Effect of natural brood size variability on growth and survival of thornbird nestlings

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Abstract

For many bird species, brood size is a highly variable trait. Several aspects of the development and survival of nestlings are affected by brood size. Most scientific evidence comes from brood manipulation experiments, and the complementary information offered by studies of natural variability has received little attention in tropical and subtropical species. Here, we provide data on the effect of brood size on the development and survival of two furnariid species under natural conditions. Weekly during two breeding seasons, two forest patches (40 ha. each) from central Argentina, were exhaustively examined for active nests. Nestlings were monitored repeatedly from hatching to fledging. Factors that were considered potential confounders or effect modifiers were also recorded and included in the statistical analysis. We found a positive effect of brood size on growth, and a negative effect on survival. The first effect was only observed when preceding weeks were not rainy, and the latter was present in only one breeding season, so both effects appeared to depend on environmental conditions. Our results suggest that the benefit of a large or small brood size is dependent on context. In the studied populations, plasticity in or within-population genetic diversity in brood size may be advantageous in the light of the unpredictable circumstances that will prevail during the breeding season.

Introduction

In many bird species, the number of eggs laid, and consequently the size of the brood, is a highly variable trait (e.g. Fargallo, 2004; Rubolini & Fasola, 2008). Several factors, either genetic (e.g. heritability – Sheldon, Kruuk & Merilä, 2003; gene flow – Postma & Van Noordwijk, 2005) or ecological (e.g. density of active nests – Ahola et al., 2009; climatic variables – Laaksonen et al., 2006; nest predation risk – Martin & Briskie, 2009; food abundance – Sofaer et al., 2013), may cause variability in the brood size of a particular species, even within populations. In altricial birds, brood size is an important component of the reproductive effort (Dijkstra et al., 1990). Large broods may increase current reproductive investment, affecting future reproductive success by decreasing the fitness and survival of parents (Dijkstra et al., 1990). In an evolutionary context, the optimal brood size is the result of processes of continuous adjustments to environmental conditions (latitude, habitat, etc.) that act simultaneously on different life-history traits that are often correlated with brood size (e.g. laying date – Ahola et al., 2009; duration of the incubation phase – Cooper et al., 2005; timing of nesting – Sokolov, 2006). In other words, brood size results from the trade-offs between the number of chicks that can be fledged and the cost

of parental care (Drent & Daan, 1980; Murphy et al., 2000), a cost that mainly differs with the environment's productivity per unit of area (Ashmole, 1963).

Experimental studies on altricial birds showed that increases in brood size are detrimental to individual nestlings, which grow more slowly, are lighter and have a reduced probability of survival after fledging (e.g. Dijkstra et al., 1990; Hõrak, 2003; Nicolaus et al., 2009). This is in agreement with what is generally proposed for species with a slow pace of life, where adults are expected to invest more in self-maintenance than in reproduction (Russell, Yom-Tov & Geffen, 2004). However, other studies suggested that this negative impact was only present under unfavourable conditions (e.g. Nur, 1984; Young, 1996) or it did not occur at all (e.g. Murphy et al., 2000; Shutler et al., 2006). Although it has been proposed that nestling development and success are mainly determined by the feeding ability of the parents either at the individual (Pettifor, 1988) or the species levels (Lack, 1947, 1954), the inconsistency of the findings suggests that many other interacting factors may contribute to brood productivity. Small broods may suffer greater heat loss, and therefore nestlings require more energy for maintaining their body temperature (Royama, 1966; Sullivan & Weathers, 1992). Therefore, larger broods might benefit from energy savings that can potentially be redirected

to other functions, such as greater growth (Olson, 1992). Also, the increase in brood size could lead to a dilution of the parasite load (less parasites per nestling – Richner & Heeb, 1995), reducing the costs of parasitism on the host's fitness (Fessl & Tebbich, 2002).

Most scientific evidence on the relationship between brood size and nestling fitness and survival originates from experimental studies, where broods were manipulated (e.g. Dijkstra *et al.*, 1990; VanderWerf, 1992). Although experimental approaches allow a more confident establishment of a cause–effect relationship, observational studies offer valuable complementary information, because they take into account factors that differ in naturally varying brood sizes. For example, the impact of a naturally large brood on the development and survival of individual nestlings may be smaller than that on a brood that was coerced to be larger. On the other hand, observational studies may be flawed due to confounding phenomena. It is crucial that studies are designed taking into account these phenomena, and the data analysed so that potential confounders are considered and controlled for (Antoniazzi *et al.*, 2011).

Research on the effect of brood size has been focused on species of the Northern Hemisphere (see reviews by Dijkstra *et al.*, 1990; VanderWerf, 1992), whereas such studies on South American birds are scarce (but see Moreno *et al.*, 2005; Styrsky, Brawn & Robinson, 2005; Pichorim, 2011; Sousa & Marini, 2013). South American ornithofauna comprises more than 30% of the bird biodiversity of the world (Auer *et al.*, 2007) and in some cases, exhibits life-history traits contrasting those of northern species, including smaller brood sizes, many nesting attempts during the breeding season, long development periods and slow growth rates (Ricklefs, 1976; Yom-Tov, Christie & Iglesias, 1994; Russell *et al.*, 2004; Auer *et al.*, 2007). Clearly, the lack of data leaves a major gap in our knowledge about the geographical diversity in reproductive strategies.

The greater thornbird *Phacellodomus ruber* Vieillot and the lesser thornbird *P. sibilatrix* Sclater are furnariids that inhabit tropical and subtropical semi-open lowlands in South America (Del Hoyo, Elliot & Christie, 2003). In Argentina, thornbirds are conspicuous representatives of the ornithofauna of 'El Espinal' biogeographical province (de la Peña, Antoniazzi & Gamboa, 2007). Although data on the reproductive biology of local populations are available (e.g. de la Peña, 1996, 2005a), no study has as yet explored breeding strategies. Here, we determined through an observational study the associations between natural variation in brood size and nestling growth and survival in natural populations of *P. ruber* and *P. sibilatrix*.

Materials and methods

Study area

The data were collected from two native forest patches located 20 km apart in the centre of Santa Fe Province (Argentina). One is a reserve belonging to Universidad Nacional del Litoral (centre at 60°55′ W; 31°23′ S) and the other, a private field known as 'Mihura' (centre at 60°47′ W; 31°30′ S). The area sampled within each site was 40 ha. Both sites represent relicts

of the biogeographical province 'El Espinal' and are located alongside the Salado River. The climate in the region is Pampean temperate, with an average annual temperature of 18°C (mean minimum = 12°C, mean maximum = 23°C – extracted from www.climayagua.inta.gov.ar). These forests are breeding grounds for around 100 bird species, mostly Passeriformes (de la Peña, 2005b).

Studied species

The greater thornbird and the lesser thornbird overlap in distribution and habitat use, being found in forests and savannas of South America. The diet of both species mainly includes beetles, ants and spiders (Del Hoyo *et al.*, 2003). Mean body masses of Argentinian specimens at adulthood are 35 g for *P. ruber* and 15 g for *P. sibilatrix* (Alderete & Capllonch, 2010). In the study area, thornbirds reside permanently during all year, and coincide in timing of breeding (de la Peña, 2005a). On an average, *P. ruber* lays four and *P. sibilatrix* lays three eggs. In both species, the duration of the incubation period is 17 days and nestlings stay in the nest for 2 weeks before fledging (de la Peña, 2005a).

Data collection

Fieldwork spanned the breeding seasons of 2008–2009 (September–April) and 2009–2010 (September–May). Every week, each area was exhaustively examined for active nests. A total of 1493 observations (nestling measurements) were collected from 324 individuals, belonging to 117 broods. All broods of *P. ruber* ($n = 39$) and *P. sibilatrix* ($n = 78$) were examined three times a week, and every nestling was monitored repeatedly from hatching to fledging. The data collected included nestling species, body mass (g), tarsus length (mm), age and brood size. Factors that were considered potential confounders or effect modifiers were also recorded. These factors were selected considering their possible association with the response variables. For example, past precipitation and time of the season are associated with food availability, which in turn can influence nestling growth and survival, whereas nest height and support might affect survival through differential predation risk. Using HOBO Pro v2 data loggers placed in the middle of each study area, we obtained air temperature records, and precipitation was obtained from the closest meteorological station. For a detailed description of all potential confounders assessed, see Supporting Information Table S1.

Statistical analysis

Statistical analyses were performed with the R software (V. 3.1.0, The R Project for Statistical Computing; http://www.r-project.org) and the specific package used was *lme4* (Bates & Bolker, 2011).

The response variables were weight gain, tarsus growth and survival. The study unit for the statistical analysis was the individual nestling, with repeated measures in the case of weight gain and tarsus growth, and a single observation for survival. Weight gain was measured as g/day, and estimated

by calculating the difference between two consecutive measures of the body mass, divided by the number of days between samples. Similarly, tarsus growth (mm/day) was estimated comparing consecutive tarsus length measurements. Survival was estimated as success or failure, success being the observation that the nestlings reached the last period of development and failure when they were absent (or dead) during the period in which they should have been in the nest.

Two different brood size measures were used. For weight gain and tarsus growth, we used the number of chicks present at the time of the observation, but when the response variable was survival, we used the maximum number of chicks recorded for a specific brood. This is because for growth, a single nestling was sampled repeatedly at regular intervals, whereas for survival, there was a single observation per nestling.

Linear mixed models (LMM) were used to evaluate the effect of brood size on weight gain and tarsus growth and generalized linear mixed models (GLMM) with a binomial response to assess survival. To take into account that observations from the same nestling and the same brood were not independent, we included the nested random intercept 'nest ID/ nestling ID' for LMM and 'nest ID' for GLMM.

Brood size, the variable of interest, was included as a polynomial term with linear and quadratic components, to take into account possible non-linearity of the association with the response variables. Besides brood size, others terms in the maximum model included potential confounders and relevant two-way interactions (see Supporting Information Table S1). Minimum and maximum weekly mean temperatures, weekly cumulative precipitation and weekly population density of each species were assessed at different time lags (i.e. 0 to 3 weeks previously: t_0–t_{-3}). For these variables, the mean (for temperature) or sum (for precipitation) for a week were calculated using the values from seven consecutive days. So, for lags at t_0, the values included were those of the day of the observation (day$_0$) plus the ones of the preceding 6 days (day$_{-1}$ to day$_{-6}$), for lags at t_{-1}, we used day$_{-7}$ through day$_{-13}$, and so on. A year effect was also included.

To avoid collinearity problems, highly correlated variables, namely lags of temperature and temperature maximum and minimum, were assessed separately in maximum models and the one with lower Akaike information criterion (AIC) value was used. The restriction of the maximum model was conducted by stepwise elimination of unimportant terms using the AIC (Akaike, 1974) (a single term was not retained in the model if its inclusion did not reduce AIC by 2 units). The analysis was not conducted separately for each thornbird species because it was of interest to statistically assess the interaction term: brood size × species.

Results

The number of observations gathered was 729 for the breeding season 2008–2009 and 764 for the breeding season 2009–2010. The average number of observations per nestling was five and the range was 1–9. These observations belonged to 324 nestlings of 117 broods. The number of broods per year

for both species is presented in Fig. 1. The first sampling year lasted for 31 weeks, in which nestlings were detected and sampled from 24 October 2008 through 21 April 2009. The second sampling year consisted of 38 weeks (the first nestlings were detected and sampled on 9 October 2009 and the last ones on 5 May 2010). Maximum brood sizes ranged from 1 to 5 in *P. ruber* and from 1 to 4 in *P. sibilatrix*. For both species, the mode was 3. No significant differences in brood size were found between the study years (Mann–Whitney test $P = 0.521$). During the second breeding season, the precipitation levels were higher and concentrated between November and February (Fig. 2). Data on mean body mass and tarsus length at different ages by brood size for both species are offered in Fig. 3.

Relationship between brood size and growth

To evaluate the effect of brood size on body weight gain, we used 945 observations, 282 from *P. ruber* and 663 from *P. sibilatrix*, whereas for the effect on increases in tarsus length, we used 951 observations, 290 from *P. ruber* and 661 from *P. sibilatrix*. Both body weight gain and tarsus growth, were positively affected by brood size (larger broods showed greater weight gains and tarsus growth), but for both this effect depended on the precipitation fallen 1 week before (Table 1; Fig. 4). The greater the rain fallen, the smaller the positive effect on the growth parameters measured. Indeed, when previous precipitation was around 40 mm, the association between brood size and growth disappeared (Fig. 4). This pattern was consistent for both species and both years, as the interaction terms brood size × nestling sp. ($P = 0.697$ and 0.360, for body weight gain and tarsus growth, respectively, Table 1) and brood size × year ($P = 0.735$ and 0.697, for body weight gain and tarsus growth, respectively, Table 1) were not significant in either model.

Relationship between brood size and survival

Of all nestlings sampled during this study, 42.5% reached the final developmental category (fully fledged nestling). The cause of death was unknown for most of the remainder nestlings. Dead nestlings in nests were very seldom found (<3% of all mortalities) and only 12% of nestlings were found with signs of predation. Most mortality events were whole broods (75%). In many cases where whole broods were missing, the nests were found destroyed, and often this was associated with recent storms. Of all nests, 9% were found destroyed in the first year and 13% in the second. For the survival analysis, we used 320 observations: 101 from *P. ruber* and 219 from *P. sibilatrix*. When all other variables considered were held constant, brood size affected nestling survival negatively during the first year of the study (Table 2; Fig. 5), but this association was not present during the second year. Moreover, independently of all other variables analysed, survival was lower during the second year of the study. For the interaction maximum brood size × year, the coefficient was not statistically significant, $P = 0.096$ (Table 2), but the ΔAIC was 4, indicating that the interaction is important for the model goodness of fit. The
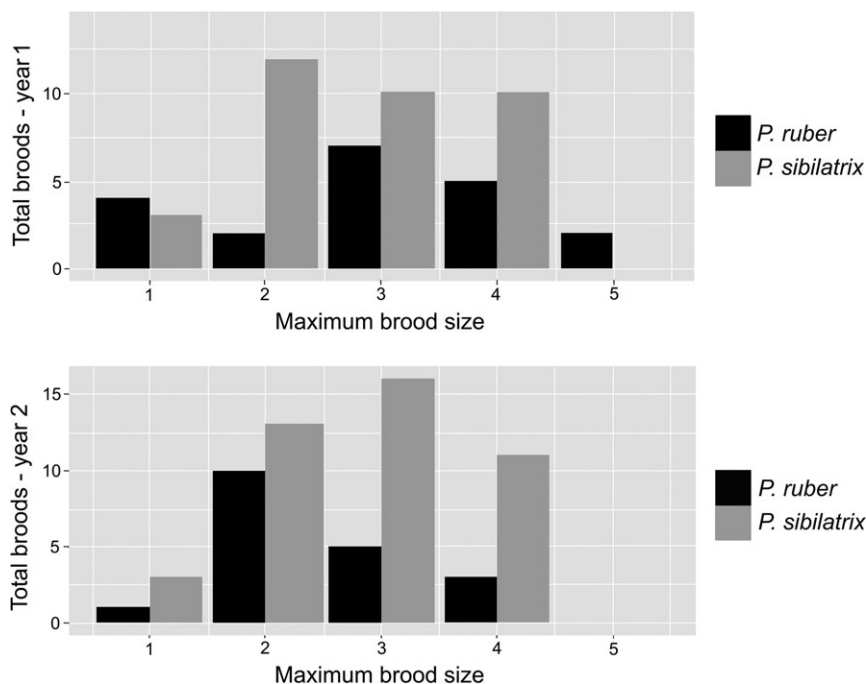
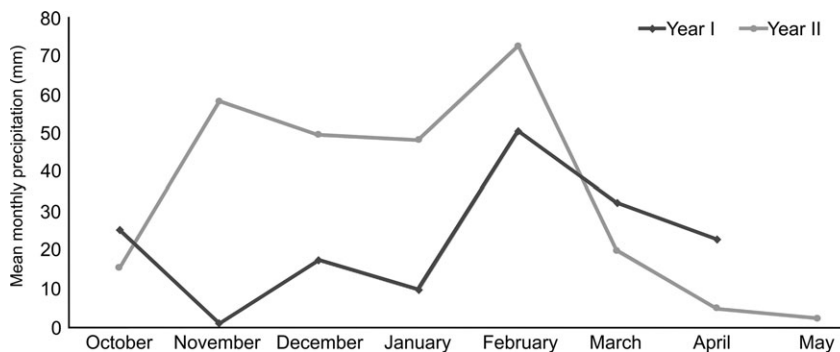**Figure 1** Number of broods per year for both species studied.

**Figure 2** Mean monthly precipitations during the 2 years of study.

effect of brood size on survival was not significantly different between bird species (the interaction term maximum brood size × nestling sp. was not statistically significant, $P = 0.283$, Table 2).

Discussion

In this study, we provided data on the effect of brood size variability on the development and survival of two passerine species under natural conditions. Although there are a few observational studies that have examined the effect of natural brood size variability while taking into account some potential confounders (e.g. Spear & Nur, 1994; Moreno *et al.*, 2005; Tarof *et al.*, 2011), rarely are intrinsic and extrinsic factors considered simultaneously, such as nestling age and weather

conditions, which could provide more accurate conclusions. After adjusting for several variables deemed potential confounders in the statistical analysis (Supporting Information Table S1), brood size was found to be significantly associated with the growth and survival of nestlings of both thornbird species. We found a positive effect of brood size on body weight gain and tarsus growth, and a negative effect on survival. Both of these effects appeared to depend on the context, as the first was only observed after low or null precipitation and the latter during the first breeding season, the least rainy one.

Brood sizes of both *Phacellodomus* species studied were within the ranges reported for furnariids of temperate regions, from 1 to 5 nestlings (Del Hoyo *et al.*, 2003). In the 2 years of study, no differences in brood size were found. The
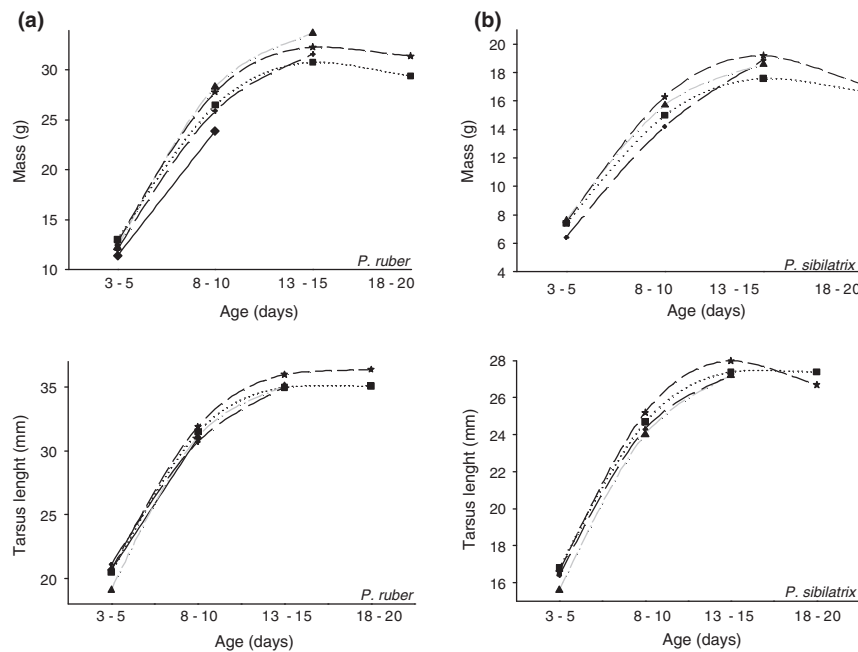
Figure 3 Mean body mass and tarsus length of *P. ruber* (a) and *P. sibilatrix* (b) nestlings at different ages and for different brood sizes.

optimum brood size for survival was 3 for *P. sibilatrix* and 4 for *P. ruber* (Fig. 4), which is the most common brood size for each species (de la Peña, 2005a).

Increases in brood size represent greater demands to be satisfied by the parents (e.g. Wright *et al.*, 2002; Neuenschwander *et al.*, 2003; Sousa & Marini, 2013). Artificially increased broods of tropical *Troglodytes aedon* presented less growth when compared to smaller broods during a year of food shortage (Young, 1996). In our study, however, larger broods showed greater growths, especially when preceding weeks were not rainy. Other studies on furnariids species have failed to find negative relationships between naturally different brood size and growth rates (Moreno *et al.*, 2005). This suggests that the size of the brood is reflecting how favourable the context and the aptitude of the parents are: parents that are of good quality, healthy and well fed are able to invest in larger broods. Also, females in good condition can better prepare their nestling for environmental conditions they may experience, via hormones and/or antibodies they deposit in the eggs (O'Neal & Ketterson, 2012). Since thornbirds feed mainly on insects (Del Hoyo *et al.*, 2003), intense precipitation may limit the activity of the parents (Radford *et al.*, 2010) or of their prey (Poulsen, 1996); thus, reducing the availability of food for nestlings. Several authors mention that insect capture by birds increases after the rain stops (i.e. Dipterans and Himenopterans – Poulsen, 1996; Kasper *et al.*, 2008; Coleopterans – Moser & Dell, 1980; Aukema, Clayton & Raffa, 2005), thus suggesting a decrease in parents' feeding activities while raining. This may explain the observed interaction with precipitation.

The association of brood size with survival, on the other hand, was strongly negative during the first sampling year (Fig. 5).

Nonetheless, it was not significant during the second year, when the probability of survival was generally low regardless of brood size. A limiting factor for nestling survival in large broods of altricial birds is reduced nestling growth (Dijkstra *et al.*, 1990; Kalmbach & Becker, 2005; Nicolaus *et al.*, 2009). However, our growth results do not indicate that greater mortality in larger broods was linked to reduced growth in that way. Instead, the opposite was observed (nestlings in larger broods grew faster). It is likely that investing extra effort to satisfy demands of a large brood decreases the probability of nestling survival (Skutch, 1949). There is evidence that parents' activity around the nest attracts predators (Martin, Scott & Menge, 2000a), and that species under greater predatory pressure tend to have smaller brood sizes (Martin *et al.*, 2000b; Sousa & Marini, 2013). Besides parental activity, other factors can affect the risk of predation of larger broods. As predators may use begging calls to locate nests (Leech & Leonard, 1997), higher begging intensities of larger broods could be easier to detect by a predator. Furthermore, predator abundance has clear effects on nest predation (Fontaine *et al.*, 2007). However, our observations on signs of predation were relatively scarce. A possible cause of mortality in the second sampling year was the weather conditions. Storms could have damaged the nests, depriving the chicks of sufficient shelter and rendering survival less likely for both large and small broods. Although for the vast majority of nestlings the cause of death was unknown, we observed a very strong association between brood disappearance and recent storms, together with the finding of destroyed nests and broken branches on the ground. Also, during that year, the number of nests found broken was higher.

In conclusion, our results suggest that the brood size of thornbirds that inhabit central Argentina in part reflects the
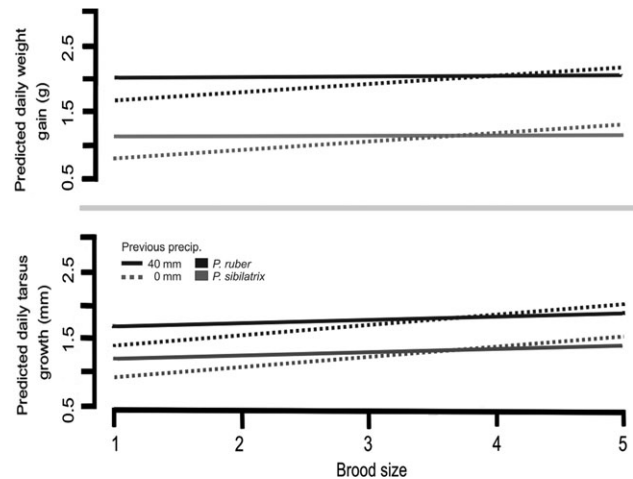
Table 1 Linear mixed models describing factors associated with nestling daily weight gain and tarsus length gain

Term	Coefficients	Std. error	*T*-value	*P*-value	ΔAIC
Model = weight gain ~ mites + brood size × precipitation$_{t-1}$ + nestling species					
Random intercept = nest ID/nestling ID					
n = 945					
Intercept	1.593	0.157	10.189	0.000	–
Mites	−0.583	0.097	−6.020	0.000	33.9
Brood size	0.135	0.045	2.977	0.003	–
Precipitation$_{t-1}$	0.010	0.003	4.134	0.000	–
Species (*P. sibilatrix*)	−0.980	0.078	−12.539	0.000	82.8
Brood size: precipitation$_{t-1}$	−0.003	0.001	−3.129	0.002	7
Model = tarsus length gain ~ brood size × precipitation$_{t-1}$ + nestling species + week + mites					
Random intercept = nest ID/nestling ID					
n = 951					
Intercept	1.398	0.168	8.306	0.000	–
Brood size	0.151	0.046	3.297	0.001	–
Precipitation$_{t-1}$	0.009	0.002	3.666	0.000	–
Species (*P. sibilatrix*)	−0.475	0.088	−5.411	0.000	22.1
Week	−0.012	0.004	−2.541	0.011	3.9
Mites	−0.508	0.088	−5.752	0.000	30.8
Brood size: precipitation$_{t-1}$	−0.002	0.001	−2.765	0.006	5.7

aptitude of the parents to embark on breeding. Parents whose quality and/or condition allowed for rearing many chicks would invest in larger brood sizes, but at the cost of increasing the risk of nestling mortality. The net effect of this differential investment seems to depend on the prevailing environmental conditions. Increasing brood size did not seem to result in a net reproductive benefit in the first sampling year, when conditions were apparently favourable (as suggested by overall survival rates), as nestlings from larger broods were less likely to survive. In the rainy year, the probability of survival was in general much lower, independent of brood size, for which larger broods had more chances of successfully producing at least one fledgling. As parents cannot foresee how favourable the conditions will be during the breeding season, variability in brood size may be advantageous. As it was observed here, there will be circumstances when small brood sizes are favoured, others when large ones are benefited. The origin of such variability could be within-population genetic diversity in brood size, perhaps resulting from fluctuating selection dynamics (Buckling & Rainey, 2002), or it might also result from phenotypic plasticity, as suggested by our findings on growth.

This study showed the natural strategy of two passerine species regarding brood size, and therefore, the effect of natural variability in that trait on the development and survival of nestlings. Since we have one wet year and one dry year, additional years of study would be needed to really understand how rainfall affects survival differences between years, and how this might vary with brood size. Further studies, including

Figure 4 Predicted daily weight gain and daily tarsus growth of nestlings of *P. ruber* and *P. sibilatrix*, according to the final linear mixed model. The figures depict the interaction between both thornbird species, brood size and cumulative precipitation fallen 1 week previously. The continuous line predicts a scenario of high preceding precipitation (40 mm) and the dotted line a scenario of no preceding precipitation.

Table 2 Generalized linear mixed model with a binomial response describing factors associated with nestling survival

Term	Coefficients	Std. error	*P*-value	ΔAIC
Model = success ~ maximum brood size × year + week				
Random intercept = nest ID				
n = 320				
Intercept	4.734	2.421	0.051	–
Maximum brood size	−2.300	0.731	0.002	–
Year 2	−7.718	3.288	0.019	–
Week	0.096	0.043	0.052	2
Maximum brood size: year 2	1.832	1.102	0.096	4
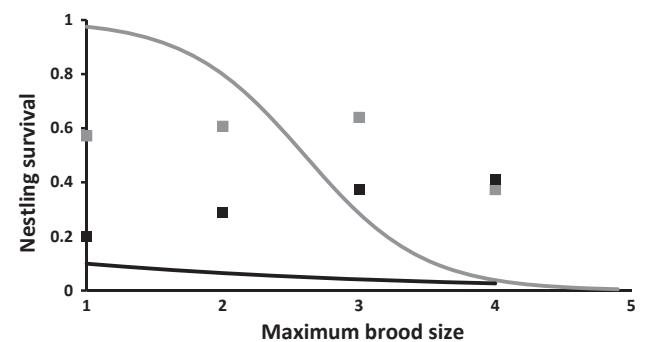
Figure 5 Survival probability (in the next 2–3 days) of *P. ruber* and *P. sibilatrix* nestlings in relation to different brood sizes. The first sampling year is depicted in grey and the second in black. Solid lines indicate the generalized linear mixed model (GLMM) predictions, and the squares, the observed data (notice that the apparent discrepancies result from the data structure, which includes repeated measures of broods and individuals; that lack of independence among observations are taken care of by the GLMM).

measurements of parental care and nest predation, might help to unveil the mechanisms underlying the associations and interactions here described.

Acknowledgements

References

Ahola, M.P., Laaksonen, T., Eeva, T. & Lehikoinen, E. (2009). Great tits lay increasingly smaller clutches than selected for: a study of climate- and density-related changes in reproductive traits. *J. Anim. Ecol.* **78**, 1298–1306.

Akaike, H. (1974). A new look at the statistical model identification. *IEEE Trans. Autom. Contr.* **19**, 716–723.

Alderete, C. & Capllonch, P. (2010). Pesos de aves Suboscines de Argentina. *Nótulas Faunísticas.* **58**, 1–5.

Antoniazzi, L., Manzoli, D., Rohrmann, D., Saravia, M.J., Silvestri, L. & Beldomenico, P. (2011). Climate variability affects the impact of parasitic flies on Argentinean forest birds. *J. Zool. (Lond.)* **283**, 126–134.

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

Auer, S.K., Bassar, R.D., Fontaine, J.J. & Martin, T.E. (2007). Breeding biology of some Passerines in a subtropical montane forest in north western Argentina. *Condor* **109**, 321–333.

Aukema, B.H., Clayton, M.K. & Raffa, K.F. (2005). Modeling flight activity and population dynamics of the pine engraver, *Ips pini*, in the Great Lakes region: effects of weather and predators over short time scales. *Popul. Ecol.* **47**, 61–69.

Bates, D.M. & Bolker, B. (2011). lme4: linear mixed-effects models using S4 classes. (R package version 0.999375-38).

Buckling, A. & Rainey, P.B. (2002). Antagonistic coevolution between a bacterium and a bacteriophage. *Proc. R. Soc. B* **269**, 931–936.

Cooper, C.B., Hochachka, W.M., Butcher, G. & Dhondt, A.A. (2005). Seasonal and latitudinal trends in clutch size: thermal constraints during laying and incubation. *Ecology* **86**, 2018–2031.

Del Hoyo, J., Elliot, A. & Christie, D. (2003). *Handbook of the birds of the world. Volume 8: broadbills to tapaculos*. Barcelona: Lynx.

Dijkstra, C., Bult, A., Bijlsms, S., Daan, S., Meijer, T. & Zijlstra, M. (1990). Brood size manipulations in the kestrel (*Falco tinnunculus*): effects on offspring and parent survival. *J. Anim. Ecol.* **59**, 269–285.

Drent, R.H. & Daan, S. (1980). The prudent parent: energetic adjustments in avian breeding. *Ardea* **68**, 225–52.

Fargallo, J.A. (2004). Latitudinal trends of reproductive traits in the blue tit *Parus caeruleus*. *Ardeola* **51**, 177–190.

Fessl, B. & Tebbich, S. (2002). *Philornis downsi* – a recently discovered parasite on the Galápagos archipelago: a threat for Darwin's finches? *The Ibis* **144**, 445–451.

Fontaine, J.J., Martel, M., Markland, H.M., Niklison, A.M., Decker, K.L. & Martin, T.E. (2007). Testing ecological and behavioral correlates of nest predation. *Oikos* **116**, 1887–1894.

Hõrak, P. (2003). When to pay the cost of reproduction? A brood size manipulation experiment in great tits (*Parus major*). *Behav. Ecol. Sociobiol.* **54**, 105–112.

Kalmbach, E. & Becker, P.H. (2005). Growth and survival of neotropic cormorant (*Phalacrocorax brasilianus*) chicks in relation to hatching order and brood size. *J. Ornithol.* **146**, 91–98.

Kasper, M.L., Reeson, A.F., Mackay, D.A. & Austin, A.D. (2008). Environmental factors influencing daily foraging activity of *Vespula germanica* (Hymenoptera, Vespidae) in Mediterranean Australia. *Insectes Soc.* **55**, 288–295.

Laaksonen, T., Ahola, M., Eeva, T., Väisänen, R.A. & Lehikoinen, E. (2006). Climate change, migratory connectivity and changes in laying date and clutch size of the pied flycatcher. *Oikos* **114**, 277–290.

Lack, D. (1947). The significance of clutch size in birds. Parts I and II. *The Ibis* **89**, 302–352.

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

Leech, S.M. & Leonard, M.L. (1997). Begging and the risk of predation in nestling birds. *Behav. Ecol.* **8**, 644–646.

Martin, T.E. & Briskie, J.V. (2009). Predation on dependent offspring: a review of the consequences for mean expression and phenotypic plasticity in avian life history traits. *Ann. N. Y. Acad. Sci.* **1168**, 201–217.

Martin, T.E., Scott, J. & Menge, C. (2000a). Nest predation increases with biparental activity: separating nest site and parental activity effects. *Proc. R. Soc. B* **267**, 2287–2293.

Martin, T.E., Martin, P.R., Olson, C.R., Heidinger, B.J. & Fontaine, J.J. (2000b). Parental care and clutch sizes in North and South American Birds. *Science* **287**, 1482–1485.

Moreno, J., Merino, S., Vásquez, R.A. & Armesto, J.J. (2005). Breeding biology of the thorn-tailed rayadito (Furnariidae) in south-temperate rainforests of Chile. *Condor* **107**, 69–77.

Moser, J.C. & Dell, T.R. (1980). Weather factors predicting flying population of a clerid predator and its prey, the Southern pine beetle. In *Proceedings of the 2nd IUFRO conference on dispersal of forest insects: evaluation, theory and management implication*: 266–278. Berryman, A.A. & Safranyik, L. (Eds). Pullman: Washington State University.

Murphy, M.T., Armbrecth, B., Vlamis, E. & Pierce, A. (2000). Is reproduction by tree swallows cost free? *Auk* **117**, 902–912.

Neuenschwander, S., Brinkhof, M.W.G., Kölliker, M. & Richner, H. (2003). Brood size, sibling competition, and the cost of begging in great tits (*Parus major*). *Behav. Ecol.* **14**, 457–462.

Nicolaus, M., Michler, S.P.M., Ubels, R., Van der Velde, M., Komdeur, J., Both, C. & Tinbergen, J.M. (2009). Sex-specific effects of altered competition on nestling growth and survival: an experimental manipulation of brood size and sex ratio. *J. Anim. Ecol.* **78**, 414–426.

Nur, N. (1984). The consequences of brood size for breeding blue tits II. Nestling weight, offspring survival and optimal brood size. *J. Anim. Ecol.* **53**, 497–517.

Olson, J.M. (1992). Growth, the development of endothermy, and the allocation of energy in red-winged blackbirds (*Agelaius phoeniceus*) during the nestling period. *Physiol. Zool.* **65**, 124–152.

O'Neal, D.M. & Ketterson, E.D. (2012). Life – history evolution, hormones, and avian immune function. In *Ecoimmunology*: 7–44. Demas, G.E. & Nelson, R.J. (Eds). New York: Oxford University Press.

de la Peña, M.R. (1996). *Ciclo reproductivo de las aves Argentinas*. Segunda parte. Buenos Aires: L.O.L.A.

de la Peña, M.R. (2005a). *Reproducción de las aves argentinas*. Buenos Aires: L.O.L.A.

de la Peña, M.R. (2005b). *Las aves de la reserva de Esperanza (Santa Fe)*. Santa Fe: Univ. Nacional del Litoral.

de laPeña, M.R., Antoniazzi, L. & Gamboa, E. (2007). Guía de aves de la Provincia de Santa Fe. Consejo Federal de Inversiones, Subsecretaría de Turismo de la provincia de Santa Fe, Fundación Hábitat and Desarrollo.

Pettifor, R. (1988). Individual optimization of clutch size in great tit. *Nature* **336**, 160–162.

Pichorim, M. (2011). The influence of clutch and brood sizes on nesting success of the biscutate swift, *Streptoprocne biscutata* (Aves: Apodidae). *Zoologia (Curitiba)* **28**, 186–192.

Postma, E. &Van Noordwijk, A.J. (2005). Gene flow maintains a large genetic difference in clutch size at a small spatial scale. *Nature* **433**, 65–68.

Poulsen, B.O. (1996). Relationships between frequency of mixed-species flocks, weather and insect activity in a montane cloud forest in Ecuador. *The Ibis* **138**, 466–470.

Radford, A.N., McCleery, R.H., Woodburn, R.J.W. & Morecroft, M.D. (2010). Activity patterns of parent great tits *Parus major* feeding their young during rainfall. *Bird Study* **48**, 214–220.

Richner, H. & Heeb, P. (1995). Are clutch size and brood size patterns in birds shaped by ectoparasites? *Oikos* **73**, 435–441.

Ricklefs, R.E. (1976). Growth rates of birds in the humid New World tropics. *The Ibis* **118**, 179–207.

Royama, T. (1966). Factors governing feeding rate, food requirement and brood size of nestling great tits *Parus major*. *The Ibis* **108**, 313–347.

Rubolini, D. & Fasola, M. (2008). Geographic patterns in reproductive parameters among nearctic herons (Ardeidae). *Auk* **125**, 374–383.

Russell, E.M., Yom-Tov, Y. & Geffen, E. (2004). Extended parental care and delayed dispersal: northern, tropical, and southern passerines compared. *Behav. Ecol.* **15**, 831–838.

Sheldon, B.C., Kruuk, L.E.B. & Merilä, J. (2003). Natural selection and inheritance of breeding time and clutch size in the collared flycatcher. *Evolution* **57**, 406–420.

Shutler, D., Clark, R.G., Fehr, C. & Diamond, A.W. (2006). Time and recruitment costs as currencies in manipulation studies on the costs of reproduction. *Ecology* **87**, 2938–2946.

Skutch, A.F. (1949). Do tropical birds rear as many young as they can nourish? *The Ibis* **91**, 430–455.

Sofaer, H.R., Sillett, T.S., Peluc, S.I., Morrison, S.A. & Ghalambor, C.K. (2013). Differential effects of food availability and nest predation risk on avian reproductive strategies. *Behav. Ecol.* **24**, 698–707.

Sokolov, L.V. (2006). Effect of global warming on the timing of migration and breeding of passerine birds in the 20th century. *Entomol. Rev.* **86**, S59–S81.

Sousa, N.O.M. & Marini, M.Â. (2013). A negative trade-off between current reproductive effort and reproductive success: an experiment with clutch-size in a tropical bird. *Emu* **113**, 8–18.

Spear, L. & Nur, N. (1994). Brood size, hatching order and hatching date: effects on four life-history stages from hatching to recruitment in western gulls. *J. Anim. Ecol.* **53**, 283–298.

Styrsky, J.N., Brawn, J.D. & Robinson, S.K. (2005). Juvenile mortality increases with clutch size in a neotropical bird. *Ecology* **86**, 3238–3244.

Sullivan, K.A. & Weathers, W.W. (1992). Brood size and the thermal environment influence field metabolism of nestling yellow-eyed juncos. *Auk* **109**, 112–118.

Tarof, S.A., Kramer, P.M., Hill, J.R. III, Tautin, J. & Stutchbury, B.J.M. (2011). Brood size and late breeding are negatively related to juvenile survival in a neotropical migratory songbird. *Auk* **128**, 716–725.

VanderWerf, E. (1992). Lack's clutch size hypothesis: an explanation of the evidence using meta-analysis. *Ecology* **73**, 1699–1705.

Wright, J., Hinde, C., Fazey, I. & Both, C. (2002). Begging signals more than just short-term need: cryptic effects of brood size in the pied flycatcher (*Ficedula hypoleuca*). *Behav. Ecol. Sociobiol.* **52**, 74–83.

Yom-Tov, Y., Christie, M.I. & Iglesias, G.I. (1994). Clutch size in Passerines of southern South America. *Condor* **96**, 170–177.

Young, B.E. (1996). An experimental analysis of small clutch size in tropical house wrens. *Ecology* **77**, 472–488.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Description of the potential confounders and relevant two-way interactions included in the analysis for LMM and GLMM models.