



Latitudinal variation in avian incubation attentiveness and a test of the food limitation hypothesis

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Avian incubation attentiveness has important fitness consequences through its influence on the number and quality of hatched young and energetic costs imposed on parents. Nest attentiveness is highly variable across species and geographical regions. We reviewed the literature and found a worldwide pattern that nest attentiveness of passerines is generally lower in south temperate and tropical regions than in north temperate regions. We also conducted a food manipulation experiment to assess the extent to which nest attentiveness may reflect proximate responses versus an evolved behaviour. We used the karoo prinia, *Prinia maculosa*, in South Africa, which has very low nest attentiveness (~49%) compared with that of many passerine birds. We provided supplemental food during early incubation to experimental females and compared nest attentiveness and on- and off-bout lengths of experimental and paired control females. Nest attentiveness of females at food-provisioned nests was significantly higher than that of control females (57% versus 49%). Food-supplemented females also spent significantly less time off the nest than did control females, whereas mean on-bout lengths did not differ. However, mean nest attentiveness of food-provisioned females was still substantially below that of other similar bird species worldwide. Food can be an important proximate influence on parental care behaviour, but proximate influences of food do not explain broad latitudinal patterns of attentiveness.

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Parental care can greatly influence reproductive success and the quantity and quality of reared young (Clutton-Brock 1991). Yet, parents inevitably face trade-offs in terms of how much energy to allocate to their developing young versus their own condition and longevity (Martin 1987; Clutton-Brock 1991; Martin 2002; Royle et al. 2004). Species differ in their parental care strategies for resolving these trade-offs (Clutton-Brock 1991; Martin et al. 2000), but the causes underlying this variation remain poorly understood.

Parental care strategies include a number of behavioural components, and one that has important fitness consequences for birds is nest attentiveness (the percentage of time that parents spend on the nest during incubation). Nest attentiveness affects egg temperatures (White &

Kinney 1974; Haftorn 1988), which influence the length of the incubation period (Price 1998; Martin 2002; Hepp et al. 2006; T. E. Martin, S. K. Auer, R. D. Bassar, A. M. Niklison & P. Lloyd, unpublished data), and thereby the extent to which young and attending parents are exposed to time-dependent mortality from nest predators (Magrath 1988; Martin 2002). Consequently, selection should favour increased attentiveness in high-predation environments in order to minimize the incubation period (Bosque & Bosque 1995; Fontaine & Martin 2006). Even within environments with high nest predation risk, however, birds display extensive interspecific variation in nest attentiveness (Martin 2002; Martin et al., unpublished data), indicating that nest predation cannot account for substantial interspecific variation. Potential causes underlying variation in nest attentiveness, therefore, remain a critical question in need of study.

Avian nest attentiveness appears to vary geographically even within a single order such as Passeriformes (Martin

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2002). Nest attentiveness of passerine species at a north temperate study site (Arizona, U.S.A.) was higher than that of phylogenetically matched pairs at a site in the southern hemisphere (Argentina; Martin 2002), and Martin (2002) argued that this was a general geographical pattern. Yet, this two-site comparison leaves open the possibility that differences simply reflect site effects rather than a generalizable geographical pattern. Thus, we reviewed the literature to assess the ubiquity of this pattern for tropical and south temperate species across the world, and examined the possible role of food in geographical patterns.

Food is not the only potential influence on geographical variation in nest attentiveness. Warmer ambient temperatures can allow lower nest attentiveness (White & Kinney 1974; Haftorn 1988; Conway & Martin 2000a), although temperatures in many south temperate locations do not differ from those of north temperate locations during the breeding season (Martin et al. 2006). Also, larger eggs can cause slower egg-cooling rates and allow longer off-bouts, but eggs are smaller in south temperate South Africa, for example, than in north temperate Arizona sites (Martin et al. 2006). Thus, neither climate nor egg size predicts consistently lower attentiveness in tropical and south temperate regions.

If food is a limiting factor in the tropics and southern regions, as has been suggested (Ashmole 1963; Cody 1966; Owen 1977; Thiollay 1988), then it may influence geographical patterns of attentiveness. Broad theory and evidence suggests that food can be an important proximate influence on nest attentiveness via its effect on energy budgets (Martin 1987; Nilsson & Smith 1988; Smith et al. 1989; Sanz 1996; Eikenaar et al. 2003; Pearse et al. 2004). Energetic expenditures during incubation are considerable, and can influence future prospects of parents (Thomson et al. 1998; Visser & Lessells 2001; Tinbergen & Williams 2002). Nest attentiveness reflects on-bouts to keep eggs warm and temporary off-bouts to forage as parents try to balance their own energetic requirements with the needs of their developing embryos (White & Kinney 1974; Conway & Martin 2000b; Deeming 2002; Martin 2002). If food availability is more limited in southern areas, then lower attentiveness in these regions could simply reflect proximate responses to greater food limitation. Of course, differences in nest attentiveness between regions can reflect evolved rather than proximate responses, but we do not know the extent to which attentiveness is an evolved

behaviour. The first step is to determine the degree to which differences between latitudes reflect proximate responses by conducting food manipulation experiments.

Experimental tests of food limits on attentiveness have not considered latitudinal patterns. Indeed, our literature survey revealed that four of six species tested were north temperate species (Table 1). Moreover, four of six species were cavity nesters. Cavity-nesting species engage in nest guarding, where they sit inside the nest at or near the opening, but not necessarily on the eggs, in order to protect the cavity from usurpers (e.g. Rendell & Robertson 1991). Therefore, presence in the nest in response to food does not clearly reflect incubation attentiveness in cavity nesters. Finally, all but one of the studies was on species with relatively high nest attentiveness (Table 1), which does not address the question of whether food limitation can explain the behaviour of species with low nest attentiveness. Thus, experimental studies are needed on non-cavity-nesting, southern species with low nest attentiveness.

We studied the karoo prinia, *Prinia maculosa* (Cisticolidae) in South Africa because it is a good example of a southern species with low nest attentiveness. The karoo prinia is a southern hemisphere warbler that builds its own nest and has low mean incubation attentiveness (49.5%, Martin et al., unpublished data) compared to other passerine species worldwide (Conway & Martin 2000b; Deeming 2002; Martin 2002). Karoo prinias, like all species at this site, experience extremely high rates of nest predation (Martin et al. 2006) and, therefore, should be under selection to increase nest attentiveness to reduce the length of the incubation period (see above). Moreover, temperature during the breeding season is similar to that experienced by breeding birds at a long-term site in Arizona, North America (Martin et al. 2006), and nest attentiveness at the latter site is greater than 70% in all species (Martin & Ghaleb 1999), thereby eliminating temperature as a cause of the low nest attentiveness. Finally, egg size of prinias is relatively small for their body size compared with similar species in Arizona (Martin et al. 2006), which should favour higher rather than lower nest attentiveness. We therefore explored the hypothesis that the low nest attentiveness of prinias reflects a proximate response to limited food availability. Specifically, we predicted that females given supplemental food would increase nest attentiveness to levels seen among similar species in the north.

Table 1. Summary of results from studies examining the effect of supplemental food on passerine nest attentiveness (%)

Species	Lat.*	Control (%)	Food (%)	Change (%)	Significant	Nest type	Source
Pied flycatcher, <i>Ficedula hypoleuca</i>	N	70	82	12	Y	Cavity	Smith et al. 1989
Bewick's wren, <i>Thryomanes bewickii</i>	N	70	82	12	Y	Cavity	Pearse et al. 2004
House wren, <i>Troglodytes aedon</i>	N	71	81	10	Y	Cavity	Pearse et al. 2004
Wheatear, <i>Oenanthe oenanthe</i>	N	78	86	8	N	Cavity	Moreno 1989
Australian reed warbler, <i>Acrocephalus australis</i>	S	51	57	6	Y	Enclosed	Eikenaar et al. 2003
Karoo prinia, <i>Prinia maculosa</i>	S	49	57	8	Y	Enclosed	This study
South Island robin, <i>Petroica australis</i>	S	79	80	1	N	Open cup	Mackintosh & Briskie 2005

*Latitude: N = north temperate; S = south temperate.

METHODS

Summary of Nest Attentiveness Across Latitudes

To assess the generality of latitudinal variation in nest attentiveness, we reviewed the literature for published estimates of nest attentiveness of passerine birds around the world. We limited our review to species with female-only incubation so as not to confound the issue with number of incubating parents. We categorized species into three latitude classes: 'northern' for those breeding in north temperate latitudes; 'tropical' for those breeding between 23.5°N (Tropic of Cancer) and 23.5°S (Tropic of Capricorn); 'southern' for those breeding at latitudes equal to or greater than 23.5°S. All attentiveness estimates were obtained from visual observations (either direct or by video recordings). If more than one source provided an estimate of nest attentiveness for the same species, we averaged estimates. We first tested for differences between the three latitude classes while controlling for phylogeny by using data from avian families that were represented across latitude classes. We used ANOVA with latitude class and avian family as fixed factors, and a Tukey post hoc test of pairwise differences between the three latitudes. In this case, species represent the error variance term within families and average values for families are compared among latitude classes (see Fig. 1).

We conducted a separate analysis for families endemic to one of the latitude classes or for which we had estimates from only one latitude class. For the raw data, we used ANOVA to simply test differences between the

three latitude classes, with a Tukey post hoc test of pairwise differences. We then conducted an analysis to correct for possible phylogenetic effects using independent contrasts (Felsenstein 1985) calculated through the CRUNCH option of program CAIC (Purvis & Rambaut 1995). We used a regression approach to ANOVA, where latitude class was represented as two (i.e. $n - 1$) dummy variables that were phylogenetically transformed and their cumulate change in sums of squares was used to test the effect of latitude class (Grafen 1989, 1992; Martins 1993; Martin 1995). The phylogeny was taken from Sibley & Ahlquist (1990).

Food Supplementation Experiment

We studied nest attentiveness of the karoo prinia and other birds during the breeding season from mid-August to early November 2000–2004 (Martin et al. 2006). We conducted our food manipulation experiment during September to early November 2004 at the Koeberg Nature Reserve (33°41'S, 18°27'E) in the Western Cape Province of South Africa. The region has a Mediterranean climate, consisting of warm, dry summers (10–38°C) and cool, wet winters (2–25°C). The reserve consists of a mosaic of strandveld succulent karoo, dune thicket and sand plain fynbos vegetation types (Nalwanga et al. 2004a). The karoo prinia is a small (9 g), territorial warbler and a common resident at this site. Nests are enclosed and dome-shaped; built off the ground in restio plants (Restionaceae) and various shrub species (Nalwanga et al. 2004b). Only females incubate the eggs, and mate feeding in this

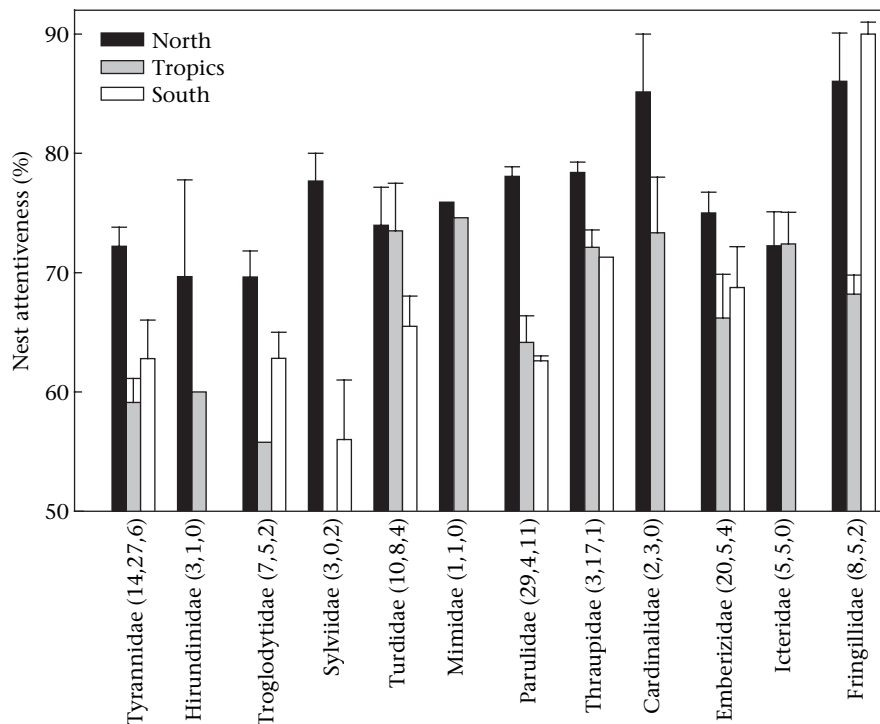


Figure 1. Paired family means (\pm SE) of nest attentiveness (% time spent on the nest) for passerine species with female-only incubation in north temperate, tropical and south temperate latitudes. Species sample sizes are indicated after the family names. Data were obtained from the literature (see Supplementary Material, Table S1).

species is minimal. Females must leave the nest intermittently to forage and meet nutritional requirements.

Prinia nests were located by observing parental behaviour during the nest-building stage (e.g. the male or female carrying nest material). We controlled for any potential confounding effects of clutch size (Thomson et al. 1998; Reid et al. 2002; Tinbergen & Williams 2002) by pairing nests of the same clutch size in 7 of 10 cases and only using nests containing the modal number of eggs (3 or 4). Moreover, because ambient temperature may influence incubation rhythms (White & Kinney 1974; Conway & Martin 2000a; Deeming 2002), we paired nests by initiation date and collected data on experimental and control nests simultaneously on the same days. For each pair of nests, we randomly assigned one to the experimental treatment and one as the control. We performed the experiment during early incubation (2 or 3 days after clutch completion) for all birds to control for possible stage effects (e.g. Deeming 2002).

Experimental nests received a small, clear plastic cup with mealworms (larvae of *Tenebrio molitor*) just below the nest entrance and within 10 cm of the nest. Initial feeding trials were conducted to determine how many mealworms the birds were willing to consume during an 8-h experimental observational period. As a result, approximately 60 mealworms (5–6 g) were placed in each cup. The average daily energy requirement for birds of similar body size to the karoo prinia is 45 kJ/day (Williams 1993). Mealworms have an energy content of 11.6 kJ/g and a minimum assimilation efficiency of 0.71 in birds (Bell 1990), so we provided females with 92–110% of their daily energetic requirements, a major energetic augmentation. Control nests received an empty cup in the same location. We placed the plastic cup with an equal number of mealworms near the nest for 6–8 h on the day prior to the actual experimental trial to ensure that experimental females: (1) were accustomed to the presence of the cup, (2) learned to take the novel food and (3) had augmented energy intake prior to measuring incubation responses. Approximately 75% of females rapidly learned to utilize the additional food. Females that did not consume at least half of the mealworms provided during the pre-experimental period were not used in actual experiments. Control nests were similarly primed, but with an empty cup.

On the day we measured responses, food containers were placed at nests within 0.5 h of sunrise. Data on nest attentiveness for experimental and control nests were collected by videotaping nests for 6–8 h beginning when the cups were in place. We calculated three parameters from the videos: mean incubation on-bout length, mean off-bout length, and overall percentage of attentiveness. Mean bout lengths were calculated by averaging all of the complete on-bouts and off-bouts observed during an entire filming. Attentiveness was calculated as the total percentage of time that the female spent on the nest incubating during the 6–8 h following Martin (2002). Mean bout lengths and percentage attentiveness for experimental versus control nests were compared using paired *t* tests. We arcsine-transformed attentiveness data for analysis, but present raw data for greater ease of interpretation. Bout length data were not transformed prior to analyses

because they were approximately normally distributed, and results of Levene tests (Dytham 2003) were nonsignificant, indicating homogeneity of variances.

RESULTS

Summary of Nest Attentiveness Across Latitudes

In comparisons of families represented across latitude classes, passerine nest attentiveness differed across latitudes ($F_{2,217} = 15.7$, $P < 0.001$) albeit to differing extents across families (family: $F_{11,217} = 5.3$, $P < 0.001$; family \times latitude: $F_{17,217} = 1.9$, $P = 0.02$; Fig. 1). Nest attentiveness was consistently higher in the north than it was for related species in tropical (Tukey: $P < 0.001$) or southern (Tukey: $P < 0.001$) latitudes, whereas attentiveness did not differ between tropical and southern latitudes (Tukey: $P = 0.97$).

In comparisons of families represented in a single latitude class (Fig. 2), we also found that attentiveness differed across latitudes ($F_{2,24} = 21.7$, $P < 0.001$), including when corrected for possible phylogenetic effects using independent contrasts ($F_{2,24} = 8.4$, $P = 0.002$). Northern taxa again had higher attentiveness than taxa in tropical

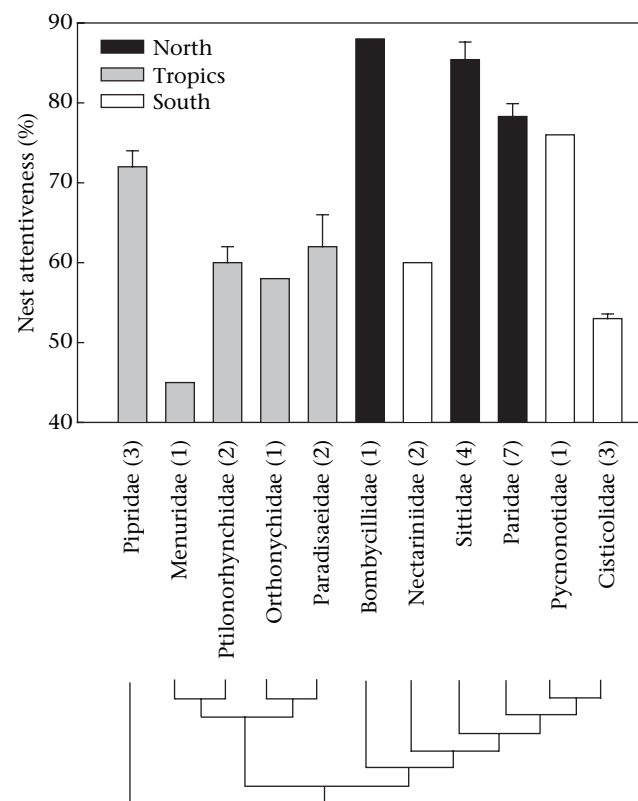


Figure 2. Mean \pm SE nest attentiveness of passerine families found primarily or exclusively in either northern, tropical or southern latitudes. Species sample sizes are indicated after the family names. Data were obtained from the literature (see Supplementary Material, Table S1), and phylogenetic relationships follow Sibley & Ahlquist (1990).

(Tukey: $P < 0.001$) or southern (Tukey: $P < 0.001$) latitudes, while attentiveness of taxa in tropical and southern latitudes did not differ (Tukey: $P = 0.89$).

Food Supplementation Experiment

We observed 20 karoo prinia nests (10 food-supplemented and 10 control). Incubation attentiveness was significantly higher in experimental nests than in control nests ($t_9 = 2.31$, $P < 0.05$; Fig. 3). On average, nest attentiveness of experimental females was 8% higher than that of paired controls. Attentiveness varied among individual females, however, ranging from 24 to 60% in controls and 40 to 74% in experimental females.

The difference in nest attentiveness between treatments was caused by a disparity in the amount of time that females spent off the nest. Mean off-bout length was significantly shorter at experimental nests ($t_9 = -3.34$, $P < 0.01$), whereas mean on-bout length was virtually identical between treatments ($t_9 = 0.18$, $P = 0.86$; Fig. 3).

DISCUSSION

Our review revealed a broad geographical pattern in an important avian breeding behaviour, as argued by Martin (2002). Passerine incubation attentiveness in tropical and south temperate species was similar and consistently lower than that for northern counterparts (Figs 1, 2). This previously unrecognized broad geographical pattern thereby raises the question of the extent to which it reflects phenotypic plasticity and proximate responses versus evolved behaviour patterns.

Food limitation is one of the most likely possibilities for proximate responses. Our food supplementation experiment yielded an increase in nest attentiveness in a southern species with low attentiveness. Moreover, attentiveness was variable among individual prinias and as high as 74% in one experimental female. Our results therefore corroborate the long-standing view that food can have important proximate effects on parental behaviours (Lack 1954, 1968; Martin 1987). Previous experimental studies of seven other bird species found that supplemental food also increased attentiveness in five species, and had no effect in two (Table 1), indicating that proximate responses to food is a common phenomenon.

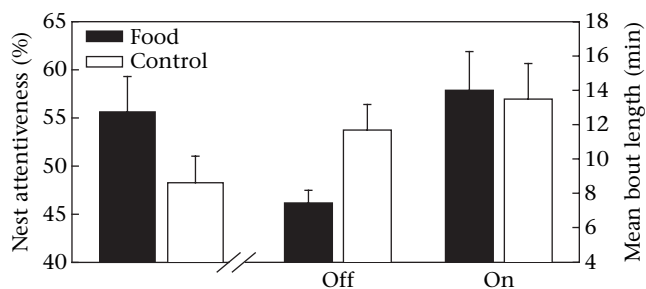


Figure 3. Mean \pm SE nest attentiveness (left) and on-bout and off-bout lengths (right) during early incubation for food-supplemented versus control nests of the karoo prinia, *Prinia maculosa* ($N = 10$ matched pairs) in South Africa during September–November.

However, responses were limited; mean \pm SE nest attentiveness for prinia females given access to unlimited food ($57 \pm 3.5\%$) remained very low relative to that of female-only incubators in North America (e.g. 75%, $N = 95$ species; Conway & Martin 2000b). We were unable to locate published estimates of nest attentiveness for north temperate members of the family Cisticolidae for comparison. However, prinias belong to the superfamily Sylvioidea (Sibley & Ahlquist 1990), and mean \pm nest attentiveness for 22 species of north temperate members of Sylvioidea averaged $74.8 \pm 9.1\%$. This attentiveness of northern relatives was nearly identical to the large sample of North American species (see above), but it was well outside the range for food-supplemented prinias in this study (one-sample t test: $t_1 = 7.40$, $P = 0.04$). The Australian reed warbler, *Acrocephalus australis*, another southern hemisphere songbird with similarly low nest attentiveness (51%; Eikenaar et al. 2003), showed the identical pattern; attentiveness increased with supplemental food, but still remained quite low (57%) compared with north temperate relatives (see above). These results suggest that proximate responses to food availability cannot explain the broad geographical differences in nest attentiveness.

The limited increase in nest attentiveness, together with the phylogenetic patterns (Figs 1, 2), suggest that latitudinal differences in attentiveness reflect evolved strategies. During our food supplementation experiment, we observed females loafing and preening at the food cup, indicating that the birds had free time that could have been allocated to nest attentiveness but was not. Similarly, after nearly a century of being introduced to a novel, food-rich environment (Vancouver, British Columbia) and where nest attentiveness is under strong selection because of effects on hatching success, the subtropical crested mynah, *Sturnus cristatellus*, still shows very low (47%) nest attentiveness, typical of southern species (Johnson & Cowan 1974). The results of our study and others, therefore, suggest that nest attentiveness in general, and latitudinal patterns in particular, are evolved and cannot be obfuscated by proximate responses to food limitation (Fig. 4). Similarly, in a comparative analysis across passerine species, Conway & Martin (2000b) found no effect of two potential correlates of food limitation (diet and foraging strategy) on nest attentiveness.

In conclusion, food may be an important proximate factor affecting the extent of parental care in birds but only within limits. Food limitation alone cannot explain large-scale, across-species geographical variation in parental care strategies, and alternative explanations for this pattern require further examination. Latitudinal variation in attentiveness is unlikely to be driven by variation in nest predation risk selecting for shorter developmental periods, because nest predation is variable both within and across latitudes and with no clear north–south gradient (Martin 1996, 2002; Martin et al. 2000). Moreover, many southern species experience very high rates of nest predation, yet maintain relatively low nest attentiveness. Climatic variation across latitudes may influence the amount of time that parents spend on the nest, although temperatures at many south temperate sites often approximate those at north temperate sites during the breeding season

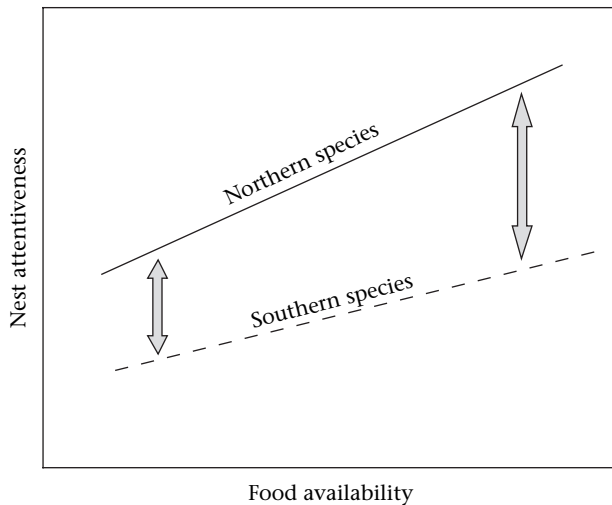


Figure 4. Hypothesized relationship of food availability and avian nest attentiveness across species and latitudes. Both northern and southern species are expected to show proximate increases in attentiveness in response to increased food availability, and preliminary data (Table 1) further suggest that northern species show slightly stronger responses. Proximate responses to food availability alone, however, cannot explain why southern species generally show lower nest attentiveness than similar northern species (grey arrows).

(Martin et al. 2006). One possible alternative explanation for geographical patterns in nest attentiveness is variation in adult mortality across latitudes (Martin 2002). According to classic life history theory (e.g. Roff 1992), if southern birds experience lower adult mortality, they should be less willing to invest as much in nest attentiveness and other components of current reproduction. Testing for the existence of an adult mortality–nest attentiveness trade-off across latitudes is therefore a critical next step in addressing geographical variation in parental care strategies.

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Supplementary Material

Supplementary material for this article can be found, in the online version, at [doi:10.1016/j.anbehav.2006.09.010](https://doi.org/10.1016/j.anbehav.2006.09.010).

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