

Adaptive phenotypic plasticity in an island songbird exposed to a novel predation risk

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Avian nest site selection and levels of parental care require assessments of numerous fitness costs and benefits. Nest site selection in open cup–nesting species is considered a relatively conservative trait; most species and genera are confined to nesting within particular vegetation strata. The nesting stratum further determines risk to nest predation, the principal cause of reproductive failure. We document predator-induced plasticity in nest site placement and levels of parental care in orange-crowned warblers (*Vermivora celata*) on an island lacking avian nest predators. We show a shift from ground nesting, characteristic of mainland populations, to off-ground nesting that appears adaptive relative to higher predation levels of ground nests. By altering the perceived nest predation risk via experimental introduction of a model avian predator prior to nest building, we demonstrate that warblers shift nest sites to more concealed ground locations. Moreover, warblers differentially adjust nest visits to feed nestlings in the presence of the predator: reducing feeding more at less concealed off-ground nests than at more concealed ground ones. Both shifts in nest site placement and feeding rate adjustments suggest adaptive phenotypic plasticity in response to increased perceived predation risk, providing evidence that birds continuously assess variation in the fitness costs and benefits of their behavioral decisions. *Key words*: adaptive phenotypic plasticity, nest site selection, parental care, predation risk. [*Behav Ecol*]

Theory predicts that animals subject to variable environments should be under selection for the ability to continuously assess the fitness costs and benefits of their behavioral decisions and modify their behavior accordingly (Shettleworth et al. 1988; McNamara 1996; Sih 1997). Predation risk is one environmental factor that often varies spatially and temporally and has been shown to impose trade-offs on the allocation of time and energy to different behaviors (Lima and Dill 1990; Sih 1992; Lima and Bednekoff 1999). Yet, in many cases, we lack an understanding of the fitness consequences of the range of decisions possible under the risk of predation (e.g., Lind and Cresswell 2005).

Nest predation is the principal cause of reproductive failure in open cup–nesting birds (reviewed by Martin 1993a). Inter-specific variation in the risk of nest predation is closely tied to differences in the strata where nests are placed, which in turn is correlated with a suite of life-history traits such as clutch size, nestling growth rate, nestling provisioning rate, and adult survival (Martin 1995; Martin et al. 2000). For example, in open cup–nesting passerines, ground nests typically face the lowest predation risk, followed by canopy and shrub nests (Yahner and Scott 1988; Martin 1993a, 1995). Presumably, because they are less constrained by the risk of attracting visually oriented predators, ground-nesting species provision their nestlings at a higher rate compared with canopy and shrub nesters (Martin et al. 2000). Yet, despite the potential benefits of being able to nest at different heights, most open cup–nesting passerines are substrate specialists (i.e., consis-

tently placing their nests on the ground, in shrubs, or in tree canopies), with high within-species stereotypy in nest placement (Martin 1988, 1993a). Consistent specialization suggests that nest placement is evolutionarily conservative either due to shared ancestry (Collias NE and Collias EC 1984) or because nest predation may exert strong stabilizing selection (Martin 1993b).

Despite the conservative nature of nest site selection, birds have been shown to exhibit the ability to assess predation cues and modify a range of reproductive behaviors. For example, experimental increases in the perceived risk of nest predation have been shown to result in the selection of more concealed or safer nesting sites within a stratum (Larson 2000; Forstmeier and Weiss 2004; Eggers et al. 2006) and a reduction in nest visitation rates (Ghalambor and Martin 2001, 2002). Similarly, experimental reduction of the risk of nest predation results in birds increasing investment in egg size, clutch mass, and visitation rates at the nest (Fontaine and Martin 2006). These results suggest that birds may be constantly assessing predation risk and adaptively adjusting their nest placement decisions to minimize fitness costs.

Here, we examine the capacity for adaptive behavioral plasticity under the risk of nest predation in an open cup–nesting, insectivorous passerine *Vermivora celata sordida*, a subspecies of orange-crowned warbler (Aves: Parulidae) endemic to the coast of southern California and the Channel Islands. Three of the 4 recognized *Vermivora celata* subspecies (*Vermivora celata celata*, *Vermivora celata orestera*, and *Vermivora celata lutescens*) and nearly all other species in the genus *Vermivora* are strictly ground nesters (Curson et al. 1994). In contrast, *V. c. sordida* exhibits unusual plasticity in nest placement on the Channel Islands: females build nests on the ground, in shrubs, and up to 8 m in tree canopies (Sogge et al. 1994; Peluc SI, personal observation). This flexibility in nest site choice could be driven by the rarity of avian nest predators on all but 1 of

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Received 9 April 2007; revised 18 January 2008; accepted 29 February 2008.

the 8 Channel Islands (see Garret and Dunn 1981). In this study, we first use field data on nest fates to test whether the shift away from ground nesting and into the shrub and canopy is an adaptive response to escape higher levels of nest predation on the ground. We then experimentally increase the apparent risk of nest predation using a common, mainland avian nest predator, the western scrub jay (*Aphelocoma californica*; see Preston and Rotenberry 2006 and references therein) to test if *V. c. sordida* have the capacity for assessing predation risk and modifying their nest site selection. Finally, we test the consequences of nest site selection (ground vs. off-ground) on parental provisioning rates in the presence and absence of a simulated avian predator.

MATERIALS AND METHODS

Study area and study system

Data presented here are based on observational and experimental studies of *V. c. sordida* breeding in two 10 ha plots in Bulrush Canyon, Santa Catalina Island, California, USA (33°22'30"N, 118°25'56"W), from March to May 2004. Plots were delineated into 25 × 25 m grids with flagging to facilitate mapping of warbler territories and finding nests. Warbler density on the plots ranged from 4 to 5 pairs per ha. Clutches of all nests considered in this paper were completed between 10 March and 10 April. Only female *V. c. sordida* build nests and incubate eggs, whereas both parents feed nestlings. Some warblers were year-round residents in the study area, but most departed after breeding, presumably to spend the July–December nonbreeding season along the coast of southern California and northern Baja California, Mexico (Sogge et al. 1994; Peluc SI, Sillett TS, Ghalambor CK, unpublished data). Dominant plant species on the study plots were island scrub oak (*Quercus pacifica*), toyon (*Heteromeles arbutifolia*), laurel sumac (*Malosma laurina*), lemonade berry (*Rhus integrifolia*), coyote brush (*Baccharis pilularis*), and poison oak (*Toxicodendron diversilobum*). The canopy was between 3 and 8 m high and the understory vegetation formed dense thickets.

Several snake and mammal species, but no bird species, were observed or suspected of depredating warbler nests in 2004: gopher snake (*Pituophis melanoleucus*), Santa Catalina Island fox (*Urocyon littoralis catalinae*), Santa Catalina Island deer mouse (*Peromyscus maniculatus catalinae*), and Beechey's ground squirrel (*Spermophilus beecheyi nesioticus*). Both feral cats (*Felis catus*) and Norway rats (*Rattus norvegicus*) are present on the island and probably depredate warbler nests as well. Avian nest predators of *V. c. sordida* are essentially absent from Santa Catalina Island (Garret and Dunn 1981). *Aphelocoma* jays do not occur, and common ravens (*Corvus corax*), while on the island, have not been observed depredating warbler nests or interacting with warblers (e.g., via predator mobbing) during 5 years of work on the island (2003–2007; authors' unpublished data).

We mapped all warbler territories on the plots (see Sillett et al. 2004), banded adults, and found and monitored nests. Adults were captured in mist nets and individually marked with a unique combination of 1 US Fish and Wildlife Service aluminum leg band and 3 colored plastic leg bands. Most nests were found during nest building, and all were checked every 2 days to determine breeding stage (i.e., building, egg laying, incubation, and nestling) and fate. Nest heights were measured after nests fledged or failed.

Experiment 1: increased predator cues during prebuilding stage

To test if *V. c. sordida*'s nest site selection could be influenced by the presence of an avian nest predator, we randomly assigned 36 territories to 1 of 3 treatments: scrub jay presenta-

tion (predator), house finch presentation (*Carpodacus mexicanus*; nonpredator), or no model presentation. Scrub jay and finch treatments consisted of presentations of taxidermy models and broadcast vocalizations of each species while warbler females were prospecting for nest sites, but before they started nest building. The combination of taxidermy mounts with vocalizations was used to prevent habituation to the mounts alone (Ghalambor and Martin 2000, 2001, 2002). Females were exposed to presentations between 0600 and 1400 h. On each experimental territory, a scrub jay or finch mount was attached to a branch approximately 1 m above ground, and a speaker playing the mount species' vocalizations (both calls and songs) was concealed in vegetation directly below the mount. Vocalizations were played on a loop for 20–25 s followed by 20–25 s of silence, then repeated, to mimic natural singing behavior. Mounts and speakers were relocated within territories every 30–60 min. We visited the 12 "no model" territories with the same frequency as those receiving model presentations. An observer watched each focal female's behavior daily to determine when and where nest building began. We terminated presentations and territory visits when a female started to build; thus, treatments varied in duration among territories because females took up to 10 days to prospect for a nest site. Focal territories were at least 50 m apart and, when possible, in different drainages to prevent mounts and vocalizations from one experimental unit affecting another. All nests were monitored with equal effort. Only first nesting attempts were included in this experiment to avoid confounding factors, such as fate of previous nest that might influence nest site selection. After nest fledging or failure, we quantified nest height and nest concealment. Nest concealment was measured following a BBIRD protocol after Martin et al. (1997). Briefly, we quantified the amount of the nest obscured by vegetation from 1 m over the nest looking down (percentage of overhead cover), as well as the percentage of the nest obscured by vegetation from 1 m north, east, west, and south of the nest at nest height (percentage of side cover). These measurements were combined, and the mean percentage of concealment was calculated for each nest.

Experiment 2: increased nest predation risk during nestling stage

To test the consequence of different nest site selection decisions on parental risk taking, we sequentially presented taxidermy mounts and vocalizations of a scrub jay (predator) and a house finch (control), in random order, to parents feeding nestlings. Mounts and speakers were placed approximately 5 m from nests so that parents could detect the models and continue feeding nestlings, without eliciting a nest defense response (Ghalambor and Martin 2000, 2001). Scrub jay and finch mounts were attached approximately 1 m high in tree saplings, and speakers were hidden directly below mounts. Vocalization playbacks followed the protocol in Experiment 1. To simulate the movements of a real jay or finch and thus minimize habituation of parents to the mounts (Ghalambor and Martin 2000, 2001), a string was tied to the base of the sapling and used by an observer at 10 m distance to gently move the sapling and mount during presentations. The experiment was conducted at 16 randomly selected warbler territories (8 ground nests and 8 nests located 1–4 m above ground) between 0600 and 1200 h and within 1 day of nestlings breaking primary pinfeathers, to control for stage of nestling development on feeding rates and levels of parental investment. Our experimental design consisted of an initial control period of 45 min followed by a 45-min model presentation period of either the scrub jay predator or the finch control, randomly chosen, followed by another 45-min presentation period of the other model. An observer recorded the number and time of all feeding trips before and during

presentations. No warbler pairs selected for this experiment were involved in Experiment 1.

Analyses

Daily nest survival probability (S) of nonexperimental nests was analyzed with a maximum likelihood approach in program MARK (White and Burnham 1999; Shaffer 2004) because some nests were found after females began incubation. We considered 2 candidate models in which S was either conditional on nest height (S_{height}) or constant (S). Nest height was not standardized prior to analysis. Models were fit using a logit link function and ranked by second-order Akaike's information criterion (AIC_c) scores. Relative likelihood of each model was estimated with AIC_c weights (w_i ; Burnham and Anderson 2002).

Individual warbler pairs and their nests were treated as independent sample units for analyses of experimental data, which were conducted with programs SAS/STAT and JMP (SAS Institute 2003, 2006). When necessary, data were transformed to meet model assumptions. However, summary statistics are presented as means \pm 1 standard error from untransformed data. Experiment 1: The distribution of warbler nest heights in our sample was highly skewed, with many nests on the ground, that is, nest height = 0, and some nests as high as 5 m. Therefore, we used a generalized linear model (GLZ) with a negative binomial error distribution and a log link function (McCullagh and Nelder 1989; Cameron and Trivedi 1998) to compare nest heights among the 3 experimental treatments and a fourth treatment comprised of the nonexperimental nests monitored on our study plots. Analysis of variance was used to compare concealment between ground and off-ground nests. All experimental nests were found during nest building, that is, prior to egg laying, which allowed us to employ logistic regression to test if nest fate (i.e., fledged or failed) was related to nest height in the 3 experimental treatments. Experiment 2: A matched-pairs t -test was used to analyze the effect of model presentation on parental provisioning rates. For each nest, we compared control (i.e., pretreatment) feeding rates with feeding rates in the presence of the finch and jay models. Nest height class (ground or off-ground) was modeled as an independent group variable.

RESULTS

Nest height and survival on Santa Catalina Island

We found and monitored the fates of 63 nonexperimental *V. c. sordida* nests. Nest height ranged from 0 to 5 m (Figure 1) and was not correlated with clutch completion date ($r = -0.09$, $P = 0.46$). Daily survival probability increased with nest height (model S_{height} : $AIC_c = 275.64$, $w_i = 0.98$; model S : $AIC_c = 283.67$, $w_i = 0.02$), indicating that nests located above ground were more likely to fledge young than those on the ground (Figure 2).

Experimentally increased nest predation risk during the prebuilding stage

Experiment 1 had a dramatic effect on *V. c. sordida* nest heights (GLZ, overall treatment effect: $\chi^2_3 = 19.79$, $P = 0.0002$; goodness-of-fit for negative binomial model: $\chi^2_{95} = 85.21$, $P = 0.75$). The experimental introduction of scrub jay mounts and vocalizations to warbler territories resulted in an absolute change in nest site selection: all 12 females in the scrub jay treatment built their nests on the ground (Figure 1). The 24 females not exposed to predator cues built nests at variable heights, similar to the 63 nonexperimental females (Figure 1). Indeed, heights of nests in the 3 "control" treatments (house

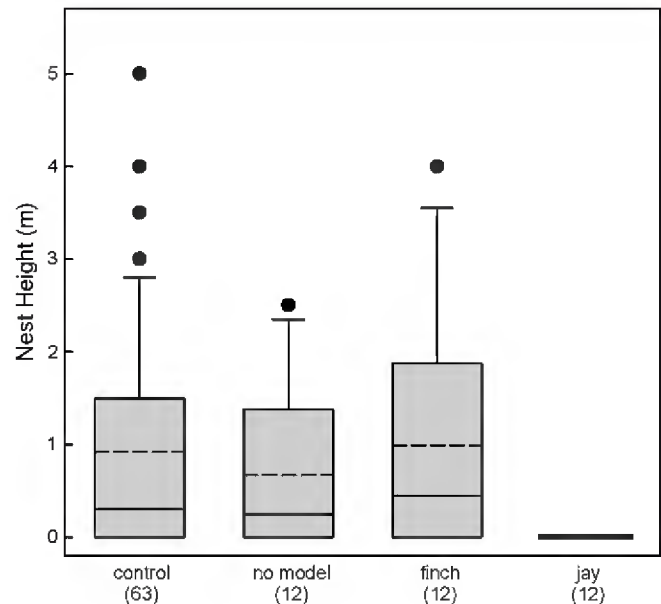


Figure 1

Distribution of orange-crowned warbler nest heights in 4 treatment groups. Solid lines within boxplots denote medians, and dashed lines indicate means; top and bottom of the boxes indicate 25th and 75th percentiles; error bars give 5th and 95th percentiles, and points indicate outliers.

finch, no model, and nonexperimental) were not statistically different from each other (GLZ pairwise contrasts: $\chi^2_1 < 0.23$, $P > 0.63$); nearly half of these 87 females placed their nests on the ground (house finch: 5/12; no model: 6/12; nonexperimental: 29/63). However, mean nest heights in the 3 control treatments were significantly different from 0, the height of all nests in the scrub jay treatment (GLZ contrast: $\chi^2_1 = 19.13$, $P < 0.0001$). Concealment of the experimental nests was negatively correlated with nest height ($r = -0.84$, $P < 0.0001$). Thus, mean concealment at ground nests (0.93 ± 0.03) was

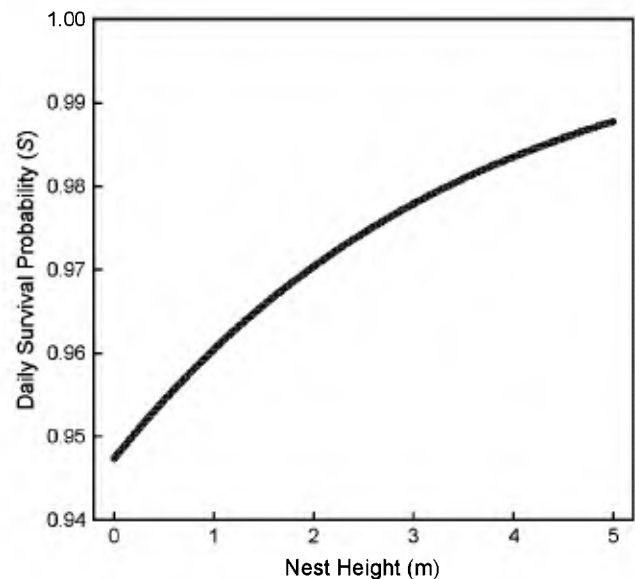


Figure 2

Daily survival probability estimated from 63 orange-crowned warbler nests on Santa Catalina Island, California, USA.

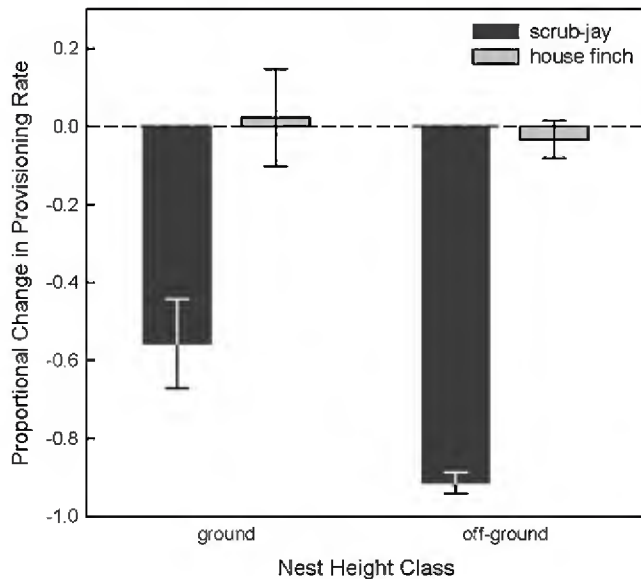


Figure 3

Proportional changes in the number of food deliveries per hour to nestling orange-crowned warblers in 2 nest height categories. Change in feeding rate = (model presented – control)/control.

significantly greater than that of nests built above ground (0.55 ± 0.03), indicating that ground nests were more hidden from visually oriented predators ($F_{1,33} = 77.63$, $P < 0.001$). Like the 63 nonexperimental nests, the probability of fledging young increased with nest height for the 36 experimental nests ($\chi^2_1 = 7.09$, $P = 0.008$, unit odds ratio for height = 3.27 ± 2.34). Thus, experimental females that nested on the ground were less likely to fledge young compared with those nesting off-ground.

Effect of increased immediate nest predation risk on nestling provisioning rates

Scrub jay and finch model presentations had different effects on nestling provisioning rates depending on nest height. All parents exposed to scrub jay presentations during the nestling period responded by significantly decreasing their provisioning rates relative to the prepresentation period (2 tailed $t_{15} = 7.10$, $P < 0.0001$) but did not change their provisioning rates when exposed to house finch cues (2 tailed $t_{15} = 1.00$, $P = 0.33$). Proportion changes in feeding rates are presented in Figure 3. In the presence of the scrub jay model, parents often arrived near the nest with food in their bills and left without feeding nestlings. This behavior was never observed in the presence of the house finch decoy. However, the change in nestling provisioning rate differed significantly between ground and above-ground nests. Parents at above-ground nests reduced their feeding rates to a greater degree in the presence of the scrub jay predator than did adults provisioning young at ground nests (Figure 3; between-group comparison, control vs. scrub jay: $F_{1,15} = 7.67$, $P = 0.02$), whereas nest height class did not affect provisioning rates in the presence of the house finch model (between-group comparison, control vs. finch: $F_{1,15} = 1.00$, $P = 0.33$).

DISCUSSION

For individuals to modify behavior adaptively, they must have the ability to monitor and interpret changing environmental conditions (Moran 1992). Indeed, individuals that can assess

environmental variation, such as the risk of predation, and modify their behaviors may have a fitness advantage over those individuals that exhibit nonplastic fixed responses (Swaigood et al. 1999). Experimental manipulations of the perceived risk of predation have previously demonstrated that birds can assess changes in predation risk and modify a suite of reproductive behaviors in ways that appear adaptive (e.g., Ghalambor and Martin 2001, 2002; Eggers et al. 2006; Fontaine and Martin 2006). Here, we demonstrate that the *V. c. sordida* on Santa Catalina Island exhibit adaptive phenotypic plasticity in nest site selection and nestling provisioning when under the risk of predation from a novel avian nest predator. The observed plasticity suggests a sophisticated ability to assess the fitness costs and benefits of different behaviors and the retention of the ability to recognize *Aphelocoma* jays as predators, even though this avian predator is absent from the island. Collectively, these results provide insight into the 1) patterns of nest site selection on the island versus the mainland, 2) the ability to adjust activity patterns at the nest, and 3) the evolution of behavioral novelty on islands. Below, we discuss these ideas in more detail.

Nest site selection

Is *V. c. sordida*'s shift in nest site selection from the ground—the only stratum used by the 3 mainland subspecies of *V. celata*—into the shrub layer and tree canopy adaptive? This appears to be the case, as the average daily survivorship of nests increases with nest height (Figure 2). Thus, nests located above ground are more likely to succeed than those on the ground. On an island where small mammals and snakes are the main predators and avian predators are absent or rare, it is likely that nests placed above ground, although less concealed, are safer from the predominant nest predators. Whereas well-concealed sites on the ground may therefore be advantageous against visually oriented predators (i.e., foliage cover may reduce transmission of visual cues from nests to potential predators; Martin 1993b), the presence of other predators less dependent on visual cues may impose no, or even opposite, selection pressures for other types or degrees of nest concealment (Clark and Nudds 1991; Martin and Joron 2003; Remes 2005).

Intraspecific stereotypy in nest site use could reflect the fact that nest predation is an unpredictable environmental factor and thus may not favor the evolution of plasticity to shift nest sites between different strata (Kulesza 1990; Sieving 1992; Martin 1995). Yet, nest predation does tend to vary predictably between strata. For example, shrub nests are generally thought to be more vulnerable to avian predators, whereas ground nests are thought to be more vulnerable to snakes and mammalian predators (Martin 1987; Nour et al. 1993; Söderström et al. 1998; Patten and Bolger 2003). The ability of *V. c. sordida* to nest in vegetation strata other than the ground, and at the same time assess *Aphelocoma* jays as potential nest predators and subsequently change their nest site selection to the ground, leads to the question why other species or *V. celata* subspecies do not exhibit the same degree of plasticity in nest site selection. One possible explanation is that in addition to lacking avian nest predators, Santa Catalina Island also lacks much of the diversity of shrub and canopy nesting bird species found in similar habitats on the mainland. This allows *V. c. sordida* to space themselves out vertically and further reduce the opportunity for specialization by predators if their nests were concentrated into one substrate (Martin 1988, 1993a). Thus, a combination of directional selection to shift nest sites higher to reduce nest predation (e.g., Figure 2) and a lack of potentially competing species that might otherwise discourage orange-crowned warblers from

nesting within the shrub and canopy layers may have favored the evolution of nest site plasticity in this population.

Predator recognition and parental care

A reduction in nestling feeding is assumed to be an adaptive ecological and evolutionary strategy that reduces the risk of drawing the attention of visually oriented predators to the nest (Skutch 1949; Ghalambor and Martin 2000, 2001, 2002; Martin et al. 2000). Nevertheless, by reducing their feeding trips to nests, adults also trade off the benefits of reduced predation risk assessment as well as the behavioral response to predator encounters should be a dynamic process (Schmidt 1999; Swaisgood et al. 1999, 2003) and birds that perceive different vulnerability to predation at different nest sites should benefit from the accurate incorporation of the risk level to their response. Warblers nesting above ground reduced nestling provisioning rates in the presence of *Aphelocoma* jays even more than those with ground nests, indicating that shrub- and tree-nesting individuals perceived a greater risk of nest predators than did the ground-nesting individuals, even when both were exposed to the same predator stimulus. Our results are consistent with a previous study by Ghalambor and Martin (2002), who found that the response to a model nest predator increased with increasing risk of nest predation. Our results also demonstrate that even after a nest site has been selected, warbler parents continue to assess their environment and modify their behavior accordingly.

Surveys of island faunas that lack predators often find that antipredator behaviors are lost or diminished (Blumstein et al. 2004; Blumstein and Daniel 2005). Several reasons could explain the retention of avian predator recognition in *V. c. sordida* on Santa Catalina Island. First, warblers nesting on the island probably encounter *Aphelocoma* jays on the mainland during the nonbreeding season. However, scrub jays are not predators of adult warblers. Second, *V. c. sordida* also breed on nearby Santa Cruz Island, home of the endemic Island Scrub Jay (*Aphelocoma insularis*), such that gene flow between island warbler populations could allow for the persistence of predator recognition alleles on Catalina. Third, although we have not documented nest predation by ravens, they are present on Santa Catalina and may opportunistically depredate nests. Thus, although jays are absent, the presence of ravens may be sufficient to maintain the ability to recognize avian predators under the “multipredator” hypothesis (Blumstein 2006). Finally, predator recognition might just be innate (e.g., Veen et al. 2000), and thus, it may not require specific experience with the predator.

Although predator-induced nest site plasticity within a vegetation stratum (e.g., the shrub layer) has been shown for several bird species (Larson 2000; Forstmeier and Weiss 2004; Eggers et al. 2006), the present study is the first to quantify the ability of a bird to use variable vegetation strata in response to variable levels of nest predation risk. Our results also imply that apparent risk of scrub jay predation overrides other predator cues on Catalina and drives females to nest on the ground, a stratum that is actually less safe from predation on the island. Given that nest stratum influences nest temperature and humidity (Peluc 2006), as well as nest size and materials (authors' unpublished data), our data suggest that the conditional use of multiple strata by *V. c. sordida* involves the assessment of a complex suite of variables including nest site availability, microclimate, and predation risk.

The evolution of behavioral novelty on islands

Like many island bird communities, the bird fauna on Santa Catalina Island, and the Channel Islands as a whole, represents

a subset of the total number of species found in similar habitats nearby on the mainland (Garrett and Dunn 1981). One hypothesis to explain the differential colonization of new environments like islands is that species with larger brains are more successful in adapting to novel conditions because of their ability to produce more innovative behaviors (e.g., Sol et al. 2005). Innovation in foraging behavior has previously been used as an indicator of cognitive ability to predict successful colonization of new environments (Sol et al. 2005); however, few studies have considered nest-building behavior from the perspective of cognitive ability. Although the prevailing dogma argues that nest placement is a highly conservative trait and that nest building is largely an innate, stereotyped behavior in most bird species (Collias NE and Collias EC 1984), the observed plasticity in nest placement reported here suggests a striking behavioral innovation. Whether such innovation facilitated colonization of the islands or evolved in response to the island environment after colonization will require comparative studies of mainland and island populations. Nevertheless, given the important fitness consequences of nest placement, the ability to modify nest placement has likely contributed to the success of orange-crowned warblers on the Channel Islands.

FUNDING

Smithsonian Institution; the University of California—Riverside; an American Ornithologists' Union Research Award (S.I.P.).

This paper benefited from the comments of David Reznick, Marlene Zuk, and 2 anonymous reviewers. The Catalina Island Conservancy (CIC) generously provided affordable housing, vehicles, and gasoline. We thank Angela Aarhus and Frank Starkey of the CIC for logistical support and Jill Coumoutso, Hannah Montag, and Jongmin Yoon for help with fieldwork. The research presented here was conducted under all necessary State, Federal, and University banding and Institutional Animal Care and Use Committee permits.

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