Testing ecological and behavioral correlates of nest predation

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Variation in nest predation rates among bird species are assumed to reflect differences in risk that are specific to particular nest sites. Theoretical and empirical studies suggest that parental care behaviors can evolve in response to nest predation risk and thereby differ among ecological conditions that vary in inherent risk. However, parental care also can influence predation risk. Separating the effects of nest predation risk inherent to a nest site from the risk imposed by parental strategies is needed to understand the evolution of parental care. Here we identify correlations between risks inherent to nest sites, and risk associated with parental care behaviors, and use an artificial nest experiment to assess site-specific differences in nest predation risk across nesting guilds and between habitats that differed in nest predator abundance. We found a strong correlation between parental care behaviors and inherent differences in nest predation risk, but despite the absence of parental care at artificial nests, patterns of nest predation risk were similar for real and artificial nests both across nesting guilds and between predator treatments. Thus, we show for the first time that inherent risk of nest predation varies with nesting guild and predator abundance independent of parental care.

Predation is a major evolutionary and ecological process that can shape both individual behaviors and community structure and function (Reznick and Endler 1982, Martin 1988, 1996, Begon et al. 1996, Pianka 2000). Understanding causes of variation in predation rates is necessary to advance our understanding of phenotypic traits. Predation risk is influenced by predator abundance, habitat structure, and predator and prey behavior (Lima and Dill 1990, Begon et al. 1996, Soderstrom et al. 1998, Chalfoun et al. 2002). While predation risk is influenced by prey behavior, it also shapes the evolution of prey behavior. This complex dynamic between predation risk and prey behavior complicates the generalization of predation processes across different habitats and species, because causes of predation risk are difficult to isolate from changes in prey behavior. For example, ecological conditions (i.e. habitat structure, nesting guild, predator abundances) can influence nest predation risk (Martin 1995, 1998,

Chalfoun et al. 2002, Fontaine and Martin 2006a, 2006b). Parental care behaviors typically change across habitats and nesting guilds with assumed differences in intrinsic predation risk, but changes in parental care behaviors can also alter measured rates of nest predation and mask ecological sources of predation risk (Martin and Ghalambor 1999, Ghalambor and Martin 2000, Martin et al. 2000b, Ferretti et al. 2005, Fontaine and Martin 2006a). Here we attempt to separate the independent influences of parental care, predator abundance and nesting guild on nest predation risk by conducting two artificial nest experiments.

Researchers have long assumed that nesting guild (i.e. cavity vs open-cup) is a major ecological factor driving differences in nest predation rates among species (Lack 1948, Nice 1957, Martin 1995, Owens and Bennett 1995, Martin and Ghalambor 1999). Patterns of increasing nest site safety from open-cup to secondary cavity to primary cavity are well established, and

are generally explained by differences in predation risk inherent to each nesting guild (Lack 1948, Nice 1957, Martin 1995). However, species occupying different nesting guilds also differ in parental care behaviors that can influence predation risk (Skutch 1949, Marzluff 1985, Montgomerie and Weatherhead 1988, Martin 1992, Kleindorfer and Hoi 1997, Martin and Ghalambor 1999, Martin et al. 2000a, Tewksbury et al. 2002). In particular, mate-feeding rates are higher at safer nests, and are associated with higher nest attentiveness (Martin and Ghalambor 1999). This relationship could suggest that safe nest sites allow high rates of mate-feeding, which facilitates high nest attentiveness (Skutch 1949, Martin and Ghalambor 1999, Martin et al. 2000a). Conversely, the causal arrows could be reversed, where increased nest attentiveness reduces predation risk but requires higher mate-feeding rates (Marzluff 1985, Montgomerie and Weatherhead 1988, Martin 1992, Kleindorfer and Hoi 1997, Tewksbury et al. 2002). In the latter case, nests with low nest predation risk may result from parents exhibiting high nest attentiveness rather than from some inherent influence of the nesting guild. Direct tests of these alternative directions of causality and the assumption that different nesting guilds have inherent differences in risk are lacking because no tests have separated the influence of parental care behaviors from the influence of nesting guild. Here, we tested for differences in nest site safety across four nesting guilds known to differ in predation rates by using artificial nests to remove the potentially confounding effects of parental care behaviors.

Differences in predator abundance are also often assumed to explain differences in nest predation rates between habitats or among years (Skutch 1949, Chalfoun et al. 2002). However, direct tests of the influence of predator abundance on predation risk independent of habitat structure and parental behavior are lacking. Parental care behaviors can change with predator abundance (Fontaine and Martin 2006a) and may affect predation risk and confuse the influence of predator abundance on predation rates. Recent experimental manipulation of a predator community demonstrates that predator abundance alone cannot predict predation outcomes (Fontaine and Martin 2006a, 2006 b). Nest predation rates on predator reduction plots decreased by only 25–50% across a diverse suite of breeding birds, despite a 90–95% decrease in predator abundance (Fontaine and Martin 2006a, 2006b). This contrast raises the question of why we fail to see similar changes in actual nest predation rates despite apparent changes in environmental risk of nest predation as reflected by predator abundance?

An increase in mate-feeding rate and a decrease in nest attentiveness coincided with a decrease in predator abundance (Fontaine and Martin 2006a), and may have increased nest predation rates beyond that predicted by predator abundance alone. Alternatively, other predators may have switched to this food resource because of increased nest density (Fontaine and Martin 2006b). To distinguish between these alternatives we conducted another artificial nest experiment overlaid on a predator removal experiment to examine how changes in predator abundance affect predation outcomes independent of the influences of parental care.

We used artificial nests to test: 1) if the pattern of decreasing nest predation rate from shrub < ground < secondary cavity < primary cavity nesters observed in real nests (Martin 1995) exists independent of parental behaviors, and 2) if predator abundance determines nest predation risk independent of parental behaviors, or if the expression of risky parental behaviors changes nest predation risk.

Methods

Study area and species

We studied nest predation in a community of birds breeding in a series of snowmelt drainages located along the Mogollon Rim in central Arizona from 1998–2004. This system is particularly appropriate for examining the effects of nest predation on breeding birds because nest predation accounts for 98% of nest failure (Martin 1998) and is known to influence both population trends and individual bird behaviors (Martin and Ghalambor 1999, Martin et al. 2000a, Ghalambor and Martin 2002, Fontaine and Martin 2006a). The vegetation and climate are typical of western mixed conifer forests (Martin 1998). Study species included 13 species of passerine birds representing a diverse continuum of ecological and behavioral characteristics and known to differ in nest predation risk and nesting guild (Table 1).

The primary nest predators in this system include: red squirrel *Tamaiasciurus hudsonicus*, gray-neck chipmunk *Eutamias cinereicollis*, deer mouse *Peromyscus maniculatus*, white-footed mouse *P. leucopus*, and Steller's jay *Cyanocitta stelleri* (Martin 1993, 1998). Although the predator community of artificial and real nests may not be the same for different nesting guilds or habitats (Thompson and Burhans 2003, 2004), this is unlikely in this system because of the limited predator community and the focus on a single habitat type. Dental imprints of clay eggs as well as photo and video documentation of predation events indicate that squirrels and chipmunks are by far the most important predators for all nesting guilds in this system and for both real and artificial nests (Martin 1993, 1998, unpubl.). Additional nest predators may exist but have rarely been documented depredating either real or artificial nests in this system (Martin 1993, 1998, unpubl.).

Table 1. Species occupy different nesting guilds.

Nesting guild	Common name	Scientific name
Primary cavity	Red-breasted nuthatch	Sitta canadensis
Primary cavity	Pygmy nuthatch	Sitta pygmaea
Secondary cavity	White-breasted nuthatch	Sitta carolinensis
Secondary cavity	Mountain chickadee	Parus gambeli
Secondary cavity	House wren	Troglodytes aedon
Secondary cavity	Western bluebird	Sialia mexicana
Ground	Orange-crowned warbler	Vermivora celata
Ground	Virginia's warbler	Vermivora virginiae
Ground	Red-faced warbler	Cardellina rubrifrons
Ground	Gray-headed junco	Junco hyemalis
Shrub	Green-tailed towhee	Pipilo chlorurus
Shrub	MacGillivray's warbler	Oporornis tolmiei
Shrub	Hermit thrush	Catharus guttatus

Experiment 1. Predation risk across nesting guilds

From May to July of 1998 and 1999, we created artificial nests that replicated four nesting guilds known to differ in nest predation rates: primary cavity, secondary cavity, ground and shrub. We chose all artificial nest sites based on nest height and substrate characteristics typical of the species they represented (Li and Martin 1991, Martin 1998). To begin, we established sampling points for artificial nests by locating naturally occurring secondary cavities with entrance (2.5 to 4 cm) and internal dimensions (7–25 cm) typical of natural house wren nests. To control for spatial and temporal variation in predation risk we created nest clusters by placing nests representing all nesting guilds within 25 m of these natural secondary cavities and baited all nests at the same time. Spatial clumping of nests across nesting guilds is common for natural nests in this system (unpubl.). We created primary cavity nests modeled after red-breasted nuthatches in a different tree of the same species and at the same height as the artificial house wren nest. Using a power drill, we excavated cavities with entrance (2.5 cm diameter) and internal dimensions (7–15 cm diameter) typical of a red-breasted nuthatch nest. We created shrub nests modeled after hermit thrushes (12.5 cm Ø, 6 cm height) from small wicker baskets covered with lichen and placed at a height of 0.5–2.5 m. Finally, we created ground nests by excavating a depression at the base of a stem, similar in size to an orange-crowned warbler nest (9–12 cm Ø, 2–3 cm deep), and lined with dried grasses.

Twenty replicate nests representing each nesting guild were set out in the last week of May of each year. We separated nest clusters by a minimum of 50 m

to mimic natural variation (Martin 1993, 1996, Whelan et al. 2003). Due to high variation in nest predation within open-cup nests, an additional 40 pairs of ground and shrub nests were set out in the second week of June 1999 in the same series of drainages. We baited each nest with one zebra finch (Poephila guttata) and one buttonquail (Turnix sp.) egg. By using eggs of different sizes we simultaneously ensure that small predators can depredate nests (zebra finch egg), and that the energy value of nests is large enough to entice larger predators (buttonquail egg). To determine nest fait, we checked nests every two days for a period of 13 days, a typical incubation period for these species (Martin 2002). Nests in which any of the eggs were disturbed or removed were considered depredated and monitoring was discontinued.

Artificial nests may not adequately replicate real nests, and their utility for examining questions relative to nest predation is unclear (Major and Kendal 1996, Moore and Robinson 2004). However, when artificial nests are coupled with studies of real nests, as we do here, they can be a useful experimental tool, but care must be paid to design and assumptions. We specifically designed nests to replicate actual nests in size, shape, substrate and material (Martin 1987). The nest predator community in this system is simple and the primary predators are the same at both artificial and real nests, limiting potential differences between nest predators of real and artificial nests (Moore and Robinson 2004, Thompson and Burhans 2004). Both artificial and real nests were visited and had their contents handled in a similar manner to control for possible differences in human scent and sign between groups. Additionally, our nests included egg sizes typical of eggs found in real nests and therefore did not limit our predator community (Major and Kendal 1996). We chose sites for artificial nests that mimicked real nests as closely as possible based on many years of experience in this system (Li and Martin 1991, Martin 1998). Any biases should be similar across nesting guilds and therefore we assume that any observed differences in nest predation rates reflect inherent differences in risk. Finally, we are not suggesting that artificial nests represent real nests (Sieving and Willson 1998). Indeed, we specifically used artificial nests to remove parental behaviors at real nests to test general patterns of predation risk across environmental gradients.

We located and monitored real nests (Martin and Guepel 1993) in drainages adjacent to experimental sites for use in comparing nest predation rates. Only nests monitored during incubation are considered here. We grouped all nests by nest guild to compare to artificial nests (Table 1) and used traditional estimates of nest predation rates (Mayfield 1961, 1975, Hensler and Nichols 1981) to identify general patterns of nest predation risk. We pooled data across years and used

Kendall's coefficient of concordance to test whether artificial nests showed the same pattern of increasing nest site safety (i.e. shrub ground < secondary cavity < primary cavity) as previously observed for real nests (Martin 1995). We predicted that if nesting guild is the major determinant of nest site safety, then artificial and real nests should show the same pattern of nest site safety. We followed this by using GLM to test whether nest predation rates differed among nesting guilds and between nest types. For this analysis, we calculated nest predation probabilities for a subset of the nests found prior to the first day of incubation. By using nests of known age, we were able to calculate individual predation probabilities for each nest based on the ratio of days survived to the average incubation period for that species (Martin unpubl.), enabling us to compare real and artificial nests directly. We used a global GLM model on these data to examine possible differences in nest predation rates among nesting guilds and nest types as fixed factors, while blocking by year, plot, and nest cluster as random factors to control for autocorrelation or interactions among samples.

To test whether parental care behaviors explained variation in nest predation risk, we examined only real nests and conducted another global GLM that included nest attentiveness and mate-feeding rate as covariates and blocked by year and plot. We log-transformed mate-feeding rate for all analyses given that previous analyses showed a curvilinear relationship (Martin and Ghalambor 1999) and visual inspection indicated the same for our data. We assessed parental behaviors by videotaping nests for approximately six h starting within 30 min of sunrise (Martin and Ghalambor 1999, Martin et al. 2000a, Martin 2002). We scored tapes for both nest attentiveness and mate-feeding rates (Martin and Ghalambor 1999, Martin et al. 2000a). Behavioral data gathered in the study years did not differ from a much broader sample gathered from 1987 to 2004 for any behaviors ($F_{1,45} < 1.461$, $p > 0.233$). Consequently, we used behavioral data from all years because we were interested in the most robust estimates. We calculated nest predation probabilities for a subset of the nests with recorded parental care behaviors and again limited our analysis to nests found prior to the first day of incubation.

We used separate global GLMs for nest attentiveness and mate-feeding rates to test whether variation in each behaviour was explained by nesting guild (and the associated differences in nest predation rates – Fig. 1, also Martin 1995) and residual variation in nest predation not encompassed by nesting guild. Again, we blocked by year and plot and tested for differences among guilds with a LSD post hoc test. Parental care behaviors may influence one another, so we conducted a follow-up test with the other parental care behavior as a covariate. For all models, we used individual pairs and
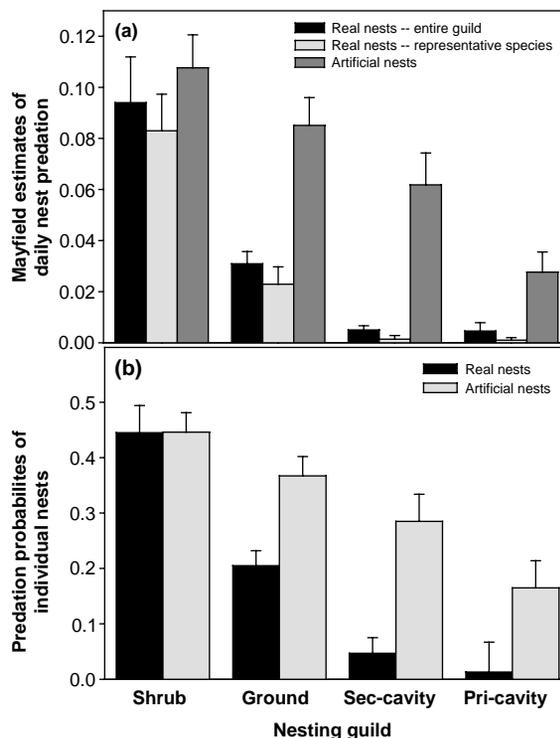

Fig. 1. Nesting guild is a major determinant of both Mayfield estimates of nest predation and individual nest predation probabilities. (a) Real nests for the entire guild, real nest of representative species, and artificial nests showed the same pattern of increasing nest site safety (shrub-ground-secondary-primary) across guilds based on Mayfield estimates of daily nest predation rates (nests: shrub, n = 903 real, 40 hermit thrush, 60 artificial; ground, n = 2327 real, 25 orange-crowned warbler, 60 artificial; secondary, n = 1784 real, 82 house wren, 20 artificial; primary, n = 841 real, 64 red-breasted nuthatch, 20 artificial). (b) Individual predation probabilities of nests also showed a similar pattern of increasing nest site safety (shrub-ground-secondary-primary) across guilds (nests: shrub, n = 26 real, 60 artificial; ground, n = 84 real, 60 artificial; secondary, n = 78 real, 20 artificial; primary, n = 21 real, 20 artificial). Data are means ± SEM.

their nests as independent samples, and excluded non-significant variables or interactions from trial models.

Experiment 2. Predation risk with varying predator abundance

We created artificial nests in sites typical of orange-crowned warblers (see above) on plots undergoing predator removals (removal plots) and plots with intact predator communities (control plots) from April to July of 2002, 2003 and 2004 (see Fontaine and Martin 2006a for a detailed description of predator removal experiment). Twenty artificial nests were set out on a series of four removal and four control plots in the last

week of May of each year, for a total of 240 nests for each treatment. Artificial nests were created, distributed and monitored using the same techniques (see above), and plots received the same treatment in all years. We also monitored real nests on these plots (see above) to compare relative nest predation rates.

We predicted that if changes in parental care behaviors lead to elevated nest predation rates on removal plots then the between-treatment difference in predation rates on artificial nests would be greater than for real nests. Alternatively, if parental care behaviors are relatively unimportant in influencing predation risk between treatments, then the between-treatment differences in predation rates of artificial and real nests should be similar. To determine which hypothesis was best supported, we calculated daily nest predation rates for real and artificial nests on each plot and used GLM to test for differences between treatments and nest type (i.e. real or artificial) while

blocking by plot and year as random factors. Because absolute values may differ between real and artificial nests, but changes between treatments may be similar we used the data to calculate the percent difference between the two treatments $[((\text{removal} - \text{control})/\text{control}) \times 100]$ for both nest types in each year on each plot and compared them using GLM.

Results

Experiment 1. Predation risk across nesting guilds

Mayfield estimates of daily predation rates were perfectly correlated across the four nesting guilds for real nests of all species, real nests of representative species, and artificial nests meant to simulate those species (Fig. 1a; $W_2 = 1$, $p = 0.018$). Nest predation probability differed among nesting guilds and was
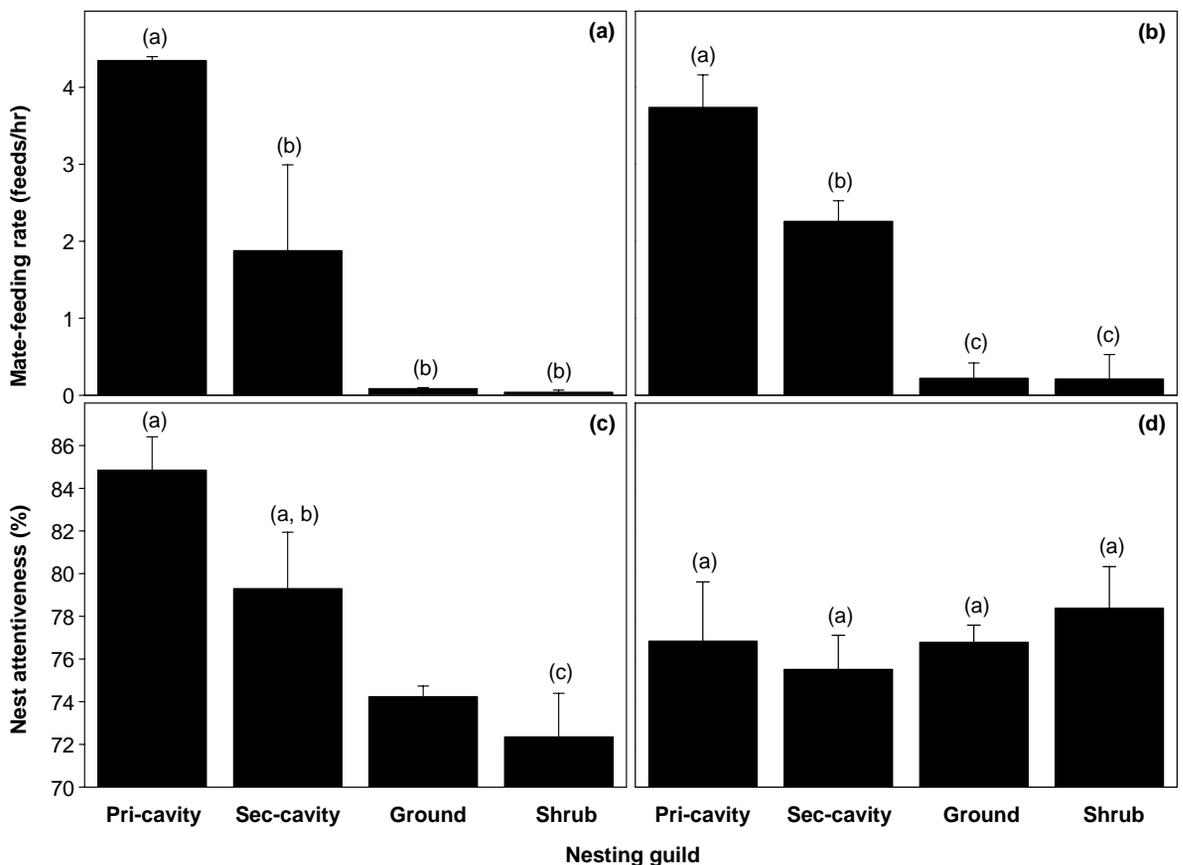

Fig. 2. Parental care behaviors are influenced by nesting guild. Nesting guild significantly influenced mate-feeding rate (rate at which males feed incubating females on the nest) (a), even after including the effects of nest attentiveness (b). In contrast, nesting guild appears to influence nest attentiveness (percentage of time female is on the nest) (c), but after including the effects of mate-feeding rate this relationship is lost (d). Columns denoted by different letters are significantly different at the 0.05 level according to an LSD post hoc test. Data are means (a, c) or marginal means (c, d) $\pm$ SEM (nests: primary, n = 21; secondary, n = 32; ground, n = 142; shrub, n = 23).

greater for artificial than real nests (i.e. nest type) even when including possible year effects (Fig. 1b; guild, $F_{3,449} = 24.805$, $p < 0.001$; nest type, $F_{1,449} = 32.947$, $p < 0.001$; nest type by year $F_{2,449} = 4.973$, $p = 0.007$). When we examined only real nests and added parental care behaviors to the model, nesting guild remained the primary factor explaining nest predation, although nest attentiveness was marginally significant (guild, $F_{3,218} = 11.971$, $p < 0.001$; nest attentiveness, $F_{1,218} = 3.763$, $p = 0.054$).

Mate-feeding rate differed strongly among nesting guilds even when accounting for nest initiation date and year (Fig. 2a; guild, $F_{3,218} = 120.224$, $p < 0.001$; nest initiation date, $F_{1,218} = 8.870$, $p = 0.003$; year, $F_{11,218} = 2.039$, $p = 0.026$). Nest predation rates are strongly predicted by and encompassed by nesting guild (see above), and when guild is not included in the model, then nest predation is the primary predictor of variation in mate-feeding rates (nest predation: $F_{1,218} = 6.857$, $p = 0.009$; year, $F_{11,218} = 4.632$, $p < 0.001$). Variation in mate-feeding rate continued to differ among guilds even when nest attentiveness was included as a covariate (Fig. 2b; guild, $F_{3,218} = 114.775$, $p < 0.001$; nest initiation date, $F_{1,218} = 9.435$, $p = 0.002$; nest attentiveness, $F_{1,218} = 19.662$, $p < 0.001$; year, $F_{11,218} = 1.990$, $p = 0.031$).

Nest attentiveness also differed strongly among guilds, with some marginal variation explained by residual variation in nest predation (Fig. 2c; guild, $F_{1,218} = 4.413$, $p = 0.005$, nest predation, $F_{1,218} = 3.763$, $p = 0.054$). This pattern among guilds was largely due to correlated variation in mate-feeding rates as mate-feeding rate strongly predicted nest attentiveness (Fig. 3; $F_{1,218} = 33.612$, $p < 0.001$). Nest attentiveness did not differ among guilds once mate-feeding rate was included in the model (Fig. 2d; guild, $F_{3,218} = 1.689$,
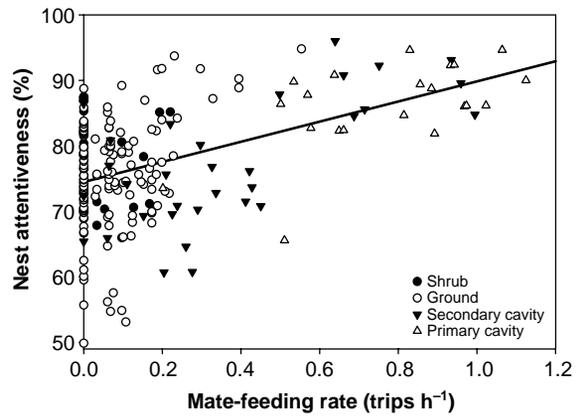

Fig. 3. Mate-feeding rate predicts nest attentiveness across guilds. Increasing mate-feeding rate leads to increased nest attentiveness across nesting guild. Data are comparisons of individual nests; mate-feeding rates have been log transformed (nests: primary, n = 21; secondary, n = 32; ground, n = 142; shrub, n = 23).

$p = 0.170$; nest predation, $F_{1,218} = 3.617$, $p = 0.059$; mate-feeding rate, $F_{1,218} = 20.539$, $p < 0.001$).

Experiment 2. Predation risk with varying predator abundance

Predator removals resulted in a significant decrease in nest predation risk (Fig. 4a; treatment, $F_{1,43} = 17.095$, $p < 0.001$; nest type, $F_{1,43} = 42.663$, $p < 0.001$; year, $F_{2,43} = 5.028$, $p = 0.011$), and although absolute predation rates varied by year and nest type, differences between treatments did not differ for real vs artificial nests (Fig. 4b; nest type, $F_{1,17} = 0.024$, $p = 0.878$; year, $F_{2,17} = 0.806$, $p = 0.463$; plot, $F_{3,17} = 2.114$, $p = 0.136$).
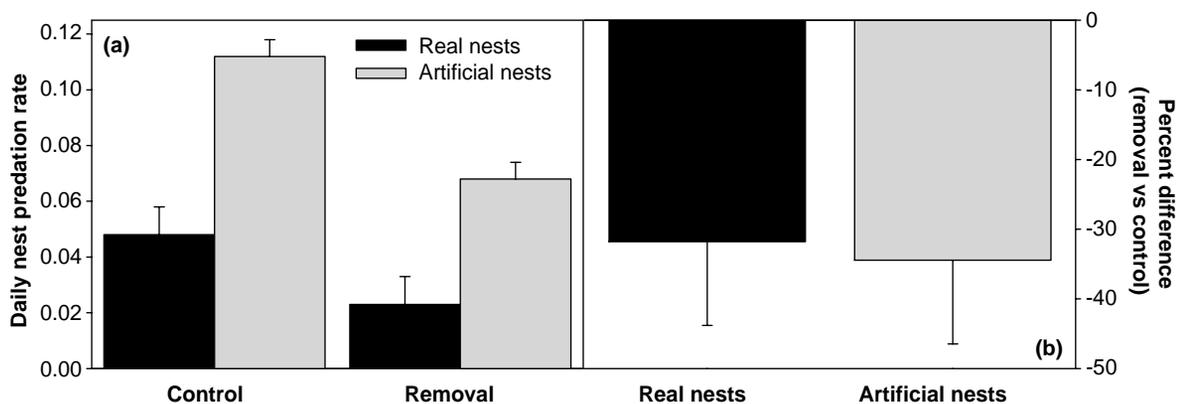

Fig. 4. Predator reductions lead to consistent changes in nest success for real and artificial nests. (a) Artificial nests experienced greater nest predation rates than real nests in both treatment groups (nests: n = 103 real, 240 artificial), but (b) the change in nest predation rates between the treatment groups, illustrated by percent difference [(removal-control)/control × 100], did not differ between real and artificial nests. All data are means ± SEM.

Discussion

Predation is a major ecological force influencing biological systems at a multitude of levels. Yet, our understanding of how differences in predation risk influences the phenotypic expression of complex sets of traits and how these traits can feedback to influence predation risk remains unclear. Here we attempted to distinguish between sources of predation risk inherent to the environment (i.e. predator density and nesting guild) and sources of predation risk imposed by prey behavior (i.e. mate-feeding rate and nest attentiveness), using both experimental and statistical approaches.

Our data demonstrate that differences in nesting environments can readily influence nest predation risk. Similar to previous studies, but based on two distinct approaches, we found a pattern of increasing nest site safety across nesting guilds (shrub < ground < secondary cavity < primary cavity) (Fig. 1), and despite the complete removal of parental care behaviors at artificial nests, the pattern of nest site safety did not change (Fig. 1). These data support the common, but previously untested, assumptions that predation risk is strongly determined by nesting guild, independent of parental behaviors. Indeed, based on our analysis, observed differences in parental care behaviors among nesting guilds (Fig. 2) do not appear to influence nest predation, although the marginally significant relationship with nest attentiveness requires further exploration. What appears more likely is that differences among nesting guilds lead to differences in parental care behaviors potentially reflecting responses to variation in nest site vulnerability (Martin and Ghalambor 1999, Martin et al. 2000a); however, even this relationship is complicated. While a cursory analysis suggests that nesting guild predicts parental care behaviors (Fig. 2a, 2c) further analysis including the other behavior as a covariate reveals that nesting guild predicts mate-feeding rate (Fig. 2b) but not nest attentiveness (Fig. 2d). However, because of the strong correlation between mate-feeding rate and nest attentiveness (Fig. 3), nesting guild may indirectly drive nest attentiveness through mate-feeding rate.

Parental care behaviors were also unable to explain the relatively limited reduction in nest predation rates on plots that underwent predator removals. Despite a 90–95% decrease in predator abundance (Fontaine and Martin 2006a) on removal plots, nest predation rates only decreased by 25–50% (Fontaine and Martin 2006b). Parents on removal plots increased mate-feeding activity and reduced nest attentiveness (Fontaine and Martin 2006a), both of which can increase predation risk, but our artificial nest study suggests that these changes did not lead to a significant increase in nest predation rates (Fig. 4b). Instead, prey switching by alternative predators may more easily explain the

limited influence of the predator reduction on nest predation rates (Fontaine and Martin 2006a, b). While individuals nesting in safer nest sites, either due to nesting guild or predator abundance, express more risky parental care behaviors, these behaviors appear appropriate and do not appear to exaggerate their risk.

Differences in nest predation between real and artificial nests (Fig. 1, Fig. 4a) suggest the possibility that other factors beyond nesting guild or predator abundance may influence nest predation risk. These differences could simply reflect our inability to adequately simulate nest sites chosen by real birds, or could reflect the importance of parents in reducing nest predation risk by passive or active defense (Montgomerie and Weatherhead 1988, Burke et al. 2004). Indeed, the marginally significant effects of nest attentiveness on predation risk suggest such a possibility. These findings contrasts previous research demonstrating the negative impacts of parental behaviors on nest success (Skutch 1949, Martin et al. 2000a), indicating that the influence of parental care on nest predation risk requires further study.

Our experiments showed that inherent differences in nest site vulnerability, independent of parental behaviors, exist among nesting guilds and habitats with different predator communities. Individuals or species with safe nests are afforded the luxury of expressing behaviors that would be costly if expressed in unsafe nests (Martin and Ghalambor 1999, Martin et al. 2000a, 2000b, Ghalambor and Martin 2002, Fontaine and Martin 2006a). Ultimately, consideration of both inherent differences in nest site safety and parental care strategies is critical to understanding variation in nest predation and life-history traits in birds.

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