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RISK OF NEST PREDATION INFLUENCES REPRODUCTIVE INVESTMENT IN AMERICAN KESTRELS (*FALCO SPARVERIUS*): AN EXPERIMENTAL TEST

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ABSTRACT.—Nest predation is the primary cause of nest failure in birds. Individuals should therefore adjust parental investment to minimize the costs associated with this constraint; evidence suggests that nest predation influences nest-site selection, and drives variation in both clutch size and parental behavior. Here, we test how the perception of the risk of nest predation from red squirrels (*Tamiasciurus hudsonicus*) influenced nest-site selection and reproductive investment of American Kestrels (*Falco sparverius*) breeding in the boreal forest. For this purpose, we conducted audio playbacks of squirrel vocalizations and altered nest boxes to experimentally increase cues of the presence of Red Squirrels in the vicinity of potential nests. Experimental manipulations of the risk of nest predation did not influence nest-site selection; however, experimentally increasing the perceived risk of nest predation induced kestrels to initiate breeding later, and to lay larger clutches. Parents did not appreciably alter incubation behavior in response to our manipulation, although the duration of incubation was longer where natural squirrel threat was higher. Our results showed that kestrels are capable of making facultative adjustments to current reproductive investment in response to their perception of the risk of nest predation.

KEY WORDS: *American Kestrel*; Falco sparverius; *red squirrel*; Tamiasciurus hudsonicus; *audio playback*; *incubation*; *nest predation*; *nest-site selection*; *reproductive investment*.

EL RIESGO DE DEPREDACIÓN DEL NIDO INFLUENCIA LA INVERSIÓN REPRODUCTIVA EN *FALCO SPARVERIUS*: UNA EVALUACIÓN EXPERIMENTAL

RESUMEN.—La depredación del nido es la principal causa de fracaso del nido en las aves. Los individuos deben por la tanto ajustar la inversión parental para minimizar los costos asociados con esta restricción; la evidencia sugiere que la depredación del nido influencia la selección de los sitios de anidación, y conduce a variación en el tamaño de la nidada y en el comportamiento parental. Aquí evaluamos como la precepción del riesgo de depredación del nido por parte de la ardilla roja *Tamiasciurus hudsonicus* influenció la selección de los sitios de anidación y la inversión reproductiva de halcones *Falco sparverius* que nidifican en el bosque boreal. Para este propósito, realizamos reproducciones de vocalizaciones de ardilla previamente grabadas y alteramos cajas nido para incrementar experimentalmente signos de la presencia de ardillas rojas en la vecindad de los nidos potenciales. Las manipulaciones experimentales del riesgo de depredación no influenciaron la selección del sitio de anidación; sin embargo, el incremento experimental de la percepción del riesgo de depredación del nido indujo a los halcones a iniciar la cría más tarde y a poner nidadas mayores. Los padres no alteraron de un modo apreciable su comportamiento de incubación en respuesta a nuestras manipulaciones, aunque la duración de la incubación fue más larga en donde la amenaza natural de las ardillas fue mayor. Nuestros resultados mostraron que los halcones son capaces de realizar ajustes facultativos en la inversión reproductiva en un momento determinado en respuesta a sus percepciones del riesgo de depredación del nido.

[Traducción del equipo editorial]

Although resource availability is thought to drive variation in life-history strategies (Martin 2002), nest predation is the primary cause of nest failure in birds (Ricklefs 1969, Martin 1995) and a key predictor of productivity (Thompson 2007). During breeding, birds may incur costs associated with resource limitation, competition, suboptimal weather, and predation risk (Martin 1996, Fontaine and Martin 2006a); minimizing these costs should contribute to overall fitness (Martin 1998, Smith et al.

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2000, Morris 2003). The risk of nest predation, defined as risk of mortality or danger (the probability of mortality) imposed by a predator (Lank and Ydenberg 2003), should therefore be an important constraint driving the evolution of avian parental investment strategies. For example, risk of nest predation has been shown to influence nest-site selection and induce breeding dispersal in a number of avian species, and in some systems nest predation affects variation in clutch size and parental behavior (reviewed in Lima 2009).

Decisions concerning space-use are understood to be influenced chiefly by the distribution and abundance of both resources and predators (Willems and Hill 2009). If habitat selection is adaptive, it should confer increased reproductive success (Martin 1998), so when all else is equal, birds should choose a nest site with the lowest possible risk of nest predation. To assess the risk of nest predation, settling individuals may use past experience; most studies to date have examined the influence of nest predation on nest-site selection in subsequent years (e.g., Doligez and Clobert 2003). Individuals may also use indirect cues from conspecifics or heterospecifics, but direct cues are presumably the most reliable (Thomson et al. 2006). Researchers assessing parental decision-making typically describe the trade-offs animals make among both direct and indirect influences on breeding-site selection (Brown 1988) but have seldom measured the perception of predation risk as opposed to actual predation risk (but see Fisher and Wiebe 2006).

Theory predicts that increased nest predation will select for reduced clutch size (Lima 1987, Martin 1993), which allows for shorter laying and nestling periods, smaller and less conspicuous nests, more satiated (quieter) young, and fewer parental nest visits during the nestling phase. These allowances provide parent birds the advantage of fewer opportunities for nest detection by predators, and a reduction in both the period of time eggs and nestlings are exposed to predators and the amount of time parents must engage in antipredator behavior (Skutch 1949, Martin et al. 2000a, 2000b). Furthermore, smaller clutches require less energy, thereby increasing an adult's chance of successfully producing and rearing a second brood should the first be depredated (Martin 1995). Although lower rates of nest predation are thought to account for larger clutch sizes in cavity-nesting birds (Martin and Li 1992), there is very limited support for this and the effect of nest predation on reproductive strategies of cavity nesters remains equivocal.

Although there is evidence that nest predation is a factor in shaping the evolution of clutch size, the influence of nest predation on other aspects of reproductive investment is less studied. There is little evidence for the role of parental evaluation of the risk of nest predation in influencing initiation date and if, as Skutch (1949) hypothesized, greater parental activity at the nest increases nest predation, then birds should adjust their incubation behavior to minimize the amount of attention they draw to the nest. The behavior of incubating parents directly influences hatching success (Ghalambor and Martin 2002) but few (e.g., Fontaine and Martin 2006b) have experimentally tested how parents may adjust incubation rhythms in response to nest predation.

We tested the hypothesis that the perception of the risk of nest predation drives variation in nest-site selection and reproductive investment of American Kestrels (*Falco sparverius*) in the boreal forest of north-central Saskatchewan, Canada. American Kestrels (hereafter, kestrels) are secondary cavity nesters and in our study area, red squirrels (*Tamiasciurus hudsonicus*) prey on kestrel eggs and hatchlings, and are also an important nest competitor (Dawson and Bortolotti 2006a). The causes and consequences of settlement decisions of this species are poorly understood; little is known about how kestrels perceive predation risk, and whether these cues influence their antipredator decision making. We conducted audio playbacks of squirrel vocalizations and altered nest boxes to experimentally increase cues of the presence of red squirrels in the vicinity of potential nests. We predicted kestrels would use these cues to preferentially select nest sites associated with lower perceived risk of predation, and adjust reproductive investment and incubation behavior to minimize the anticipated costs associated with higher predation risk.

METHODS

Study Area. We studied American Kestrels breeding in nest boxes in the boreal forest near Besnard Lake, Saskatchewan (55°N, 106°W). The study area comprised a network of nest boxes situated along gravel roads. Nest boxes were located either in mature mixed forests composed of both deciduous and coniferous cover or adjacent to harvested cut blocks with regeneration (jack pine, *Pinus banksiana*) lower than the height of the box. Kestrels begin arriving on the study site in mid- to late April (Dawson and

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Bortolotti 2002); our experiment was conducted between late April and July 2008.

Cues of Predation Risk. We used playbacks of red squirrel vocalizations as cues to simulate the presence of a territorial squirrel near nest boxes. Although visual cues may signal the potential risk of nest predators, we chose squirrel vocalizations because these would seem a direct representation of reality in comparison with other approaches such as a dummy display. In addition, kestrels are sensitive to researcher presence near the nest box during the initiation phase, and the use of a playback allowed us to minimize the time we spent near the nest box while maximizing exposure to the cue. We chose nest boxes that kestrels had bred in at least once during the previous five years; 29 of these were randomly assigned as experimental boxes, 29 were assigned to the control group. We created playback recordings that were a combination of warning barks, chips, and trills of red squirrels interspersed with silence. These were broadcast at experimental boxes on a continuous loop for 7–12 hr, every third day, beginning 28 April. Squirrel vocalizations were played from a small compact disc player (Durabrand, model CD-566, Lennox Electronics Corp., Edison, New Jersey, U.S.A.) with portable speakers (ILO Digital Active Speaker System, DSP-26A, 1.5 W RMS, Lennox Electronics Corp., Edison, New Jersey, U.S.A.); the playbacks were audible to us at a distance of at least 100 m. Male kestrels establish territories; however, upon pair formation, females may choose from multiple nest holes that the male presents to her (Balgooyen 1976; J. Greenwood unpubl. data); thus, in order to concentrate the audio cues around only our nest boxes, we placed speakers 20 paces from the nest box in a random direction. Kestrels feed on a diverse array of prey, including birds (Dawson and Bortolotti 2006a); therefore, we did not subject control boxes to playbacks of a non-predator (e.g., songbird) to avoid confounding effects of perceived resource availability or distribution. Rather, we visited a random location, 20 m from each control box, on the same schedule as experimental boxes. Playbacks were conducted until laying was largely finished throughout the study area and, in the case of occupied boxes, until hatching.

In addition to audio playbacks, we altered nest boxes slightly to simulate use or prospecting by red squirrels. In the early stages of nest-building, squirrels often deposit neatly wound balls of grass in nest boxes before constructing a full nest of grass and leaves. Furthermore, boxes frequented by squirrels routinely exhibit chewed entrance holes. We mimicked these two cues to simulate the presence of squirrels on the territory and in the box. We placed three balls of grass (collected from squirrel nests throughout the study area) in each experimental box, and the entrance holes of the boxes were chiseled (but not enlarged) in a manner similar to the incisor marks left from squirrels. Control boxes were left empty, and entrance holes were not altered.

Nest-box Selection and Reproductive Rate. Starting in early May, we visited nest boxes every 3–5 d to determine selection of boxes as nest sites, and clutch initiation dates in those boxes where eggs were laid. Upon clutch completion, we returned to determine clutch size and measure eggs; at this time we also captured adults by hand in nest boxes. We measured the length (l) and breadth (b) of each egg, and for male and female parents we measured length of tarsus, culmen, 10th primary feather, central and outer rectrices, and unflattened wing chord. We also recorded mass, and scored the integumentary color of the cere, lores, and tarsi on a six-point scale (Dawson and Bortolotti 2006b); on our scale, a lower score indicates brighter coloration.

Although the first individuals to arrive on a breeding area are thought to secure the highest quality nest sites (Fontaine and Martin 2006a), intraspecific interactions as a result of mate choice and resource limitation (food, nest sites) may complicate this relationship. The outcome of these interactions can be a function of individual quality, and so we examined several measures to test whether the quality of males and females differed among those that chose control or treatment boxes. We calculated two measures of adult quality. First, we used the first component (PC1) of a principle components analysis (PCA) that was calculated using the six linear size measurements taken from all adults (first capture only) caught on the study area in 2007 and 2008. Data from males (n = 130, 49.89% variance explained) and females (n = 105, 48.30% variance explained) were analyzed separately (Bortolotti and Iko 1992). As an index of body condition of male parents we used the residuals from a linear regression of body mass, measured during incubation, on PC1 (Dawson and Bortolotti 2000). Body condition of kestrels can vary during the breeding season (Dawson and Bortolotti 1997); however, we detected no relationship between capture date and

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condition residuals so did not correct for capture date. There was no relationship between mass (measured during incubation) and PC1 ($r = 0.01$, $P = 0.90$, $n = 99$) among females in our study area in 2008, so we used mass as a proxy.

The second measure of adult quality we used was the sum of color scores for the cere, lores, and tarsi. Skin color is correlated with carotenoid concentration in plasma (Bortolotti et al. 2003), and is influenced by prey abundance (Bortolotti et al. 1996), and indirectly, an individual's ability to secure prey. In addition, carotenoid-dependent color may signal the ability to manage parasite infections (Dawson and Bortolotti 2006b), and although environment-dependent, skin color is regulated in a manner that suggests it is a sexually selected trait (Negro et al. 1998). Consequently, in addition to body condition, integumentary color may be considered one measure of individual quality (Bortolotti et al. 1996).

Incubation Behavior. During visits to nests to capture adults, a data logger was installed in some nests to monitor incubation patterns. A small probe was fitted with a rubber sleeve (to prevent damage to the eggs), threaded through the bottom of the nest box, and secured in a position in the middle of, and flush with, the top of the eggs. Probes were connected to HOBO data loggers (Onset Computer Corporation, Massachusetts, U.S.A.) which were programmed to record the temperature at the tip of the probe every 1.6 min.

We used the program Raven and the plug-in Rhythm (Cooper and Mills 2005) to determine the periods when an adult was incubating the eggs (on-bouts) and periods of nonattendance (off-bouts), based on temperature fluctuations. We validated our interpretations by verifying that off-bouts were recorded at the times we captured an adult from the nest ($n = 7$). Off-bouts were not verifiable or readily interpretable for all nest boxes, and some nests were abandoned some time after we installed the probes, so samples sizes for these analyses varied. To maximize sample size, we analyzed incubation rhythms of each box for only one 12-hr period. This 12-hr period was between 08:00 and 20:00 H, within 3 d following installation of the temperature loggers, and on a treatment (playback or control) day, between 9–16 d after clutch completion. We chose a day soon after installation in the event that adults in treatment boxes became desensitized to the playbacks.

Quantifying Natural Squirrel Threat. We estimated the density of red squirrels by conducting surveys in the vicinity of each nest box, over a period of 3 d, within the first week of beginning playbacks. Three parallel transects were walked, within 100 m of each box; the middle transect began in a randomly determined direction 25 m from the box. Each line was 50 m long, and 50 m from adjacent grid lines. When feeding, squirrels leave behind piles of conebracts which can become large over time. In addition, they often leave obvious signs of digging when burying or searching for food (fungi, cones) in the moss layer (Mahon and Martin 2006). We tallied the total number of feeding piles and digging sites encountered within a 4-m swath of grid lines at each nest site (3 transects). We also tallied the number of squirrels encountered (seen or heard) within a 100-m belt of grid lines, taking care to count each individual only once (Mahon and Martin 2006). We conducted these transects near the beginning of the experiment to determine squirrel density at a time when most birds are arriving and prospecting. We also recorded whether squirrels were detected (seen or heard within 100 m of nest boxes) at each nest visit (two per day, every third day) and calculated the proportion of visits on which squirrels were detected for each nest site.

To control for squirrel density and prevalence we calculated an index of natural squirrel threat using PC1 (52.76% variation explained) from a PCA that included for each nest site the total number of feed piles, total number of digs, number of squirrels detected (seen or heard), and the proportion of visits where a squirrel was detected (seen or heard). Higher (more positive) values of PC1 are associated with greater numbers of feed piles, digs, and squirrel detections at each site.

Data Analysis. We used binary logistic regression to asses nest-site (box) selection (selected, unselected) as a function of experimental manipulations (control, treatment), surrounding habitat composition (mature mixed forest, harvested), natural squirrel threat (PC1), and treatment-by-squirrel threat interaction. We used a backwards stepwise approach to sequentially remove terms that did not improve model fit. We evaluated each model by comparing the log-likelihood to that of the null model using a goodness-of-fit χ^2 to test the null hypothesis that at least one of the coefficients equaled zero (Quinn and Keough 2002). The inclusion of predictor terms was evaluated by using the likelihood ratio test to determine loss of fit with the individual exclusion of each variable in a given model; we used this in addition to the Wald statistic

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because it yields greater power with small sample sizes (Quinn and Keough 2002).

We used analysis of covariance (ANCOVA), with natural squirrel threat as a covariate, to test whether male or female body condition or integumentary color differed among individuals that chose treatment or control nests. We also tested for differences in the size of males and females according to treatment; size can influence the energy budget (Vedder et al. 2005) and aerial agility (Bortolotti and Iko 1992) of kestrels and therefore may influence the ability to secure a mate, and provision nestlings.

We used ANCOVA to test for the effects of treatment on clutch-initiation date, clutch size, mean egg volume in each nest, hatching success, percent of time spent off the nest during incubation, mean incubation off-bout duration, number of incubation off-bouts per 12 hr, and duration of incubation. Treatment group was the categorical variable and natural squirrel threat was the covariate in each model. Although kestrels usually begin continuous incubation when the third egg is laid (Bortolotti and Wiebe 1993), we could not confirm that all birds began incubating at this time, so we calculated a coarse estimate of the duration of incubation as the number of days between clutch completion and the day the first egg hatched. Egg volume was calculated as $0.51*l*b^2$ (Hoyt 1979) and hatching success was calculated as the ratio of the number of nestlings hatched to the number of eggs laid. For analyses of clutch size and egg volume, we also included mass of females and clutch initiation date as additional covariates, and for analyses of hatching success, clutch size and male size were included as additional covariates. For all analyses we iteratively removed terms that did not approach significance ($P < 0.10$), but we included experimental treatment as a fixed factor and natural squirrel threat as a covariate in all final models because we were interested in both the influence of our experiment and the background risk of nest predation from squirrels on the variables we tested.

All data were examined visually and statistically for distributional violations. Parametric tests were used in all cases because we detected no severe departures from normality, and no statistically significant inequality of group variance. In cases where the homogeneity of regression slopes assumption was violated, we examined each experimental group individually. All analyses were performed using SPSS 13.0 (Norušis 2000) and results were considered significant at $P = 0.05$. We present means ±1 SE and show final statistical models only.

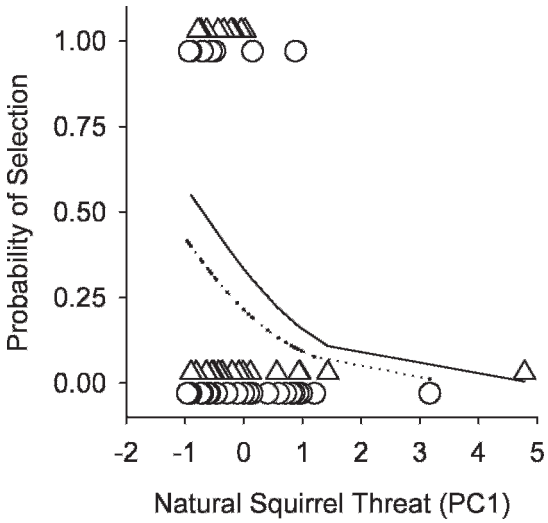


Figure 1. Observed and predicted probabilities of American Kestrels (*Falco sparverius*) selecting nest boxes where the perceived risk of nest predation was experimentally increased (open circles, dashed line) or control boxes (open triangles; solid line) in relation to the natural threat of nest predation imposed by squirrels present in the vicinity of nest boxes. Observed values have been slightly offset by treatment group to illustrate their distribution on the plot.

RESULTS

Nest-box Selection. Kestrels initiated clutches in seven treatment, and nine control boxes ($n = 29$ boxes for each experimental group). Summary statistics for reproductive measures are shown in Table 1; all kestrels that bred in 2007 and 2008 are provided for reference. The logistic regression model including treatment group and squirrel threat as explanatory variables performed significantly better than the null model ($\chi^2_2 = 6.42$, $P = 0.04$). In this model, neither treatment group ($\beta = 0.61$, ±0.60 SE, Wald = 1.01, $P = 0.32$) nor natural squirrel threat ($\beta = -0.99 \pm 0.54$ SE, Wald = 3.42, $P = 0.06$) had coefficients that were significantly different than zero; however, natural squirrel threat approached significance, and the fit of the full model was significantly better than the reduced model that excluded natural squirrel threat ($\chi^2_1 = 3.79$, $P = 0.05$), but not treatment group ($\chi^2_1 = 1.29$, $P = 0.26$). This indicates that although our manipulations of perceived predation risk did not affect nest-site selection, the threat imposed from background squirrel presence near potential nest sites likely had some negative influence on nest-site selection (Fig. 1).

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Table 1. Summary statistics of reproductive measures of American Kestrels (*Falco sparverius*) breeding in north-central Saskatchewan in 2007 and 2008.

Year	Experimental Group	Clutch-initiation Date			Clutch Size			Hatching Success			Number of Young Fledged		
		Mean	SE	Range	Mean	SE	Range	Mean	SE	Range	Mean	SE	Range
2007	None	134.70	1.16	115–173	4.94	0.09	2–7	0.64	0.06	0–1	2.81	0.30	0–5
2008	None	142.51	1.18	128–162	4.60	0.09	3–5	0.83	0.06	0–1	3.20	0.25	0–5
	Control	137.38	1.48	134–145	4.75	0.16	4–5	0.72	0.16	0–1	2.38	0.75	0–5
	Playback	145.86	2.28	136–153	4.57	0.37	3–6	0.40	0.19	0–1	0.71	0.71	0–5

There were no differences in male or female size (PC1), male condition, female mass, or male color scores between individuals that selected treatment versus control nests; natural squirrel threat was not significant in any of these analyses (Table 2). Although the integumentary color of females that nested in treatment boxes was duller than those in controls, there was a significant interaction between treatment and natural squirrel threat so we were unable to test the significance of this difference using an ANCOVA. Analyses conducted separately for each treatment group showed that in control boxes, females with duller (higher) color scores during incubation settled in boxes with a higher natural squirrel threat ($r = 0.77$, $P = 0.01$, $n = 9$), whereas in treatment boxes, we detected no relationship ($r = 0.01$, $P = 0.99$, $n = 6$).

Reproductive Effort. Although natural squirrel threat affected nest-site selection, it did not significantly influence clutch-initiation date, clutch size, mean egg volume, or hatching success (Table 3). Kestrels that laid clutches in treatment boxes initiated later than kestrels that laid clutches in control boxes (Fig. 2a, Table 3). After controlling for clutch-initiation date, we found that clutch sizes in the treatment group were larger than those in the control group (Fig. 2b, Table 3). We found no difference between experimental groups in mean egg

Table 2. ANCOVA parameters of final models testing for differences in individual adult quality among American Kestrels (*Falco sparverius*) that chose nest boxes where perceived threat of predation was experimentally increased or control nest boxes. Natural squirrel threat is an index of the background risk of nest predation posed by squirrels using PC1 from a PCA that included four measures of squirrel presence at each nest site.

Dependent Variable	Mean ±SE[a]		Independent Variables[b]	*F*	df	*P*
	Control	Playback Treatment				
Female size (PC1)	0.52 ± 0.46	−0.46 ± 0.46	Experimental group	2.30	1,11	0.16
			Natural squirrel threat	0.71		0.42
Female mass (g)	132.67 ± 4.37	128.67 ± 4.33	Experimental group	0.35	1,12	0.56
			Natural squirrel threat	0		0.99
Female color	10.67 ± 0.62	11.17 ± 0.54	Experimental group	2.08	1,11	0.18
			Natural squirrel threat	7.14		0.02
			Experimental group-by-natural squirrel threat	7.23		0.02
Male size (PC1)	−0.10 ± 0.34	−1.13 ± 0.57	Experimental group	3.53	1,10	0.09
			Natural squirrel threat	0.01		0.94
Male condition	−3.44 ± 2.32	−.41 ± 1.73	Experimental group	0.78	1,10	0.40
			Natural squirrel threat	0.01		0.93
Male color	7.63 ± 0.42	7.0 ± 0.32	Experimental group	1.09	1,10	0.32
			Natural squirrel threat	1.31		0.28

[a] Raw means.

[b] In all cases, experimental group is the independent variable of interest, subsequent independent variables are covariates.

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Table 3. ANCOVA parameters for final models testing for differences in reproductive effort and incubation vigilance of American Kestrels (*Falco sparverius*) that chose nest boxes where perceived threat of predation was experimentally increased or control nest boxes. Natural squirrel threat is an index of the background risk of nest predation posed by squirrels using PC1 from a PCA that included four measures of squirrel presence at each nest site.

	MEAN ±SE[a]					
DEPENDENT VARIABLE	CONTROL	PLAYBACK TREATMENT	INDEPENDENT VARIABLES[b]	*F*	df	*P*
Julian clutch-initiation date	138.27 ± 1.73	145.94 ± 1.96	Experimental group	8.60	1,13	0.01
			Natural squirrel threat	2.10		0.17
Clutch size	4.25 ± 0.21	5.14 ± 0.23	Experimental group	6.52	1,11	0.03
			Natural squirrel threat	1.10		0.32
			Clutch initiation date	19.34		0.001
Mean egg volume (cm^3)	14.23 ± 0.33	14.44 ± 0.41	Experimental group	0.16	1,11	0.70
			Natural squirrel threat	0.003		0.96
			Female mass	5.41		0.04
Hatching success	0.47 ± 0.15	0.50 ± 0.18	Experimental group	0.01	1,10	0.93
			Natural squirrel threat	1.07		0.34
			Clutch size	5.57		0.05
			Male size (PC1)	4.65		0.07
Time off (%)	7.10 ± 2.10	7.40 ± 2.70	Experimental group	0.01	1,7	0.95
			Natural squirrel threat	0		1
			Clutch size	4.26		0.085
Number of off-bouts/12 hr	7.04 ± 1.65	5.17 ± 2.25	Experimental group	0.41	1,8	0.54
			Natural squirrel threat	0.26		0.62
Incubation duration (d)	26.76 ± 0.44	28.48 ± 0.62	Experimental group	5.08	1,6	0.065
			Natural squirrel threat	6.19		0.047

[a] Marginal means.
[b] In all cases, experimental group is the independent variable of interest, subsequent independent variables are covariates.

volume or hatching success, although hatching success was positively related to clutch size and negatively related to male size (Table 3). We observed that more pairs that nested in treatment boxes appeared to abandon their nests altogether prior to hatching (four out of seven) than those that nested in control boxes (two out of nine); however, a logistic regression showed that neither playback treatment or natural squirrel threat predicted abandonment ($\chi^2_2 = 2.37$, $P = 0.31$).

Incubation Behavior. There was a nonsignificant trend for percent of time nests were left unattended to decrease with larger clutches, but we found no experimental effect on the percent of time off, or on the number of off-bouts in a 12-hr period (Table 3). Although mean off-bout duration was slightly longer for playback treatment nests (9.68 min ± 1.95) than controls (9.12 min ± 1.75), the assumption of homogeneity of regression slopes was violated (natural squirrel threat-by-experimental group: $F_{1,12} = 6.33$, $P = 0.04$; Fig. 3) so we did not examine this difference for statistical significance. Both experimental and control groups showed positive relationships between natural squirrel threat and off-bout duration, but this was significant only for the control nests (Fig. 3). In addition, hatching success decreased as the mean off-bout duration increased ($r = 0.70$, $P = 0.02$, $n = 11$).

Natural squirrel threat was a significant covariate in our analysis of incubation duration, and although mean incubation duration was longer for treatment boxes, this effect only approached significance (Table 3). It is also noteworthy that although sample sizes were limited, correlation analyses showed that boxes with longer mean off-bout durations had longer incubation durations ($r = 0.80$, $P = 0.02$, $n = 8$).

DISCUSSION

Nest-box Selection. We directly manipulated cues of the risk of nest predation to determine the importance of this interspecific interaction on nest-site decisions. Increasing the perceived risk of nest predation by using squirrel vocalizations and altered nest boxes did not have a direct influence on nest-site selection by American Kestrels in our study area. Males establish territories, and for females, the

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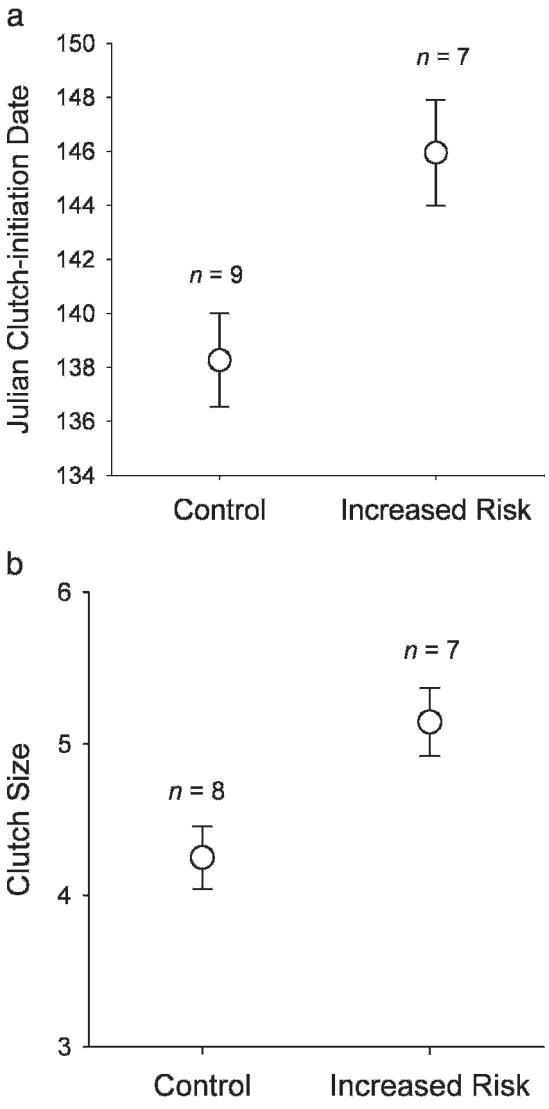


Figure 2. Marginal means (±1 SE) of Julian clutch-initiation dates (2a) and clutch sizes (2b) of American Kestrels (*Falco sparverius*) that initiated breeding in control nest boxes and boxes where the perceived risk of nest predation was experimentally increased, after controlling for natural squirrel threat (2a) and for clutch-initiation date and natural squirrel threat (2b).

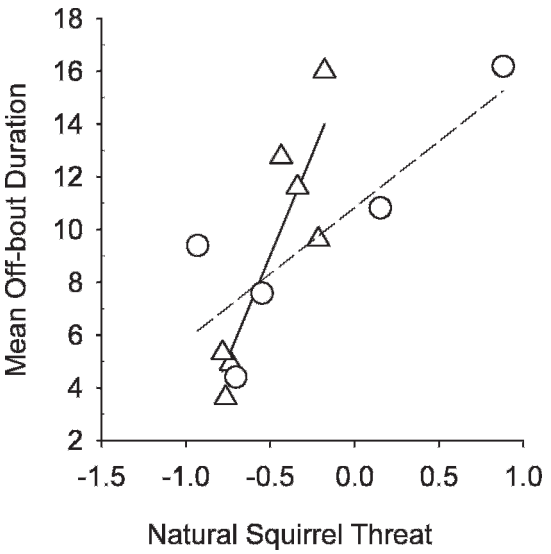


Figure 3. Mean off-bout duration (min) of American Kestrels (*Falco sparverius*) in control boxes (open triangles, solid line; $r^2 = 0.78$, $P = 0.008$) and boxes where the perceived risk of nest predation was experimentally increased (open circles, dashed line; $r^2 = 0.73$, $P = 0.065$) in relation to natural squirrel threat.

choice of a mate likely involves not only an assessment of the individual male, but of the quality of the territory he has secured. Ultimately, females choose a nest site from among several the male may present to her on his territory (Balgooyen 1976); this is the finest scale decision made with regard to breeding habitat selection (Orians and Wittenberger 1991). This series of decisions should factor in the relative value of potential nest sites so that, on balance, the chosen nest site is one that will maximize fitness (Martin 1998, Morris 2003, Fontaine and Martin 2006a). We controlled for background levels of the threat of nest predation, and examined settlement outcomes with respect to individual quality, but we did not quantify all possible factors that may signal nest-site quality and interact with the risk of nest predation to influence parental decisions. For example, resource availability (e.g., food availability, the number of potential nest sites/territory) is known to influence reproductive success of kestrels (Wiebe and Bortolotti 1994, Dawson and Bortolotti 2000, 2002) and may also have played a role in nest-site selection.

Although we made small physical adjustments to experimental nest boxes to mimic use by squirrels, the primary cue that we used was auditory. Our results showed that these cues did not significantly alter nest selection behavior, but that the natural squirrel threat did. All but one of the measures of natural squirrel threat that we used were visual cues. If a squirrel is detected near a box at a given point

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in time, either by sight or sound, it may be a resident of that territory, or simply moving through the area. Consequently, an audio cue therefore may not be the most reliable indicator of the threat of squirrel presence throughout the nesting phase; however, physical (visual) cues, such as digging and feeding piles, which can grow large over time, are indicative of the persistent presence of squirrels in an area. Kestrels may utilize these physical cues as indicators of the long-term threat imposed by squirrels when assessing potential nest sites. Furthermore, kestrels hunt by sight and may also rely most heavily on visual cues in their initial assessment of predation risk.

We found no indication that adults that had brighter integument color or were in better condition were more likely to nest in control boxes (Table 2). However, skin color and condition can vary throughout the different phases of breeding (Dawson and Bortolotti 1997, 2006b) so it is possible that we found no pattern in settlement as a function of adult quality because we captured and measured adults during incubation rather than settlement. Among females that nested in control boxes, those that were duller during incubation nested in boxes with higher natural squirrel threat, but differences in color, mass, or size of females that nested in treatment boxes did not differ from those in control boxes. So although we found a relationship between female color and natural squirrel threat in control boxes, our results are not suggestive of the idea that higher quality adults were more successful at securing boxes they perceived to be associated with a lower risk of nest predation. Alternately, there was little suggestion that there may be some cost to nesting in boxes with a higher perceived risk of nest predation.

Reproductive Investment. Birds that initiate breeding earlier typically realize higher reproductive success; this may occur as a function of parental quality or temporal changes in the environment that influence resource availability, resulting in lower survival probability of avian offspring with later onset of breeding (Verhulst and Nilsson 2008). We found that birds that chose treatment nests initiated breeding more than one week later than pairs that selected control nests. If this were a function of competitive interactions that resulted in lower quality birds selecting treatment boxes, we would have expected to detect differences in adult quality between those that settled in treatment and control boxes. Given that we found no evidence of such differences, we suggest a facultative delay in the timing of breeding by kestrels. It is possible that once females selected a mate whose territory included a treatment box, they required a longer period of time to weigh the benefits of breeding in treatment boxes against the associated risk of nest predation that they perceived.

The increase in clutch size that we observed is contrary to both theory and empirical evidence suggesting that birds reduce clutch size in response to increased nest predation (Slagsvold 1984, Doligez and Clobert 2003, Eggers et al. 2006). Martin and Li (1992) found that secondary cavity nesters (non-excavators) had larger clutch sizes than primary cavity nesters (excavators) or open cup nesters, even though they experienced higher failure rates than excavators. Subsequently, Martin (1993) suggested that the evolution of clutch size in cavity nesting birds is driven by variation in nest-site limitation more than nest predation; non-excavators are more constrained by the availability of nest sites than excavators. Although squirrels can depredate entire clutches or young broods, often only partial clutch loss occurs (J. Greenwood unpubl. data). Double-brooding has not been documented at our study area, so where nest sites and subsequent breeding attempts are limited, a facultative increase in clutch size may increase a pair's chance of fledging at least one young during their first attempt, even if they experience partial predation of their clutch.

It is also possible that the increase in clutch size we observed was a function of the delay in clutch initiation. This delay allowed females in treatment boxes an additional week to acquire nutrients, which may have enabled them to lay more eggs. Studies of Eurasian Kestrels (*F. tinnunculus*) have shown that the typically negative relationship between clutch-initiation date and clutch size can become decoupled when food availability is manipulated (Aparicio 1994). Regardless, previous experiments conducted at our study area indicated that although kestrels laid larger eggs in response to food supplementation, they did not increase clutch size (Wiebe and Bortolotti 1994). We did not observe any difference in mean egg volume of birds that initiated breeding later (Table 3), and so it seems unlikely that acquisition of additional nutrient reserves by delayed females can account for our results.

Red squirrels have been observed using parental activity to locate nests of open cup and cavity nest-

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ing passerines (Ghalambor and Martin 2002), and heightened parental activity at the nest is associated with significant proximate increases in nest predation in open-cup and ground-nesting birds (Wiebe and Martin 1997, Martin et al. 2000b). Faced with increased nest predation, open-cup nesters have been shown to adopt longer on- and off-bout durations thereby reducing activity at the nest (Conway and Martin 2000). We found that off-bout durations were indeed longer at nest sites with higher natural squirrel threat, but were unable to evaluate the significance of longer off-bout durations in playback treatment nests.

Although the effect of experimentally increased risk of predation on off-bout duration was inconclusive, the incubation duration was 1.7 d longer than that in control boxes. This delay approached significance, and higher natural squirrel threat also produced longer incubation periods (Table 3). Short incubation periods have been shown to increase hatching success in other birds (e.g., Lyon and Montgomerie 1985) and our data showed that hatching success decreased with longer mean incubation duration. This relationship suggests an indirect cost to the perception of increased risk of nest predation. However, although parental decisions that result in decreased hatching success lead to reduced fitness (Brown 1988), the cost is presumably lower than would be incurred in the event of complete nest failure in the absence of anti-predator strategies.

Our manipulations showed that kestrels adjust their reproductive strategies in response to the risk of nest predation they perceive, but further studies are required to establish the cause of delayed clutch initiation, and the ultimate function of, and mechanism for, increased clutch sizes. The increase in clutch size that we observed in experimental boxes would be of enhanced interest if, in fact, lower quality females were securing higher risk boxes and initiating later. In this case, we would expect reduced clutch sizes in these nests. Larger, longer-term studies may clarify this phenomenon, in addition to whether and how kestrels adjust incubation behavior in response to this constraint. Theory surrounding the role of nest predation in influencing reproductive decisions will be greatly improved by an increased body of experimental work that quantifies the relative influence of resource availability and nest substrate, and that spans multiple avian taxa.

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