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fects on the acquisition of social knowledge and that the possession of enhanced discriminatory abilities by the oldest individual in a group of advanced social mammals can influence the social knowledge of the group as a whole. These findings have important implications for conservation as well as evolutionary biology. Tusk size in elephants is related to age, and hunters focus their efforts on individuals that have large tusks (21). In view of our results, it is clear that the removal of matriarchs from elephant family units could have serious consequences for the conservation of this endangered species. Indeed, in many mammal societies, the oldest individuals are also the largest, and these tend to be particular targets of hunters (22) and poachers. If groups rely on older members for their store of social knowledge, then whole populations may be affected by the removal of a few key individuals.

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8. Families were considered to encounter another family during the year if they were sighted at least once within the same group. We calculated the number of families encountered per year by each of the 21 families of subjects that were part of the current study for the years of the study (from January 1993 to December 1999). On this basis, the mean number of families encountered per year was 24.8, with a standard error of 1.35.
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11. Contact calls recorded from a total of 20 adult females, all known individuals in the study population, were used as playback stimuli. All recordings were made on digital audio tape using equipment specialized for low-frequency recording: a Sennheiser MKH 110 microphone linked to a Sony TCD D10 DAT recorder (with DC modification) or a HHb PortaDAT PDR 1000 DAT recorder. The system for playback was composed of a custom-built 6th-order bass box loudspeaker (Aylestone, Cambridge, UK) with two sound ports linked to a power amplifier [a Kenwood KAC-PS400M or amplifiers described in (9)], which had a lower frequency limit of 10 Hz and a response that was flat  $\pm$  4 dB from  $\sim$ 15 Hz on one sound port and  $\sim$ 20 Hz on the other. Each of 21 families of subjects received playbacks of contact calls from a mean of 8 different callers (range: 4 to 11), none of which were members of their own family unit or bond group. Calls were only played if the subjects were

- within their home range and had no calves of less than 1 month. Playbacks to the same family unit were always separated by at least 7 days, and playbacks of callers of different association indices with the subjects were given in random order. In each playback, a single contact call was played at peak sound pressure levels of 105 dB at 1 m (corresponding to the natural volume of a medium loud contact call) from a Landrover vehicle that was located 100 m from the subjects. The vehicle was positioned at right angles to the direct line of sight to the elephants, and vocalizations were played through the rear door. Responses to playbacks were observed through binoculars and recorded on videotape. Out of a range of behaviors monitored during playback experiments, two key behaviors were used to classify subjects' reactions in this study: (i) Bunching: scored as occurring if subjects bunched together into defensive formation so that the diameter (estimated in terms of elephant body lengths) of the whole group, or of constituent subgroups, decreased. (ii) Smelling: scored as occurring when any of the subjects used the tip of their trunk to smell, in lowered, mid-, or raised positions.
12. Data on the ranging and association patterns of female study animals were obtained from regular monitoring of elephant family units. Association indices were calculated for the period from January 1993 to December 1999 as  $NAB/(NA + NB + NAB)$ , where NAB = number of times families A and B are sighted in association in the same group; NA = number of times family A is sighted without B; and NB = number of times family B is sighted without A. This "same-group" measure of association is more restrictive than that used in our previous study (9). The association indices for the 21 families in our study were based on a total of 6685 sightings of these families.
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23. We thank the Biotechnology and Biological Sciences Research Council for providing the major funding for this work (grant no. 85/S07659 to K.M.). Additional financial support or equipment came from the African Wildlife Foundation; the Association for the Study of Animal Behaviour; Newnham College (Cambridge); the Natural Environment Research Council; the Nuffield Foundation; the Royal Society; the Tusk Trust; the University of Sussex; and the Institute of Zoology. We are grateful to the Kenyan Office of the President and to Kenya Wildlife Services for permission to conduct the work in Amboseli National Park; to the African Wildlife Foundation and P. B. Allen for logistical support; to K. Sayialel and N. Njiriana for assistance with fieldwork; and to P. Harvey, G. Mace, and D. Reby for comments on the manuscript.

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## Fecundity-Survival Trade-Offs and Parental Risk-Taking in Birds

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Life history theory predicts that parents should value their own survival over that of their offspring in species with a higher probability of adult survival and fewer offspring. We report that Southern Hemisphere birds have higher adult survival and smaller clutch sizes than Northern Hemisphere birds. We subsequently manipulated predation risk to adults versus offspring in 10 species that were paired between North and South America on the basis of phylogeny and ecology. As predicted, southern parents responded more strongly to reduce mortality risk to themselves even at a cost to their offspring, whereas northern parents responded more strongly to reduce risk to their offspring even at greater risk to themselves.

Should parents place themselves, or their offspring, at greater risk of mortality when threatened with predation? Theoretical models of life history evolution predict that the resolution to this dilemma will vary among species depending on offspring number and the probability of survival for the parents (1–5). Parents should tolerate greater risk to

themselves, but not their young, in species with many offspring and reduced adult survival because the fitness value of the current brood is high and the probability of surviving to breed in the future is low (i.e., residual reproductive value is low). In contrast, parents of species with fewer offspring and higher probability of adult survival should tolerate

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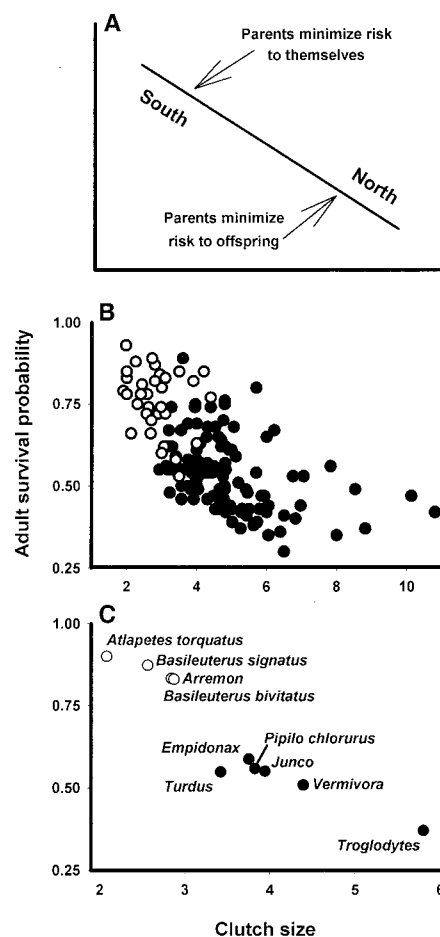
less risk to themselves, even at a cost to their young, because the fitness value of current offspring is lower and prospects for producing young in the future are greater. This choice between responding to the risk of mortality directed toward offspring versus parents in the face of predation is a fundamental challenge faced by all organisms that provide parental care and is highlighted by birds with altricial young that require frequent feeding visits to the nest.

Parental feeding visits to the nest can increase the risk of predation to both parents and young by attracting the attention of predators (5–11). When faced with an immediate risk of predation, parents temporarily decrease visitation rates to reduce risk to themselves or their young (5, 6), but such responses should vary among species according to their life histories. In particular, when predation risk is directed at parents, species with fewer young and higher adult survival should reduce risk to themselves by reducing feeding visits relatively more than species with many young and lower survival, even if offspring suffer from reduced food delivery (1–5) (Fig. 1A). Conversely, when offspring are at risk of predation, species with more young and lower adult survival should reduce feeding visits relatively more than less fecund species to reduce risk toward their greater investment in current reproduction (1–5) (Fig. 1A). These predicted differences in parental care tactics have not been tested, but contrasting life histories of birds from southern and northern latitudes provide a broad-scale opportunity to test them.

Tropical and Southern Hemisphere birds have small clutch sizes that historically

were thought to be associated with increased adult survival compared with northern species (7–10), but latitudinal differences in adult survival have been challenged in recent years (12, 13). These challenges, however, came from studies that relied on passive capture and recapture of marked birds in nets, which may underestimate survival probabilities, particularly in southern regions (14, 15). Supplementing recapture with resighting data of breeding territorial adults provides improved estimates of survival (14, 15). We obtained data on clutch size and adult survival from published studies that used such resighting methods for 182 passerine species of Northern (Europe and North America) and Southern (Australia, New Zealand, and South Africa) Hemispheres (16). We found a strong negative relation between clutch size and adult survival within and between regions, where southern species have smaller clutch sizes and higher adult survival than northern species (Fig. 1B). To verify that this general relation applied to our study systems, we analyzed data for species that were intensively color-banded and resighted at our sites in Argentina and Arizona (17). Again, we found a strong negative relation, with species from Argentina having higher adult survival associated with smaller clutch sizes compared with birds from Arizona (Fig. 1C). Three pairs of species (*Atlapetes-Pipilo*, *Arremon-Junco*, and *Basileuterus-Vermivora*) are closely matched phylogenetically and ecologically between the two sites (10), and these six species show survival to be higher in Argentina (Fig. 1C) independent of phylogeny (paired  $t = 12.4$ ,  $P < 0.003$ ). At the same time, clutch sizes of Southern Hemisphere species are smaller when closely related species that have the same numbers of broods are compared between regions (Table 1) [also (10, 18)]. Given these clutch size and adult survival differences between northern and southern regions (Table 1, and Fig. 1, B and C) [also (10, 15,

18)], we tested the predictions that southern parents should more strongly reduce risk to themselves whereas northern parents



**Fig. 1.** Annual adult survival probability and parental risk-taking relations relative to clutch size. (A) Life history theory (1–5) predicts that parents of species with fewer young and higher adult survival probability, as typical of southern regions, should minimize risk of mortality to themselves even at a cost to their young. In contrast, parents of species with more young and lower adult survival probability should minimize risk of mortality to their young, even at a cost to themselves. (B) Clutch size is negatively related to estimated annual adult survival probability from studies (17) that used resighting in addition to capture/recapture techniques ( $r = -0.63$ ,  $P < 0.0001$ ,  $n = 182$ ), and Southern Hemisphere species (open symbols) show higher survival and smaller clutches than north temperate species (closed symbols). This relation remains significant after controlling for phylogeny with independent contrasts ( $r = -0.55$ ,  $P < 0.0001$ ,  $n = 172$ ). (C) Clutch size is also negatively related to estimates of annual adult survival on our Arizona and Argentina study sites ( $r = -0.92$ ,  $P < 0.0001$ ) (18), even when controlled for phylogeny ( $r = -0.94$ ,  $n = 9$  independent contrasts). Species from Argentina (open symbols) have consistently smaller clutch sizes and higher annual adult survival compared with species from Arizona (closed symbols).

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**Table 1.** Species pairs used for experimental tests in North and South America.

North America*	Clutch size†	South America*	Clutch size
<i>Empidonax occidentalis</i> (6)	<i>Tyrannidae</i> (niche nesters, single-brooded)‡	<i>Lathrotriccus euleri</i> § (6)	2.3
<i>Turdus migratorius</i> (6)	<i>Turdidae</i> (shrub nesters, multibrooded)	<i>Turdus rufiventris</i> (6)	2.6
<i>Troglodytes aedon</i> (7)	<i>Troglodytidae</i> (hole nesters, double-brooded)	<i>Troglodytes aedon</i> (6)	3.7
<i>Junco hyemalis</i> (6)	<i>Emberizidae</i> (ground nesters, multibrooded)	<i>Arremon flavirostris</i> (6)	2.8
<i>Vermivora celata</i> (7)	<i>Parulidae</i> (ground nesters, single-brooded)	<i>Basileuterus bivittatus</i> (5)	2.9

\*Numbers in parentheses denote numbers of pairs (i.e., nests) tested in experiments (21). †Mean number of eggs laid per nesting attempt. ‡Numbers of broods are the same between regions within each of our taxonomic pairs of species (10). §Previously placed in the genus *Empidonax*.

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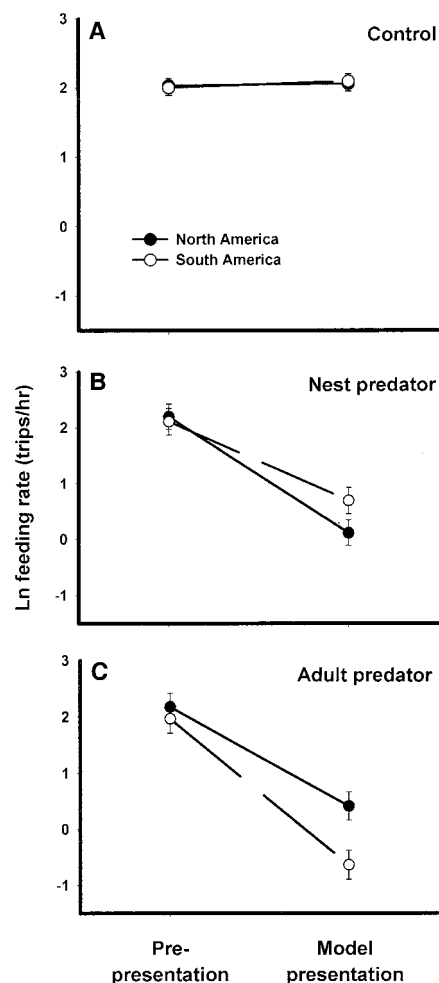
should reduce risk to their offspring (Fig. 1A).

We manipulated predation risk to parents versus offspring at 61 nests of 10 species that were paired between North and

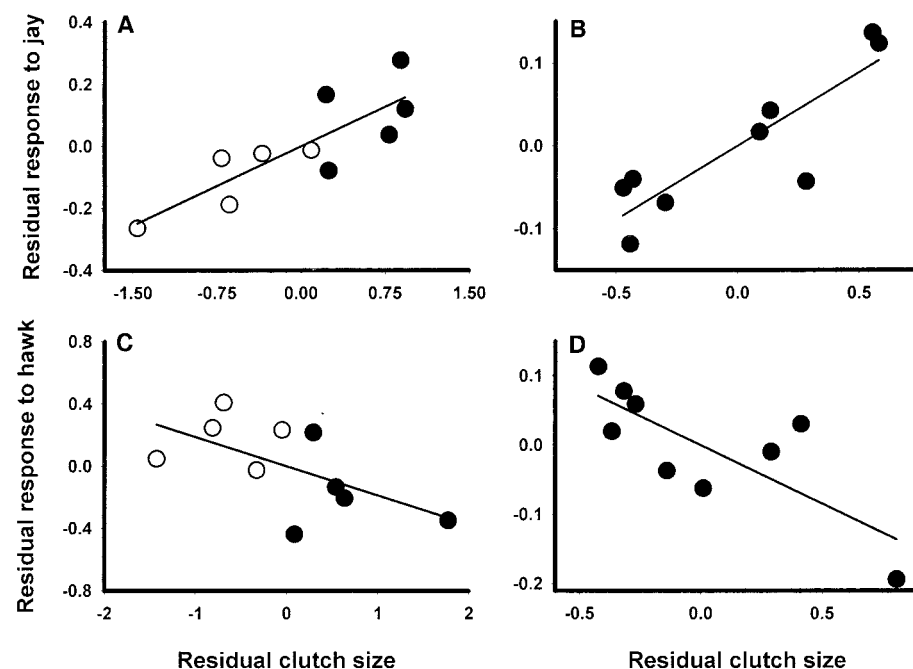
South America (19) on the basis of ecology and phylogeny and that had smaller clutch sizes and higher adult survival in South America (Table 1 and Fig. 1C). We presented a common predator of adults (hawk) and nestlings (jay) and a control that represented no predation threat (tanager) to examine the extent that parents risk themselves versus their offspring when making feeding trips to the nest (20). We found that parents did not change the rate that they visited the nest to feed offspring during control presentations (Fig. 2A). In contrast, parents strongly reduced visitation rate when presented with either a nestling (Fig. 2B) or adult (Fig. 2C) predator. Thus, parents differentiated among presentations and reacted appropriately to reduce potential threats to themselves and their offspring by reducing feeding visits to the nest. Responses to predation threats differed between regions and types of predators. Parents decreased feeding rates more in North than South America when the predation threat (i.e., jay) was directed at the offspring (Fig. 2B). However, this result was reversed when the predation threat (i.e., hawk) was directed at the parent; South American species decreased feeding rate

more than North American species (Fig. 2C). In short, North American species reacted more strongly to reduce risk to their offspring, whereas South American species reacted more strongly to reduce risk to themselves. These differences in parental responses between regions are consistent with theoretical predictions that life history differences should predict variation in parental behavior (Fig. 1 and Table 1). However, because such responses could be confounded by environmental effects unique to North and South America, it is important to examine species-specific responses as a function of their life histories.

Life history differences exist between regions, but life histories also vary along a continuum within as well as between regions (Fig. 1, B and C). Hence, we predicted that parental investment tactics should vary among species on the basis of their position along this continuum (Fig. 1). To test this prediction, we examined parental responses of each species relative to its clutch size. Clutch size reflects current investment in reproduction and is correlated with adult survival (Fig. 1C), a measure of residual reproductive value. Clutch size therefore reflects both factors that should influence how par-



**Fig. 2.** Log-transformed rates ( $\bar{x}/90 \text{ min} \pm 1 \text{ SE}$ ) that parents visit the nest to feed young before presentation (prepresentation) and during presentation (presentation) of control and predator models for 10 species of birds paired between North and South America (Table 1). (A) Feeding rates did not change when a control model (tanager) that presents no predation threat was presented [ $F(1, 59) = 3.13, P > 0.05$ ]. (B) Feeding rates decreased in North and South America [ $F(1, 57) = 140.19, P < 0.001$ ] in response to increased nestling predation risk from jay presentations. The interaction between treatment and location was not significant, but feeding rates during presentations were significantly lower in North than South American species (one-tailed phylogenetically paired  $t = 2.42, df = 4, P = 0.036$ ). (C) Feeding rates also decreased in response to increased adult predation risk from hawk presentations in North and South America [ $F(1, 56) = 105.71, P < 0.001$ ]. As above, the interaction term was not significant, but feeding rates during presentations were lower in South than North American species (one-tailed phylogenetically paired  $t = -3.41, df = 4, P = 0.013$ ).



**Fig. 3.** Partial regression plots of parental responses, measured as the percentage (arc-sin transformed) that feeding rates decreased, relative to clutch size for 10 bird species paired between North (closed symbols) and South (open symbols) America. Larger responses reflect greater decreases in feeding rates and risk. (A) Species with larger clutch sizes had larger responses to nestling predator (jay) presentations (one-tailed  $r_p = 0.83, df = 7, P = 0.003$ ) controlling for differences in the natural risk of nest predation among species (6, 10). (B) Independent contrasts that control for any phylogenetic effects and nest predation showed the same response to jay presentations (one-tailed  $r_p = 0.87, df = 6, P = 0.003$ ). (C) In contrast, species with smaller clutch sizes had larger responses to adult predator (hawk) presentations (one-tailed  $r_p = -0.60, df = 7, P = 0.04$ ) controlling for body mass. (D) Independent contrasts showed the same response to hawk presentations when controlling for body mass (one-tailed  $r_p = -0.77, df = 6, P = 0.01$ ).



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ents respond to a juvenile versus an adult predator (Fig. 1A, see earlier). We found strong predicted relations between clutch size and parental responses to juvenile and adult predators across all 10 species (Fig. 3). Specifically, the magnitude of responses to a juvenile predator increased with increasing clutch sizes, as typical of northern species (Fig. 3, A and B). In contrast, magnitude of responses to an adult predator intensified with decreasing clutch sizes, reflecting higher annual adult survival (Fig. 1C), as typical of southern species (Fig. 3, C and D). Thus, parental responses to juvenile and adult predator manipulations can be predicted from their life histories independent of whether species are from northern or southern regions but yield differences between regions because of latitudinal differences in clutch size and survival.

These data provide two important sets of results. First, all species reduce risk when faced with a predation threat by reducing the rate that they visit the nest to feed offspring (Fig. 2, B and C). Hence, parents appear to trade off the costs associated with reduced food delivery to their young against a reduction in the risk of mortality to themselves or their offspring. Species differentially express this trade-off depending on whether risk is directed at the parents or their offspring, and expression is predicted by clutch size and associated adult survival among species (Figs. 1 and 3). Interspecific covariation of life history traits such as clutch size and adult survival has been commonly explored (3, 4, 21–23), but covariation of these traits with parental behavior, as shown here, has been previously undocumented. Second, higher adult survival rates in southern species have been debated in recent years (12–15), potentially because of methodological differences in how survival is measured (14, 15, 18). Our review of published studies that incorporate resighting (Fig. 1B) and our own efforts (Fig. 1C) indicate that southern birds have higher survival than related northern birds. Additionally, our finding that parents of southern species respond more strongly than northern species to risk of adult mortality (Figs. 2C and 3, C and D) follows from higher adult survival in southern birds (Fig. 1A). This increased adult survival of southern birds is correlated with smaller clutch sizes (Fig. 1, B and C). Yet, no previous study has shown that clutch size and adult survival are correlated along a continuum that includes hemispheric differences (i.e., Fig. 1, B and C). Our demonstration that life history differences among southern and northern species accurately predict differences in parental risk-taking behavior provides empirical support for generalized models of life history evo-

lution and offers insight into the underlying factors responsible for interspecific variation in parental care tactics within and among latitudes.

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- We obtained data on clutch size and used estimates of adult survival that were based on resighting techniques from published reviews (22, 23) for the Northern Hemisphere (North America and Europe) and from individual published reports for the Southern Hemisphere (Australia, New Zealand, and South Africa; data available from T.E.M.). These data were analyzed with linear regression and were controlled for body mass. To control for any nonindependence due to phylogeny, we used independent contrasts and forced all regressions through the origin (21, 22).
- Study sites were at 34°N in mixed conifer forest near Flagstaff, AZ, and at 26°S in mixed subtropical forest in El Rey National Park, Salta, Argentina (10). Annual adult survival probabilities were estimated on the basis of intensive color-banding and resighting of breeding adults over 8 years in Arizona and 3 years in Argentina for all species except *Turdus migratorius* and *Pipilo chlorurus*. *Turdus* was not color-banded, and so estimates were from capture-recapture only. Pipilo data are from (24). We used a Cormack-Jolly-Seber model (25) with constant year and sex for survival but allowed these to vary for recapture probability to obtain the best fit model based on the program MARK (26) for species-level estimates of annual adult survival probabilities. Sample sizes and associated standard errors (*n*, SE) for each species are *Junco*, 377, 0.05; *Vermivora*, 307, 0.04; *Troglodytes*, 234, 0.07; *Empidonax*, 181, 0.09; *Turdus*, 167, 0.12; *B. bivittatus*, 38, 0.14; *B. signatus*, 14, 0.38; *Arremon*, 16, 0.27; and *Atlapetes*, 14, 0.23.
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- We conducted experiments on 10 species paired by phylogeny and ecology in Arizona and Argentina (Table 1). We used species paired within five avian families to provide five replicates that were independent of phylogeny. Nests were located and intensively monitored every 1 to 4 days to determine the fate of broods. Clutch size and daily probability of nest predation for the five Arizona species were estimated from a sample of >1800 nests over 12 years and for the five Argentina species from >330 nests over 3 years to provide robust estimates (70).
- We manipulated the risk of predation during the nestling period using vocalizations and presentation of stuffed models and followed the same protocol at all sites. Nests were observed for a 90-min presentation control period, followed by 90-min presentations of a nest predator, an adult predator, and a control. The perceived risk of adult predation was increased with a taxidermic mount and taped vocalizations of a common adult predator species that exists on both study sites, the sharp-shinned hawk (*Accipiter striatus*). Because *Accipiter* hawks are typically silent, the taxidermic mount was used in conjunction with the taped vocalizations to ensure that parents identified the potential risk. The risk of nest predation was increased with taped vocalizations of phylogenetically related and common nest predators at both sites: Steller's jay (*Cyanocitta stelleri*) in Arizona and push-capped jay (*Cyanocorax chrysops*) in Argentina. Video cameras at nests used to record parental behavior over 9 years in Arizona and all 3 years in Argentina confirm both species of jay to be common nest predators [see also (10)]. Both jay species are highly vocal and conspicuous nest predators that frequently elicit strong nest defense behavior from almost all species of breeding birds. In preliminary tests, we found that use of a jay model resulted in a group mobbing effect, where neighboring pairs of breeding birds would join the target parents to attack the model. This group mobbing effect obfuscated the response of our target parents alone. However, when the jay vocalizations were played without the model, the group mobbing effect was eliminated, while still eliciting a clear response to a potential threat from the parents. Response to the predators was compared with vocalizations of the phylogenetically related western tanager (*Piranga ludoviciana*) in Arizona and sayaca tanager (*Thraupis sayaca*) in Argentina, because these species represent no known risk to parents or young. To control for time of day effects and the order in which presentations were made, we made presentations of predators and the control in a stratified random order with a 60-min break between each treatment. Experiments were conducted on five to seven nests per species; however, in eight cases, circumstances prevented each nest from receiving all three treatments. To control for differences in developmental stage of young, we carried out all presentations on the same day and within 1 to 2 days of the nestling pin feathers breaking their sheaths. The breeding season is slightly longer in Argentina, so we conducted all experiments in Argentina during the second half of the breeding season to minimize any possible differences in reneating potential on parental risk-taking. Behavioral changes in response to experimental manipulations were analyzed with general linear models, in which prepresentation and presentation time periods were compared for the three treatment categories (control, nest predator, and adult predator). Differences between North and South America were first examined by testing the interaction between the response to presentations and continents and then by using a paired *t* test for species phylogenetically paired between North and South America. The relation between magnitude of response to presentations and clutch size of all 10 species was analyzed with partial regression analysis that controlled for significant confounding variables and used independent contrasts to control for phylogeny.
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