

## LETTER

## Parent birds assess nest predation risk and adjust their reproductive strategies

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### Abstract

Avian life history theory has long assumed that nest predation plays a minor role in shaping reproductive strategies. Yet, this assumption remains conspicuously untested by broad experiments that alter environmental risk of nest predation, despite the fact that nest predation is a major source of reproductive failure. Here, we examined whether parents can assess experimentally reduced nest predation risk and alter their reproductive strategies. We experimentally reduced nest predation risk and show that in safer environments parents increased investment in young through increased egg size, clutch mass, and the rate they fed nestlings. Parents also increased investment in female condition by increasing the rates that males fed incubating females at the nest, and decreasing the time that females spent incubating. These results demonstrate that birds can assess nest predation risk at large and that nest predation plays a key role in the expression of avian reproductive strategies.

### Keywords

Clutch size, egg size, nest predation, parental care, reproduction.

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### INTRODUCTION

Past attention to putative causes of variation in avian reproductive strategies has focused extensively on variation in the abundance of food (Lack 1948; Martin 1987). Indeed, experimental tests of food limitation abound in the literature (see Martin 1987). Yet, food does not explain considerable variation in reproductive strategies within and among species (Martin 1995; Martin *et al.* 2000a; Ferretti *et al.* 2005). As a result, the environmental causes of broadly differing reproductive strategies observed in nature remain unclear.

Nest predation is the primary cause of reproductive failure for most birds and, thus, represents an important source of natural selection (Ricklefs 1969; Martin 1995). Correlative evidence suggests that this source of selection can influence the expression of reproductive strategies (Lack 1948; Slagsvold 1982; Martin 1995; Martin *et al.* 2000a). Yet, the causal influence of nest predation risk on the expression of reproductive strategies by diverse species remains largely untested experimentally. Moreover, the ability of birds to assess variation in nest predation risk in the environment at large and adjust their reproductive strategies remains untested and unknown.

Here, we reduce nest predator populations to directly test the ability of 12 coexisting passerine species (Table 1) to assess variation in background levels of nest predation risk and whether they alter their reproductive strategies in response.

If individuals can assess nest predation risk in the environment, phenotypic responses to varying risk can shed light on the role of nest predation in the expression of reproductive strategies (West-Eberhard 1989; Ghalambor & Martin 2001, 2002). For example, greater risk of nest predation may favour reduced investment in current clutches as a means of bet-hedging to allow increased energy for re-nesting (Slagsvold 1984; Roff 1992; Martin 1995). As a result, clutch size, egg mass and clutch mass, all of which contribute directly to fitness (Roff 1992; Williams 1994; Saino *et al.* 2004), might be reduced in the face of high nest predation risk. Similarly, nest attentiveness (percentage of time females spend incubating) is a major energetic investment (Williams 1996), and might also be reduced under elevated nest predation risk as a means of bet-hedging. Alternatively, greater nest predation risk may favour increased attentiveness because of the potential benefits from camouflaging the nest contents or being present to deter predators that discover the nest (Marzluff

**Table 1** Study species differ in background nest predation risk

Species code*	Nest		Study species		Number of nests (control, removal)				
	predation rate†	site‡	Common name*	Scientific name	Egg mass	Clutch size	Clutch mass	Nestling feeding	Attentiveness/mate feeding
howr	0.005	Cavity	House Wren	<i>Troglodytes aedon</i>	5, 8	18, 12	5, 8	8, 6	30, 22
rbnu	0.008	Cavity	Red-breasted Nuthatch	<i>Sitta canadensis</i>	–	–	–	–	7, 5
brcr	0.012	Cavity	Brown Creeper	<i>Certhia americana</i>	–	–	–	–	9, 6
wbnu	0.014	Cavity	White-breasted Nuthatch	<i>Sitta carolinensis</i>	–	–	–	–	4, 4
moch	0.014	Cavity	Mountain Chickadee	<i>Poecile gambeli</i>	–	–	–	–	11, 5
ocwa	0.028	Ground	Orange-crowned Warbler	<i>Vermivora celata</i>	21, 22	76, 48	21, 22	16, 21	52, 32
viwa	0.030	Ground	Virginia's Warbler	<i>Vermivora virginiae</i>	16, 10	70, 34	16, 10	23, 22	37, 18
cofl	0.033	Niche	Cordilleran Flycatcher	<i>Empidonax occidentalis</i>	21, 6	81, 15	21, 6	4, 6	62, 17
rfwa	0.040	Ground	Red-faced Warbler	<i>Cardellina rubrifrons</i>	27, 5	62, 8	27, 5	27, 7	43, 9
ghju	0.041	Ground	Gray-headed Junco	<i>Junco hyemalis caniceps</i>	37, 18	120, 55	37, 18	29, 19	50, 42
amro	0.046	Subcanopy	American Robin	<i>Turdus migratorius</i>	7, 6	25, 16	7, 6	5, 8	34, 25
heth	0.085	Subcanopy	Hermit Thrush	<i>Catbarus guttatus</i>	23, 11	41, 24	23, 11	5, 3	29, 13

\*Species codes used for labels in all figures are from the American Ornithological Union and are based on common names.

†Mean daily probability of nest failure 1985–2004.

‡Nest predation rates differ among species related to their nest site.

1985; Montgomerie & Weatherhead 1988; Kleindorfer & Hoi 1997). Finally, nest predation can favour reduced activity at the nest to reduce the probability of nest detection by predators (Skutch 1949; Martin *et al.* 2000a,b; Ghalambor & Martin 2002). Thus, rates of mate-feeding (males feeding incubating females at the nest) and nestling feeding (both parents feeding young) might decrease under high nest predation risk. The potential consequences of nest predation risk for this broad suite of traits that comprise an individual's reproductive strategy remain untested experimentally. We experimentally tested all the above predictions by removing the primary nest predators of a community of passerine birds to study the reproductive response of birds nesting in reduced nest predation environments.

## METHODS

### Study area and species

From 2001 to 2004, we studied a bird community breeding in snowmelt drainages along the Mogollon Rim in central Arizona at *c.* 2300 m in elevation. The habitat in these drainages is typical of a western mixed conifer forest (Martin 1998).

Our study included 12 species of coexisting passerines representing four nesting guilds that experience different nest predation risk (Table 1; Martin 1995). Nesting begins in early May and extends into July. Species were included in analyses only when we could obtain samples (Table 1); for example, we could not obtain samples of egg mass and clutch mass for cavity-nesting birds.

### Field techniques

Nests were located using long-standing techniques (Martin & Guepel 1993). Incubating females were not flushed from nests to limit human disturbance, which birds may perceive as a predation threat. Instead, nests were either checked from afar by parental behaviour, or contents were checked when females were off during normal foraging bouts.

We measured egg mass for nests located during nest building or egg laying, and measured all eggs within 2 days of clutch completion using a calibrated digital scale accurate to 0.001 g. We only included nests known to be first attempts. These nests were also used in determining clutch mass (sum of total egg mass for a nest). Clutch size was taken from all nests found prior to hatching because partial losses are virtually never observed in this system. Again we only included nests known to be first attempts. Clutch size did not differ between the limited sample used for mass determination where we observed the complete clutch being laid and the broader sample in an analysis of variance that included species as a random factor ( $F_{1,638} = 1.867$ ;  $P = 0.172$ ).

We assessed parental behaviours by videotaping nests starting within 30 min of sunrise for 4–6 h (Martin *et al.* 2000a). When ever possible we recorded nests once in early incubation and once in late incubation and averaged to determine incubation behaviours. Tapes were scored for behaviours including: percentage of time females spent on the nest (nest attentiveness), the rate that males visited the nest to feed incubating females (mate-feeding rate) and the rate that both parents feed the young (nestling feeding rate)

(Martin *et al.* 2000a). Nestling feeding rates were measured only once at nests videotaped within 1 day of nestlings breaking primary pinfeathers to control for the influence of nestling development on feeding rates.

### Nest predator removals

Based on population densities and video evidence of nest predation events the primary predator community in this system is limited to five species: red squirrel (*Tamiasciurus hudsonicus*), gray-collared chipmunk (*Tamias cinereicollis*), deer mouse (*Peromyscus maniculatus*), white-footed mouse (*P. leucopus*) and Steller's jay (*Cyanocitta stelleri*) (Martin 1998). Additional nest predators exist within the community, but at such low densities that their effect on nesting productivity is likely minimal.

We removed nest predators from 10 plots (removal plots) to compare with 10 neighbouring plots with intact predator communities (control plots). We primarily removed mammalian predators from selected drainages through live trapping and translocation, but supplemented these efforts with lethal removals when necessary. Sherman and Tomahawk live-traps were baited with peanut butter and sunflower seeds and checked daily. All captures were transported 10 km to similar habitats separated from the study area by large canyons. Because of their increased mobility it was necessary to lethally remove all Steller's jays. All removal methods followed national guidelines and were approved and monitored under permits from the Arizona Game and Fish Department (SP635085), the US Fish and Wildlife Service (MB791101-3), and The University of Montana Institutional Animal Care and Use Committee (01-04-TMCWR-033105-01). Removals for all predator types began the second week of April, before the arrival of female migrant birds to the study site, and because plots were not fenced, we continued removal efforts through mid-July each year to offset immigration from surrounding source populations. We assessed the effectiveness of removals by comparing capture rates throughout the season.

To control for additional sources of variation in habitat quality we paired control and removal plots based on data from previous years that suggested similar bird, nest predator and plant assemblages. We removed nest predators from ten, 5–10 ha drainages. Control and removal plots were spatially paired (within 1 km) to minimize possible spatial influences, but separated by at least one intervening drainage to buffer against possible carryover effects of removals on control plots. We removed predators from the same plots each of the 4 years to maximize effect size.

We conducted aural surveys for jays and squirrels throughout the season as a index of predator abundance. Sampling consisted of a 1-min survey to determine the presence or absence of each predator. Tape recorders were

paired and randomly placed on both control and removal plots every fourth day of the season for a total of 23 sampling days per year. Because squirrels and jays, as well as our study species are most active in the morning, tapes were sampled starting at sunrise and every half-hour after for a total of six samples. Thus, we sampled six times per day for 23 days each year across all 4 years.

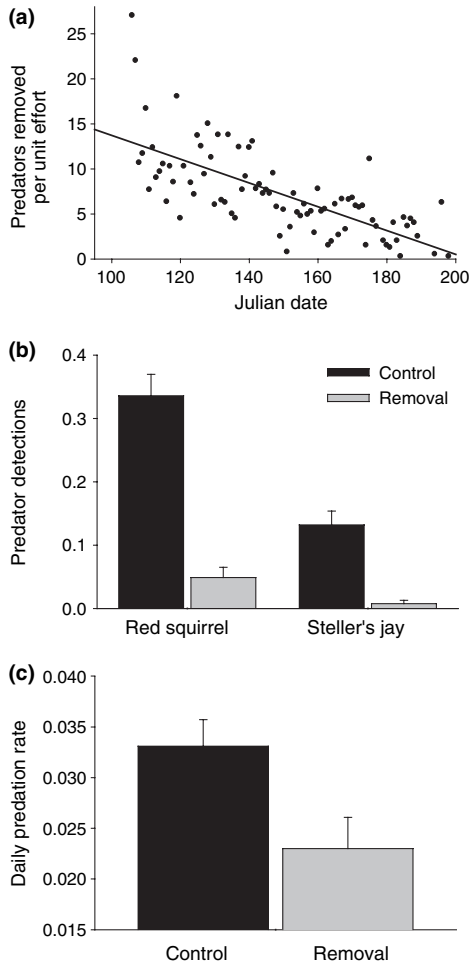
### Analyses

We examined capture rates of nest predators across the season using a simple linear regression. For nest predator surveys, we paired data by date and compared between treatments using a paired *t*-test. Mayfield estimates of daily predation rates were compared between treatments by species and year using a paired *t*-test (Mayfield 1961, 1975; Hensler & Nichols 1981). In examining parental responses, individual pairs and their nests were used as independent sample points for the analysis of behavioural and life history data. We used an analysis of covariance that included species as a random factor to test for overall differences between treatments in life history and parental care behaviours while controlling for potentially confounding effects. We excluded non-significant variables or interactions from trial models. Analyses were conducted on raw data, but differences represented in graphs are per cent change [(removal – control)/control × 100] to standardize changes for ease of visual comparison.

### RESULTS

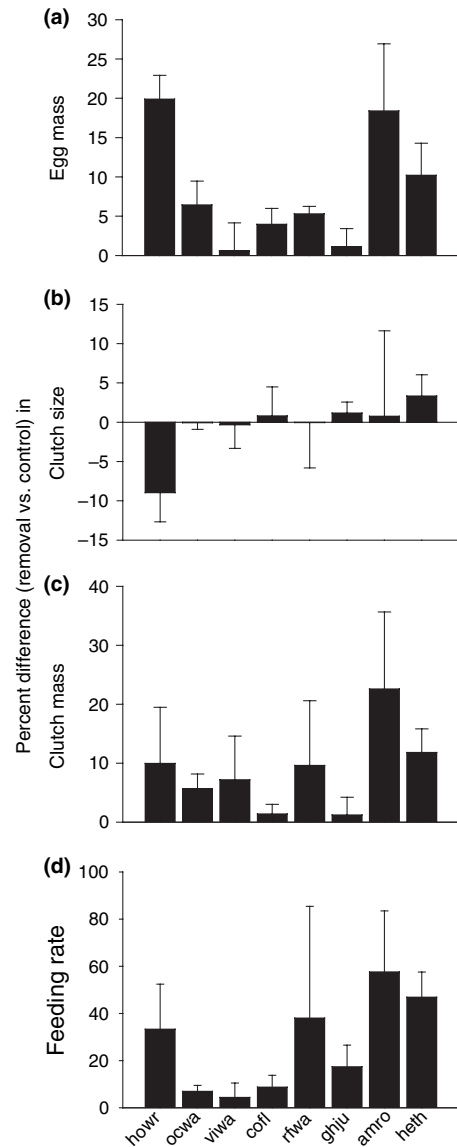
Over 4 years we removed 3791 predators from removal plots (769 red squirrel, 45 Steller's jay, 531 gray-collared chipmunk, 2446 mice spp.), and found and monitored 410 nests on removal plots and 850 nests on control plots. Differences between treatments in nest numbers reflect differences in re-nesting rates after nest failure and not increased densities on control plots (J.J. Fontaine and T.E. Martin, unpublished data). Experimental removals resulted in a reduction in capture rates on removal plots across the breeding season (Fig. 1a;  $F_{1,84} = 81.969$ ,  $P < 0.001$ ), which foreshadowed the change in nest predator detections between treatments (Fig. 1b; red squirrel  $t_{58} = -7835$ ,  $P < 0.001$ ; Steller's jay  $t_{58} = -6.058$ ,  $P < 0.001$ ). The reduction in vocalizations of two major predators is important because it reflects a reduction in predator cues and activity that might be key for assessment of risk by birds, but also telegraphs a strong reduction in actual nest predation rates (Fig. 1c;  $t_{44} = -2.02$ ,  $P = 0.025$ ).

The reduction in actual and perceived nest predation risk yielded significant changes in reproductive strategies by the diverse array of species that we studied. Parents increased investment in offspring. Mean egg mass was larger on plots



**Figure 1** Predator removals resulted in a reduction in nest predators and ultimately nest predation rates. Capture rates (a) on removal plots fell across the season and (b) vocalization rates of red squirrels and Steller's jays, as well as (c) nest predation rates were substantially reduced on removal plots when compared with control plots. Error bars indicate SEM across years.

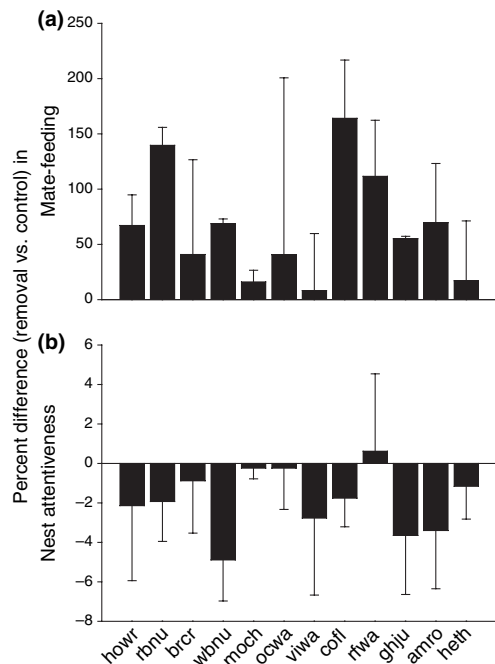
with reduced nest predation risk, as predicted (Fig. 2a; treatment:  $F_{1,249} = 54.205$ ,  $P < 0.001$ ; initiation date:  $F_{1,249} = 16.772$ ,  $P < 0.001$ ; species:  $F_{8,249} = 1475.825$ ,  $P < 0.001$ ; treatment by species:  $F_{8,249} = 12.622$ ,  $P < 0.001$ ). Yet, clutch size, a trait that other studies have found can be influenced by variation in nest predation risk (Julliard *et al.* 1997; Ferretti *et al.* 2005) showed a clear lack of response among the diverse array of species that we studied (Fig. 2b; treatment:  $F_{1,748} = 0.745$ ,  $P = 0.388$ ; initiation date:  $F_{1,748} = 65.831$ ,  $P < 0.001$ ; species:  $F_{11,249} = 75.283$ ,  $P < 0.001$ ). Nonetheless, the increase in egg mass led to an increase in clutch mass (Fig. 2c; treatment:  $F_{1,250} = 13.106$ ,  $P < 0.001$ ; species:  $F_{8,250} = 350.804$ ,  $P < 0.001$ ; treatment by species:  $F_{8,250} = 5.267$ ,  $P < 0.001$ ). Moreover, parents also increased investment in



**Figure 2** Life history traits and parental care behaviours affecting offspring were altered by predator removals. Responses are illustrated by per cent change [(removal - control)/control  $\times$  100]. Females nesting on plots with reduced nest predation risk (a) laid larger eggs, (b) did not change their clutch size, but (c) increased clutch mass. Both parents (d) increased the rate they fed nestlings. Error bars indicate SEM across years.

hatched young by feeding nestlings at a higher rate on removal plots (Fig. 2d; treatment:  $F_{1,189} = 14.458$ ,  $P < 0.001$ ; number of nestlings:  $F_{1,189} = 18.722$ ,  $P < 0.001$ ; species:  $F_{8,189} = 15.842$ ,  $P < 0.001$ ; treatment by species:  $F_{8,189} = 2.277$ ,  $P = 0.031$ ).

The reduced risk of nest predation also caused parents to invest in traits that enhance female condition. The rate that males fed incubating females increased on removal plots



**Figure 3** Behaviours affecting female parents were altered by predator removals. Responses are illustrated by per cent change [(removal – control)/control × 100]. Females nesting on plots with reduced nest predation risk (a) were fed more at the nest by their mates, and (b) reduced the percentage of time they spent incubating. Error bars indicate SEM across years.

(Fig. 3a; treatment:  $F_{1,598} = 162.429$ ,  $P < 0.001$ ; species:  $F_{12,598} = 360.612$ ,  $P < 0.001$ ; treatment by species:  $F_{12,598} = 53.428$ ,  $P < 0.001$ ), as predicted. Increased mate feeding (Fig. 3a) is known to reduce the energy constraints placed on females by the time and energy costs of incubation, and previous studies have found an increase in nest attentiveness with increased mate feeding (von Haartman 1958; Lyon & Montgomerie 1985; Smith *et al.* 1989; Halupka 1994). However, we found the opposite pattern of decreased nest attentiveness (Fig. 3b; treatment:  $F_{1,581} = 6.284$ ,  $P = 0.012$ ; year:  $F_{1,581} = 10.489$ ,  $P < 0.001$ ; species:  $F_{12,581} = 18.896$ ,  $P < 0.001$ ) despite increased mate feeding. Females on removal plots reduced nest attentiveness and accepted the double benefits of increased mate feeding and increased time off the nest caring for themselves when nest predation risk was low.

## DISCUSSION

The influence of food abundance on investment in eggs and reproductive behaviours like mate feeding and nest attentiveness has been studied extensively (von Haartman 1958; Lyon & Montgomerie 1985; Martin 1987; Smith *et al.* 1989; Halupka 1994; Sanz 1996). While food is obviously

important, nest predation is the primary source of reproductive mortality in many systems (Ricklefs 1969; Martin 1995) and therefore may impose strong direct selection on the expression of reproductive traits. We found such direct effects for a broad array of traits including the first experimental demonstration that nest predation risk may play a pivotal role in determining maternal investment in eggs, which may yield significant fitness benefits to young (Tinbergen & Boerlijst 1990; Williams 1994; Smith *et al.* 1995; Styrsky *et al.* 1999; Pelayo & Clark 2003). Furthermore, the fact that this increased investment was not limited to egg laying, but was maintained throughout the nesting cycle emphasizes the importance of nest predation in shaping many aspects of reproductive investment.

Equally as interesting as change in egg size was the lack of response in clutch size. Clutch size is known to correlate with nest predation risk across species (Martin 1995; Martin *et al.* 2000a), and has been shown to change with differences in nest predation risk across habitat gradients (Ferretti *et al.* 2005) and among years (Julliard *et al.* 1997). However, increases in clutch size represent an incremental increase in investment (i.e. from 1 to 2 to 3 eggs) that may require females to invest more in a clutch than small, continuous changes in individual eggs. Increases in clutch size also require continued investment throughout the nesting cycle (i.e. more eggs to heat, and more nestlings to feed), whereas increased egg size does not require such clear increases in future investment. Clutch size increases, therefore, require considerably more investment than egg size increases, which may be particularly important if females make mistakes in assessing nest predation risk or if risk can change within a nesting cycle. Changes in egg size rather than clutch size may represent a conservative response to relatively small changes in a strong and rapidly variable selection agent, nest predation.

In addition to showing the direct effects of nest predation risk, we also show that nest predation risk can create an indirect effect of food limitation by restricting the ability of adults to acquire food resources for themselves and their young. In particular, the reduction in nest attentiveness by incubating females despite increased mate feedings highlights the complex indirect effects of nest predation on food limitation in these systems. These results imply that females on control plots increase incubation effort in response to greater nest predation risk even when energy is more limited by reduced mate feeding. Such responses are opposite to those expected by bet-hedging. Although initially surprising, these results follow theory that suggests females should increase investment in themselves and enhance opportunities for future reproduction when the cost to current young is minimal (Roff 1992), as can be expected in low offspring mortality environments.

The fitness consequences of both direct and indirect effects of nest predation risk are clearly substantial, and emphasize the importance of considering responses to variation in nest predation risk in a relatively complete array of traits comprising reproductive strategies (Ferretti *et al.* 2005). Previous experiments that have attempted to explore the influence of nest predation risk on reproductive strategies have provided useful information on the short-term reactions of parents to the immediate threat imposed by a predator at the nest in a restricted subset of traits (Ghalambor & Martin 2001, 2002). However, when a predator is at the nest, the primary concern of the parents is deterring a predation event. Such studies do not address whether birds can assess variation in nest predation risk in the environment at large and modify their broader reproductive strategies based on such assessments. We have demonstrated here for the first time that parents can assess risk in the environment at large and adjust their reproductive strategy as a function of environmental risk of juvenile mortality. These findings highlight the importance of nesting mortality in shaping reproductive strategies both within and among species well beyond anything appreciated previously.

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#### REFERENCES

- Ferretti, V., Llambias, P. & Martin, T.E. (2005). Life-history variation of a neotropical thrush challenges food limitation theory. *Proc. R. Soc. Lond. B, Biol. Sci.*, 272, 769–773.
- Ghalambor, C.K. & Martin, T.E. (2001). Fecundity-survival trade-offs and parental risk-taking in birds. *Science*, 292, 494–497.
- Ghalambor, C.K. & Martin, T.E. (2002). Comparative manipulation of predation risk in incubating birds reveals variability in the plasticity of responses. *Behav. Ecol.*, 13, 101–108.
- von Haartman, L. (1958). The incubation rhythm of the female pied flycatcher (*Ficedula hypoleuca*) in the presence and absence of the male. *Ornis Fenn.*, 35, 71–76.
- Halupka, K. (1994). Incubation feeding in the meadow pipit *Anthus pratensis* affects female time budget. *J. Avian Biol.*, 25, 251–253.
- Hensler, G.L. & Nichols, J.D. (1981). The Mayfield method of estimating nesting success: a model, estimators and simulation results. *Wilson Bull.*, 93, 42–53.
- Julliard, R., McCleery, R.H., Clobert, J. & Perrins, C.M. (1997). Phenotypic adjustment of clutch size due to nest predation in the great tit. *Ecology*, 78, 394–404.
- Kleindorfer, S. & Hoi, H. (1997). Nest predation avoidance: an alternative explanation for male incubation in *Acrocephalus melanopogon*. *Ethology*, 103, 619–631.
- Lack, D. (1948). The significance of clutch size. Part 3. Some interspecific comparisons. *Ibis*, 90, 25–45.
- Lyon, B.E. & Montgomerie, R.D. (1985). Incubation feeding in snow buntings: female manipulation or indirect male parental care? *Behav. Ecol. Sociobiol.*, 17, 279–284.
- Martin, T.E. (1987). Food as a limit on breeding birds: a life-history perspective. *Annu. Rev. Ecol. Syst.*, 18, 453–487.
- Martin, T.E. (1995). Avian life history evolution in relation to nest sites, nest predation, and food. *Ecol. Monogr.*, 65, 101–127.
- Martin, T.E. (1998). Are microhabitat preferences of coexisting species under selection and adaptive? *Ecology*, 79, 656–670.
- Martin, T.E. & Guepel, G.R. (1993). Nest-monitoring plots: methods for locating nests and monitoring success. *J. Field Ornithol.*, 64, 507–519.
- Martin, T.E., Martin, P.R., Olson, C.R., Heidinger, B.J. & Fontaine, J.J. (2000a). Parental care and clutch sizes in North and South American birds. *Science*, 287, 1482–1485.
- Martin, T.E., Scott, J. & Menge, C. (2000b). Nest predation increases with parental activity: separating nest site and parental activity effects. *Proc. R. Soc. Lond. B, Biol. Sci.*, 267, 2287–2293.
- Marzluff, J.M. (1985). Behavior at a pinyon jay nest in response to predation. *Condor*, 87, 559–561.
- Mayfield, H. (1961). Nesting success calculated from exposure. *Wilson Bull.*, 73, 255–261.
- Mayfield, H. (1975). Suggestions for calculating nest success. *Wilson Bull.*, 87, 456–466.
- Montgomerie, R.D. & Weatherhead, P.J. (1988). Risks and rewards of nest defense by parent birds. *Q. Rev. Biol.*, 63, 167–187.
- Pelayo, J.T. & Clark, R.G. (2003). Consequences of egg size for offspring survival: a cross-fostering experiment in ruddy ducks (*Oxyura jamaicensis*). *Auk*, 120, 384–393.
- Ricklefs, R.E. (1969). An analysis of nesting mortality in birds. *Smith. Contr. Zool.*, 9, 1–48.
- Roff, D.A. (1992). *The Evolution of Life Histories Theory and Analysis*. Chapman & Hall, New York.
- Saino, N., Romano, M., Ambrosini, R., Ferrari, R.P. & Moller, A.P. (2004). Timing of reproduction and egg quality covary with temperature in the insectivorous Barn Swallow, *Hirundo rustica*. *Funct. Ecol.*, 18, 50–57.
- Sanz, J.J. (1996). Effect of food availability on incubation period in pied flycatcher (*Ficedula hypoleuca*). *Auk*, 113, 249–253.
- Skutch, A.F. (1949). Do tropical birds rear as many young as they can nourish? *Ibis*, 91, 430–455.
- Slagsvold, T. (1982). Clutch size variation in passerine birds – the nest predation hypothesis. *Oecologia*, 54, 159–169.
- Slagsvold, T. (1984). Clutch size variation of birds in relation to nest predation: on the cost of reproduction. *J. Anim. Ecol.*, 53, 945–953.

- Smith, H.G., Kallander, H., Hultman, J. & Sanzen, B. (1989). Female nutritional state affects the rate of male incubation feeding in the pied flycatcher *Ficedula hypoleuca*. *Behav. Ecol. Sociobiol.*, 24, 417–420.
- Smith, H.G., Ohlsson, T. & Wettermark, K.J. (1995). Adaptive significance of egg size in the European Starling: experimental tests. *Ecology*, 76, 1–7.
- Styrsky, J.D., Eckerle, K.P. & Thompson, C.F. (1999). Fitness-related consequences of egg mass in nestling house wrens. *Proc. R. Soc. Lond. B, Biol. Sci.*, 266, 1253–1258.
- Tinbergen, J.M. & Boerlijst, M.C. (1990). Nestling weight and survival in individual Great Tits (*Parus major*). *J. Anim. Ecol.*, 59, 1113–1127.
- West-Eberhard, M.J. (1989). Phenotypic plasticity and the origins of diversity. *Annu. Rev. Ecol. Syst.*, 20, 249–278.
- Williams, T.D. (1994). Intraspecific variation in egg size and egg composition in birds: effects on offspring fitness. *Biol. Rev. Camb. Philos. Soc.*, 68, 35–59.
- Williams, J.B. (1996). Energetics of avian incubation. In: *Avian Energetics and Nutritional Ecology* (ed. Carey, C.). Chapman and Hall, New York, pp. 375–416.

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