climate is also driven by El Niño-Southern Oscillation (ENSO) events (Power *et al.* 1999), which induce strong and unpredictable changes in temperature and precipitation. These three climatic peculiarities can have significant consequences for life-history evolution. Owing to low seasonality, bird numbers might not be so tightly regulated by conditions during the lean season, which is a prerequisite for the mechanism suggested by Ashmole (1963). Further, bet-hedging theory suggests that in unpredictable environments (e.g. highly arid ones or those driven by ENSO events; Power *et al.* 1999), the probability of breeding success is reduced and parents are thus selected to invest less energy into single clutches and lay fewer eggs (Murphy 1968; Slatkin 1974). For instance, the clutch size of southern African birds was found to be smaller in arid areas when controlled for seasonality, thereby supporting the bet-hedging strategy (Lepage and Lloyd 2009). Moreover, productivity is tied closely to

water availability, which plays an important role in avian reproduction as well (Coe and Rotenberry 2003), and thus the extensive aridity of Australia might have constrained the diversification of avian life histories.

Second, many Australian bird species reproduce during the months that have comparably low plant productivity (Figure S2 B), which might be caused by the occurrence of a marked wet season in the tropical areas, during which NDVI values increase, but might not represent ideal conditions for breeding (Foster 1974). Moreover, NDVI values can differ across habitats even within a climatic zone (Burbidge and Fuller 2007) and the NDVI probably does not fully account for seasonal changes in various types of food. Species with different diet specialisation, for instance, do not breed simultaneously, for example Australian insectivores breed earlier than seedeaters (Ford 1989), and this might not be well captured by the NDVI. Furthermore, even though food availability is seasonal

in Australia, the seasonality is lower and without sharp peaks compared to the Northern Hemisphere, which might lead to overall smaller clutches of Australian songbirds compared to Northern Hemisphere songbirds (Woinarski 1985; Ford 1989). In addition, the timing of breeding in the tropics might be affected not only by food availability but also by annual variation in nest predation or the timing of energetically demanding moult (Stutchbury and Morton 2001). Taken together, the NDVI can be a good predictor of the best time for breeding in temperate areas but not in the tropics and (southern) subtropics, which might hamper its predictive value for clutch size in these regions.

Nest predation

The nest predation hypothesis suggests that clutch size decreases with increasing nest predation rate (Skutch 1949; Slagsvold 1982). Although several studies from other continents confirmed a negative correlation between clutch size and nest predation rates (Europe: Slagsvold 1982; North and South America: Martin *et al.* 2000; Ghalambor and Martin 2001), we did not find similar evidence in Australia. One might argue that historically existing correlation between clutch size and nest predation could be obscured by increases and decreases of populations of different species of predators in Australia compared to pre-European settlement (Ford *et al.* 2001; Remeš *et al.* 2012a), including the introduction of effective exotic predators (Salo *et al.* 2007; Dickman 2009; Remeš *et al.* 2012b). However, we doubt this is a sufficient explanation for the pattern in clutch size we found, because our data include records on clutch sizes and predation rates over large spatial and temporal scales and therefore should be robust to recent biotic changes. Rather, Australian songbirds might be geared towards small clutches and spreading the risk by other factors (e.g. overall aridity and low productivity), making the effect of nest predation difficult to detect. Notice in this respect that the effect of nest predation was not negligible, occurred in the expected direction, and was almost statistically significant (Table 2; Figure 3).

Nestling development

Martin (2014) predicted that clutch size would increase with the length of nestling period. We confirmed this prediction, but only when we controlled for adult survival (Table S6) or climate and nest predation (Table 2). Adult survival together with the length of the breeding season set the total parental reproductive

effort (Martin 2014). Accordingly, nestling period became significant only when the analysis was adjusted for total reproductive effort. One is tempted to suggest that this makes sense, as Martin (2014) proposes that the per-offspring investment is set by the nestling period (via the nestling development gradient). The effect of nestling period would then become apparent when statistically accounting for factors affecting total reproductive effort per breeding attempt. However, caution is needed here, because the significance of the length of nestling period might have been caused simply by the sampling effect. The analyses re-run with the length of the nestling period as the only predictor (for the subset of 52 and 93 species; Martin's hypothesis adjusted for adult survival and the joint analysis; Tables S7 and S8) revealed that this was perhaps the case, as nestling period was significant even without the presence of adult survival, DPR, or NDVI among predictors. On the other hand this result shows that nestling period itself as well as total reproductive effort (nestling period together with adult survival) are significant predictors of clutch size at least for these subsets of species. Thus, only further detailed studies can show whether sampling effect, or real biological effects are more important.

Martin's (2014, 2015) hypothesis further assumes that species with long nestling periods enjoy benefits of well-developed offspring at fledging leading to high post-fledging survival. We tested the relationship between nestling development and the length of the nestling period and confirmed that relative body mass at fledging increased with increasing nestling period length in accordance with Martin's (2015) findings, but the effect of nestling period length on relative wing length at fledging was not significant. However, this latter analysis was probably hampered by the very limited sample size (18 species). Furthermore, Remeš and Matysioková (2016) recently confirmed that species with long nestling periods and high relative body mass at fledging enjoyed high post-fledging survival. Thus, these studies (Remeš and Matysioková 2016; this study) confirm two important components of the new hypothesis for clutch size evolution in songbirds (Martin 2014, 2015).

Other factors that may influence clutch size

Besides effects that we investigated, quite a large difference in clutch size seems to be present between old endemic families and those that underwent most of their evolution and diversification elsewhere and (re-) colonised Australia later (Moyle *et al.* 2016), and

which, in general, have larger clutches (Corvidae and most of the families between Alaudidae and Estrildidae in Figure 1). Old endemics and old invaders to Australia have smaller clutches than the ‘new’ arrivals (Woinarski 1985; Yom-Tov 1987). Besides historical effects, cooperative breeding or diet might also covary with clutch size. Based on simple graphical inspection of data, it appears that families with mostly cooperatively breeding species have somewhat larger clutches (Artamidae, Corcoracidae, Cracticidae, Maluridae, Pomatostomidae; Figure 1). Helpers might help raise larger clutches as they possibly provide extra food to offspring and help with nest defence. However, Poiani and Jermiin (1994) found the opposite effect in Australian passerines, where clutch size in cooperative breeders was smaller than that of non-cooperatively breeding species. This shows that the effect of cooperative breeding on clutch size will be complex (if any), because additional adult help might instead lift the load from the other provisioners, which does not affect chicks but increases adult survival. Moreover, the occurrence and degree of cooperative breeding might differ greatly between individual family groups within species and also might be facilitated by low environmental seasonality (Ford *et al.* 1988), and thus its relation to clutch size might be confounded by environmental factors. These hypotheses remain to be tested rigorously.

In this study, clutch size was positively associated with latitude and out of the three hypotheses we tested, guarded support was received by Martin’s (2014) new hypothesis stressing the role of the nestling development gradient. Since this developmental gradient is often driven by nest predation (Remeš and Martin 2002; Cheng and Martin 2012; Remeš and Matysioková 2016), nest predation seems to be indirectly driving clutch size evolution, at least in some Australian songbirds. However, our test of Martin’s hypothesis was indirect and on a small sample of species. We thus critically need more direct tests involving nestling developmental traits, especially wing length and body mass at fledging (Martin 2015).

In sum, we show that the evolution of clutch size in Australian songbirds might be under the influence of different factors compared to other continents. Australian birds, with their wide range of life histories, including a high incidence of cooperative breeding, and occupying a large array of habitats, provide great opportunity to shed new light on the evolution of clutch size and other life-history traits in birds.

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