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Lack of avian predators is associated with behavioural plasticity in nest construction and height in an island songbird

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Orange-crowned warblers, *Leiothlypis celata sordida*, breeding on the California Channel Islands exhibit remarkable variation in their nest structure and placement, providing an intriguing exception to the general pattern that avian nest structure and nest site selection are highly conserved characters. We examined nest construction at both the population and individual scale to test whether warblers on Santa Catalina Island change their nest construction in response to nest height. At the population level, warblers built both lighter, grass-dominated ground nests and heavier off-ground nests that contained more rigid materials and less grass. The probability of nest success was significantly and positively correlated with nest height. At the individual level, we found the same individuals were capable of building on- and off-ground nests between nesting attempts within the same season. However, nest construction was highly variable among individuals and not significantly correlated with nest success after controlling for nest height. We suggest this observed behavioural plasticity in nest construction and nest height is a hierarchical response to the absence of avian predators. Reduced risk from avian predators appears to allow the warblers to use a variety of nest sites, thereby necessitating increased flexibility in nest construction.

Behavioural plasticity, the capacity for the same genotype to predictably produce different behavioural phenotypes in response to environmental cues, results in some of the most striking examples of how individuals adaptively respond to environmental challenges (Dingemanse et al., 2009; Foster, 2013; Ghalambor et al., 2010; Snell-Rood, 2013; Stamps, 2016). Theory shows that predictable spatial and temporal environmental variation should favour the evolution of adaptive behavioural plasticity, in part to minimize the fitness costs of always producing the same phenotype across environments with different optima (e.g. Foster, 2013; Gavrilets & Scheiner, 1993; Murren et al., 2015; Sultan & Spencer, 2002). However, individuals often vary in plasticity (e.g. an individual/genotype × environment interaction; Dingemanse et al., 2009), and selection can directly act on this variation (Brommer, 2013). Quantifying variation in plasticity among individuals and its fitness consequences are therefore critical for testing the conditions favouring the evolution of plasticity. Variation in predator-induced plasticity provides a particularly good system for asking these questions because of the high fitness costs imposed by predators.

Many animals have evolved the capacity to plastically respond to visual, chemical or other cues linked to predation risk that typically improve survival (Benard, 2004; Relyea, 2001; Say-Sallaz et al., 2019). However, prey often face threats from multiple coexisting predators and may not be able to simultaneously express adaptive behavioural responses to each predator individually (Sih et al., 1998). When predators differ dramatically in the risk they pose, prey may resolve this dilemma by expressing behaviour that mitigates predation from only the most dangerous predator species present (‘hierarchy control’; McIntosh & Peckarsky, 1999; Sih et al., 1998). Such hierarchical behavioural responses to different predator communities have been observed in numerous taxa including invertebrates (Bourdeau, 2009; Hoverman & Relyea, 2007), amphibians (Relyea, 2003; Teplitsky et al., 2004), birds (Syrová et al., 2016) and mammals (Thaker et al., 2011). If such hierarchical plasticity is present, then we can predict a significant shift in

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behavioural responses when important predators are absent from a community.

Island environments provide an opportunity for testing how altered predator communities impact prey behaviour because they often have depauperate predator communities (Wright, 1980). Indeed, many island species have evolved reduced antipredator behaviour on predator free islands (Beauchamp, 2004; Blumstein & Daniel, 2005; Cooper et al., 2014; but see Yang et al., 2014). Theory predicts that behavioural plasticity in response to predators may erode and become more variable over time due to relaxed selection or if the behaviour is costly to maintain (Foster, 2013; Lahti et al., 2009). Less is known about what happens to behavioural responses when only a subset of predators become excluded from a community. For example, prey species may retain their ability to detect predator cues, but their behavioural responses may become more variable because they are under relaxed selection (Lahti et al., 2009). Tests of these ideas are rare because few studies examine how relaxed selection from the loss of dominant predators affects variation in behavioural plasticity.

The ‘dusky’ subspecies of orange-crowned warbler, *Leiothlypis celata sordida*, a songbird endemic to the California Channel Islands and the adjacent mainland coast, provides a model system to test how behavioural plasticity is affected by lack of a dominant nest predator. Almost all species in the genus *Leiothlypis* build highly concealed small cup nests on the ground (Curson et al., 1994). Mainland subspecies of orange-crowned warblers (*L. c. celata*, *L. c. lutescens*, *L. c. orestera*) are almost exclusively ground nesters and only occasionally nest off-ground in low vegetation (Gilbert et al., 2020). Throughout their breeding distribution, orange-crowned warblers coexist with a diversity of avian and terrestrial nest predators (Gilbert et al., 2020; Martin & Martin, 2001; Sofaer et al., 2013). However, on the California Channel Islands, some populations of *L. c. sordida* are notable for the frequency at which they build off-ground nests, and this shift in behaviour has been attributed to differences in the predator community (Montag et al., 2009; Peluc et al., 2008; Sofaer et al., 2013). All the California Channel Islands lack corvids and other visually oriented avian nest predators within the habitats used by *L. c. sordida* for breeding, except for Santa Cruz Island, home to the endemic island scrub-jay, *Aphelocoma insularis*. On Santa Cruz Island, orange-crowned warblers primarily build ground nests, whereas on Santa Catalina Island (hereafter Catalina Island), nests are primarily built off-ground in shrubs and trees (Montag et al., 2009; Peluc et al., 2008; Sofaer et al., 2013). Moreover, anecdotal field observations suggest Catalina Island warblers build off-ground nests that are larger than ground nests, suggesting that, in addition to nest height, nest construction behaviours may also vary between nest site locations (Montag et al., 2009). Such dramatic variation is surprising, given that many aspects of nest construction are often highly stereotypical and invariant within taxonomic families (Sheldon & Winkler, 1999; Zyskowski & Prum, 1999). The ability of the warblers on the Channel Islands to nest on and off ground likely reflects a plastic response as (1) gene flow and little genetic divergence exists between *L. c. sordida* populations (Sofaer et al., 2013) and (2) experimental exposure to scrub-jay taxidermic mounts and vocalizations caused warblers on Catalina Island to consistently nest on the ground (Peluc et al., 2008). Together, these results suggest that pervasive ground nesting on Santa Cruz and the mainland may reflect hierarchical prioritization towards ground nesting in response to avian predators (e.g. *Aphelocoma* spp.) over terrestrial predators (e.g. snakes, small mammals) and that the absence of important avian predators on most of the islands has favoured the evolution of plasticity in nest height. Yet, no study to date has investigated whether Catalina Island warblers modify nest construction in relation to nest height.

In this study, we examined the capacity for individual variation in orange-crowned warbler nest-building behaviour on Catalina Island and how nest construction is related to nest success. By deconstructing nests built at varying heights, we tested whether Catalina Island warblers predictably alter nest construction relative to nest height. Then, using records of individuals with multiple nesting attempts, we tested whether the subset of individuals whose nests failed due to predation predictably built heavier nests at greater heights and had a higher probability of nest success (Montag et al., 2009; Peluc et al., 2008; Söderström et al., 1998; Sofaer et al., 2014). Analysing the structure and placement of individual nests at both the population and individual level allowed us to determine whether variation in nest construction behaviour is plastic and whether this plasticity impacts nesting success of orange-crowned warblers on Catalina Island.

METHODS

Study Species

We collected data from breeding orange-crowned warblers on Catalina Island from March through May, from 2004 to 2005, in Bulrush Canyon (33°22′30″N, 118°25′56″W; see description in Montag et al., 2009). These warblers will renest multiple times a season, especially after nest failure (Gilbert et al., 2020). Nest site selection and construction are exclusively undertaken by females, although both sexes share duties of parental care (Gilbert et al., 2020; Peluc et al., 2008).

Data Collection

We monitored nests until a nest was successful (nestlings leave the nest; fledge) or failed due to being depredated (nest contents missing; signs of predation) or abandoned. We determined the fate of each nest by inspection of the nest, by the adults' behaviour and by visual confirmation of fledglings. We recorded nest height, male and female band identity (ID) and the presence of eggs or nestlings. If a nest failed, the suspected cause of that failure was recorded. Unbanded females were identified by their territory use, which was mapped to a grid system of 500 × 300 m plots, and pair bonds with known males. For detailed field methods see Sofaer et al. (2014), Montag et al. (2009) and Martin and Geupel (1995).

To assess variation in nest construction, we collected nests from 24 individual females that renested in the same breeding season: 19 females renested following nest failure ($N = 38$ nests); five females renested following nest success ($N = 10$ nests). Nests ($N = 100$) were weighed with an Ohaus Scout Pro 200 g scale, then deconstructed and separated into four categories of materials: grasses, twigs, bark and leaves, and ‘Other’ materials, such as moss, lichen, animal hair and seed pods. Each component category was then weighed separately and compared to the total weight of the nest to get a percentage of total weight for each category.

Data Analysis

Nest composition

To test how the composition of ground and off-ground nests differed, we conducted redundancy analysis (RDA) using the ‘LEA’ R package (Frichot & François, 2014; R Core Team, 2019) of all 100 deconstructed nests. Like principal components analysis (PCA), RDA allows the major structure of the data to be reduced to a few orthogonal axes. However, unlike PCA, which represents the major features of the data along unconstrained axes that explain the most variance, RDA is a constrained ordination procedure that allows for hypotheses of linear relationships to be specifically tested. RDA functions as a two-step process in which a matrix of linear combinations of explanatory variables are modelled to best explain variation in the response data. This produces a matrix of fitted values that is fed into a PCA to compute canonical axes that explain variation in the response data (Borcard et al., 2011). We used a matrix of nest components, including nest weight and the percentage of twigs, grasses, bark and leaves and Other as our response variables, and included nest height as our explanatory variable. We calculated adjusted R^2 statistics and assessed significance using 1000 permutations. To further test how nest components differed as a function of nest location, we conducted a discriminant function analysis (DFA) using the 'lda' function in the MASS R package (Venables & Ripley, 2002) to test whether nests could be classified as, 'on-ground' or 'off-ground' based on nest components (nest weight and percentage of twigs, grasses, bark and leaves and Other).

Behavioural plasticity and nest success

We sought to quantify how much nest placement and construction changed between nesting attempts and whether these changes in nest placement and construction influenced orange-crowned warbler nest success. To do this, we fitted linear mixed models implemented in the 'lme4' R package (Bates et al., 2015; Shaffer, 2004). We used nest height and the calculated RDA1 values from all 100 deconstructed nests as the response variable, nest attempt as a fixed variable and individual female as a random effect. To assess the effect of behavioural plasticity on nesting success, we ran two logistic exposure regression models using the 'lme4' R package. Because we wanted to focus on the potentially adaptive decisions females make following nest failure, we focused on only those females that built a second nest following initial nest failure ($N = 19$). One female's second nest failed at the onset of laying (prior to the first egg being laid) and was removed from analyses ($N = 23$ females total, 18 females for whom their first nest failed). We used only the fates of the second nests in the logistic regression as we were interested in the potentially adaptive decisions orange-crowned warbler females make following nest failure (Peluc et al., 2008). Specifically, we first tested whether nest success following nest failure increases with nest height by assigning a binary value to the second nest following nest failure as fledged (1) or failed (0), with nest height as a fixed effect. To determine whether nest construction varies significantly between nesting attempts after accounting for plastic shifts in nest height, we ran a second RDA using the nest components of nests built by females that initially failed as our response, and nest height and attempt number (1 and 2) as explanatory variables. We then ran a second logistic exposure model to determine whether nest success following nest failure is affected by nest construction.

RESULTS

Nest Composition

Orange-crowned warblers on Catalina Island altered the composition and structure of their nests at different heights, confirming previous anecdotal field observations (Montag et al., 2009; Figs 1, 2). Nest characteristics between on-ground ($N = 33$) and off-ground ($N = 67$) nests (nest weight, percentage of twigs, grasses, bark and leaves and Other) were significantly related to nest height ($P = 0.001$, $R^2_{adj} = 0.048$, eigenvalue $= 0.288$; Fig. 2b). Off-ground nests tended to be heavier, consist of more twigs and less grasses, bark and leaves than on-ground nests (Appendix, Table A1). Most variation in nest composition was driven by the relative percentage of twigs and nest weight, followed by the percentage of bark and leaves, grasses and Other materials (species scores in the Appendix, Table A1). Our DFA model was able to correctly assign 71% of the sampled nests as either 'on-ground' or 'off-ground' based on nest components.

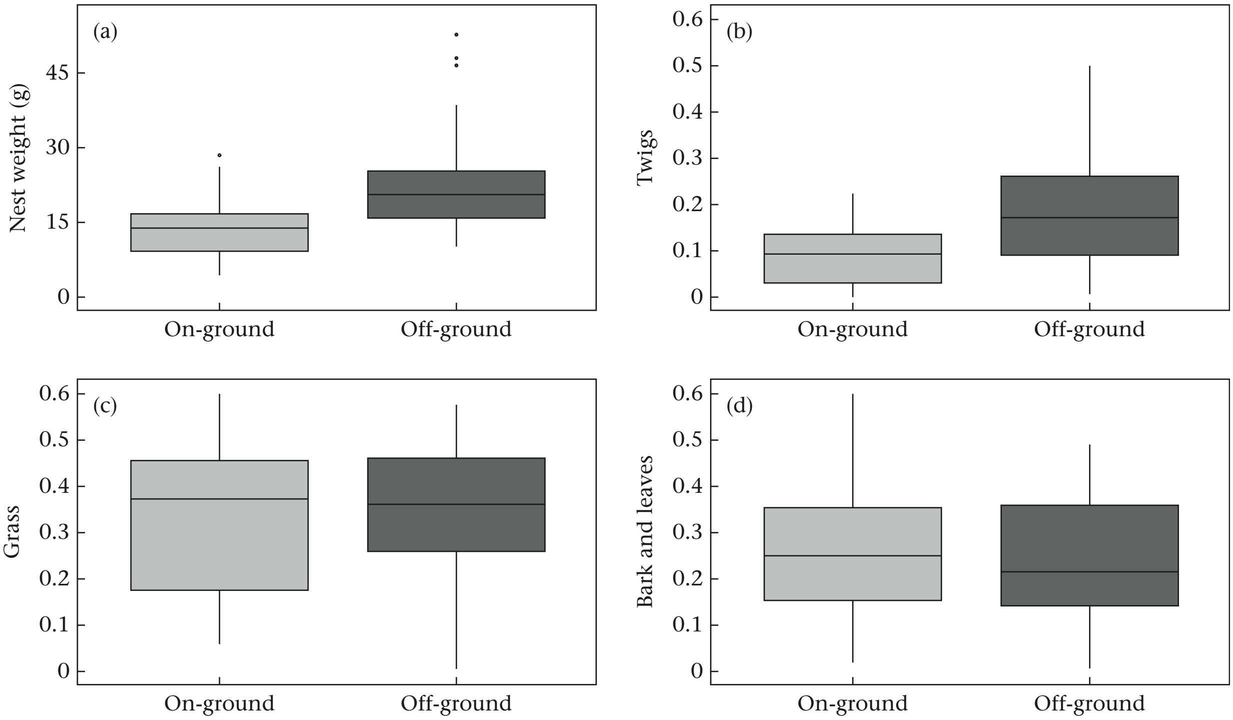

Figure 1. Box plots showing the differences between on-ground (white) and off-ground (grey) nests for (a) nest mass, (b) percentage of twigs, (c) grass and (d) bark and leaves using 100 deconstructed Catalina Island orange-crowned warbler nests. The thick horizontal lines indicate the median, the box edges depict the first and third quartiles, and the whiskers represent 1.5 times the interquartile range between the first and third quartile. Data beyond the end of the whiskers are plotted individually.

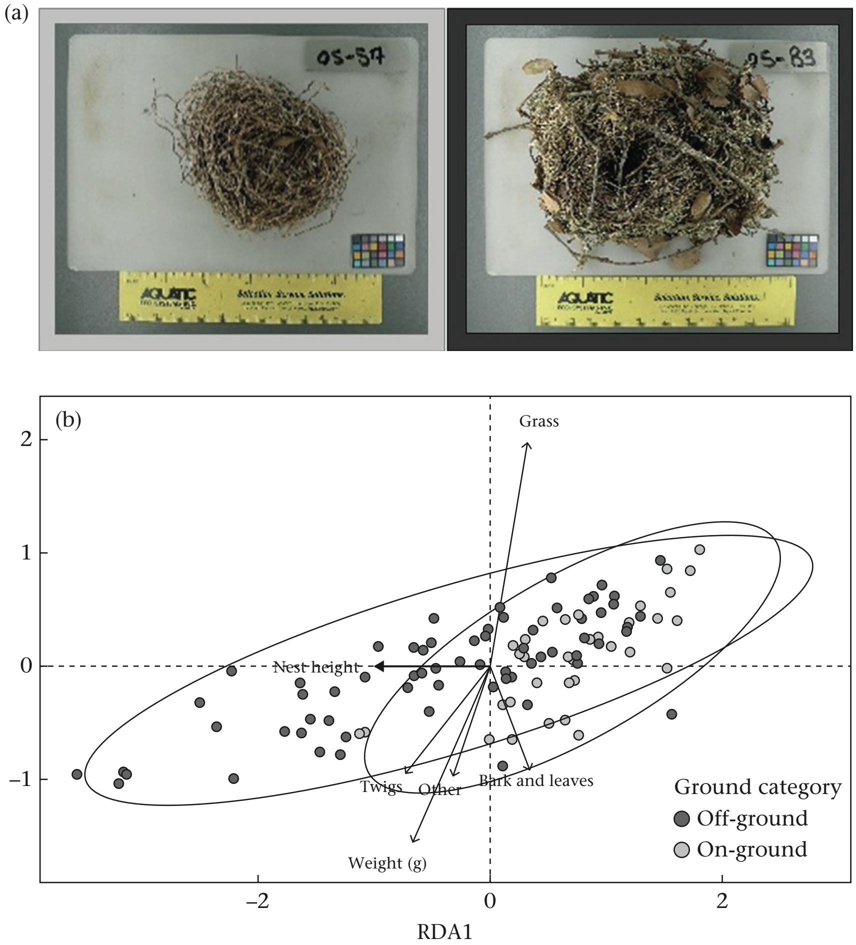

Figure 2. (a) Examples of on-ground (left) versus off-ground (right) nests of orange-crowned warblers on Catalina Island, California. (b) Redundancy analysis triplot of 100 deconstructed Catalina Island orange-crowned warbler nests shows the relative arrangement of on-ground and off-ground nests in the ordination space according to their relationship with the ordination axes. Our response variables (nest weight; percentage of twigs, grasses, bark and leaves, and 'Other'; grey vectors) were constrained by the explanatory variable of height at which the nests were built (black vector). The angles between vectors reflect their linear correlation. Points represent individual nests built coloured by whether they were built on-ground (nest height = 0 m; light grey) or off-ground (nest height > 0 m; dark grey).

Behavioural Plasticity and Nest Success

Our RDA analysing nest construction and attempt number showed that individual females did not predictably alter nest composition after nest failure after accounting for variation in nest height ($R^2_{adj} = -0.011$, eigenvalue$_{RDA1} = 0.132$, eigenvalue $_{RDA2} = 0.039$; Appendix, Table A2). Furthermore, nest construction did not significantly impact nest success ($\beta = -0.667, P = 0.123$). The likelihood of nest failure tended to decrease as nest height increased following initial nest failure ($\beta_{height} = 0.535$, $P = 0.176$; Fig. 3b). Individual females also renested up or down in the canopy a greater distance following initial nest failure compared to females that fledged their first nests (Fig. 3c). Because six of the nests failed due to abandonment under uncertain circumstances, we reran the logistic exposure models excluding females with abandoned nests, which reduced our sample size to 13 individuals, but we found a similar pattern of reduced daily predation rate with increasing nest height.

DISCUSSION

Variation in plasticity of nest-building behaviour reflects a potentially critical component of fitness differences, but few studies have quantified how the same individual differs in its capacity to alter nest structure and location (Feng et al., 2019; Healy et al., 2015). Catalina Island orange-crowned warblers are distinctive in that they commonly build off-ground nests, which are almost nonexistent in mainland populations. Here, we show that individuals in this population built off-ground nests that were significantly larger, heavier and composed of more twigs than their on-ground nests (Figs 1, 2). While smaller ground nests are generally predicted to be less conspicuous to predators (Lima, 2009; Martin, 1993), the shift in nest height appears to be an adaptive response to the absence of avian predators on Catalina Island (Fig. 3a, b; see also Peluc et al., 2008). Shifting nests from typically on-ground to off-ground substrates is not simply a shift in nest size but requires females to adjust their nest construction behaviour to secure their nests to vegetation (see Figs 1, 2a). Given that nest construction behaviour is often considered to be a highly conserved trait within a taxonomic group (Sheldon & Winkler, 1999; Zyskowski & Prum, 1999), the capacity for such plasticity is notable. We also found substantial variation within and among individuals in their capacity to alter nest composition in response to nest height (Fig. 3a). Yet, contrary to our expectations, when individuals renested after a successful or failed nesting attempt, there was considerable variation in how much they shifted their nest height up or down (Fig. 3c, Appendix, Fig. A1). Such results suggest the expectation that higher-canopy nests provide a safer haven for nesting warblers on Catalina Island does not fully explain why warblers there exhibit so much variation in plasticity of nest construction. Below, we discuss these results in more detail and suggest alternative hypotheses for the processes promoting and maintaining plasticity in this population.

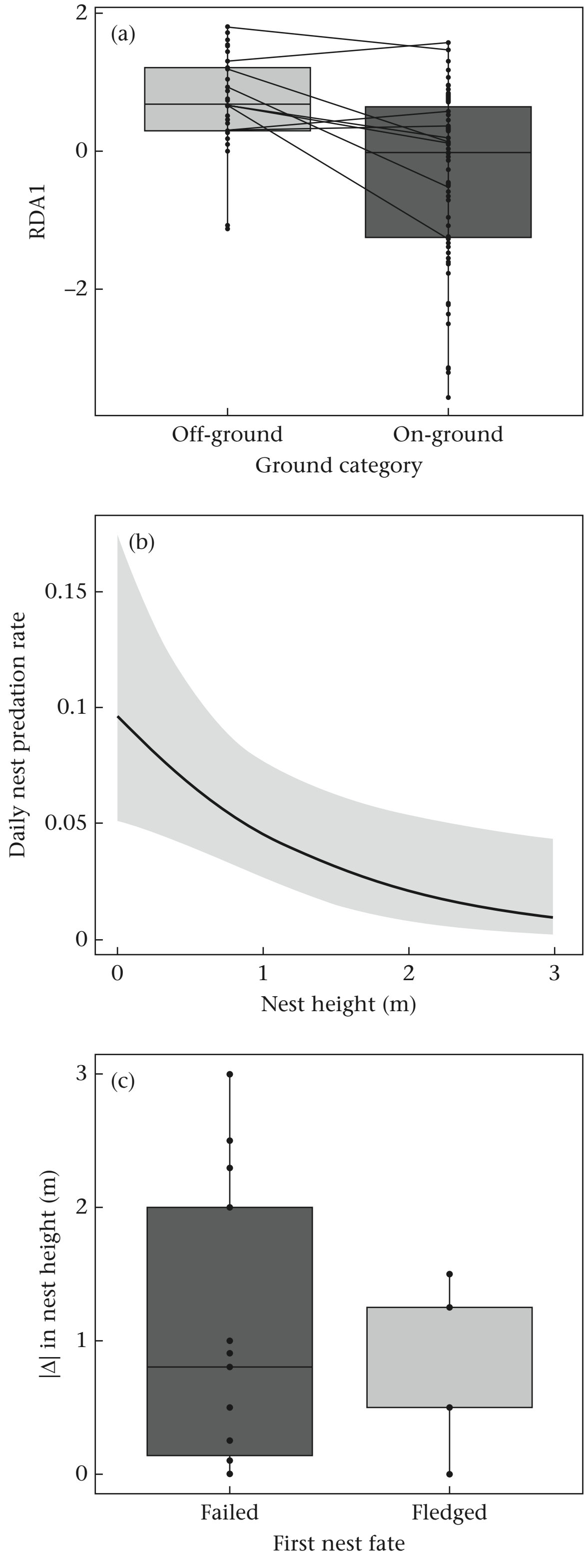

Figure 3. (a) Population level variation in nest construction (RDA1) between on-ground and off-ground orange crowned-warbler nests on Catalina Island, California. Points represent individual females with lines connecting females that built more than one nest (note that some lines are obscured due to females building consecutive on-ground or off-ground nests). (b) Logistic exposure model (95% confidence interval shaded) showing the predicted probability of a nest being depredated given nest height. (c) Absolute change in nest height between two consecutive nests built by the same female (points, $N = 23$) that failed or fledged their first nest.

Plasticity in Nest Construction

Measuring behavioural reaction norms provides insight into how individuals vary in their plastic responses to environmental cues and whether this plasticity is potentially adaptive (e.g. Brommer, 2013; Dingemanse et al., 2009; Ghalambor et al., 2010). Variation within a population is thought to reflect both a genetic predisposition to build a certain type of nest and a plastic component based on experience and the environment (e.g. Healy et al., 2015; Järvinen et al., 2017; Patrick et al., 2017; Walsh et al., 2010). Orange-crowned warbler populations breeding on the Channel Islands are thus notable because the level of variation in nest height and structure encompasses or exceeds that observed elsewhere in the genus *Leiothlypis* (Montag et al., 2009; Peluc et al., 2008; Sofaer et al., 2014). We found off-ground nests were significantly heavier and consisted of more twigs than on-ground nests. Given that the percentage of twigs and nest weight were highly correlated (0.78), most of the variation in nest weight may be attributed to the proportion of twigs. The increased use of twigs likely reflects the need for more robust structural elements to support nests on tree and shrub branches compared to the smaller and lighter on-ground nests (Hansell, 2000; Heenan & Seymour, 2011; Montag et al., 2009). Females also differed in the degree to which they changed nest composition with nest height (Fig. 2). While we have yet to measure the degree to which such variation in nest construction is heritable (Järvinen et al., 2017; Walsh et al., 2010), several other factors may also be at play, including female age (Stamps, 2016), availability of suitable building materials in a given location (Patrick et al., 2017), learned preference for certain nesting materials (Briggs & Mainwaring, 2019), the microclimate of the nest site (Perez et al., 2020; Scherr & Chalfoun, 2022) or individual condition (Berg et al., 2006). Understanding how potential genetic variation interacts with these factors to shape variation in nest construction remains a major challenge but also a future opportunity, given the large variation in nest construction behaviour among individuals.

Plasticity in Nest Height

We found a tendency for daily nest predation rate to decline with increased nest height following nest failure (Fig. 3b). These results are consistent with previous research in this population arguing that plasticity in nest height is likely to be adaptive in the absence of avian predators such as jays and crows (Peluc et al., 2008). Potential nest predators of ground nests on Catalina Island include the southern Pacific rattlesnake, *Crotalus oreganus helleri*, San Diego gopher snake, *Pituophis melanoleucus*, the Santa Catalina Island fox, *Urocyon littoralis catalinae*, Beechey's ground squirrel, *Spermophilus beecheyi nesioticus*, the Santa Catalina Island deer mouse, *Peromyscus maniculatus catalinae*, feral cats, *Felis catus*, and potentially introduced Norway rats, *Rattus norvegicus* (Garrett & Dunn, 1981; Peluc et al., 2008). While many of these species are described as terrestrial (Peluc et al., 2008), most can be arboreal even if they likely have difficulty reaching the highest nests (Remeš, 2005). Similar predators are also found on the mainland and other islands where the warblers almost exclusively nest on the ground. The only clear difference between Catalina Island and locations on both the mainland and Santa Cruz Island is the absence of corvid nest predators in habitats where the warblers breed (DeGregorio et al., 2016; Sofaer et al., 2013). Such a shift in nesting behaviour is consistent with hierarchical responses to predators that differ in the risk they pose and has been observed in other natural systems (McIntosh & Peckarsky, 1999; Sih et al., 1998). For example, ground-nesting hermit thrush, *Catharus guttatus*, avoid nesting in areas with high densities of chipmunks, but they do not experience higher nest survival where chipmunks are relatively rare (Vernouillet et al., 2020), likely because avian predators such as blue jays, *Cyanocitta cristata*, account for the vast majority of hermit thrush nest predation even though the jays themselves are relatively rare (Bouffard et al., 2020). Interestingly, similar to the orange-crowned warblers, hermit thrushes exclusively build off-ground nests in portions of their range where terrestrial nest predators are the dominant predator, suggesting that plasticity in nesting height may be more widespread than previously appreciated (Martin, 1988; Martin & Roper, 1988). Additionally, a population of dark-eyed juncos, *Junco hyemalis*, in southern California (<70 km from our study site) recently expanded into urban Los Angeles and shifted to off-ground nests (Bressler et al., 2020). The timing of this expansion roughly coincides with the spread of West Nile virus in California, which resulted in a significant decline of corvid species and may have facilitated a similar shift in nest height (Kilpatrick & Wheeler, 2019; Lanciotti et al., 1999). Collectively, these studies imply that the potential for plasticity to increase nest height is a potentially common adaptive response in ground-nesting birds but is only observed when they are released from avian predators. In contrast, when avian predators are present, this plasticity is not expressed because of the increased risk of predation when nesting off-ground.

Do Nest Predators Select for Plasticity in Nest Construction Behaviour?

Theory predicts that adaptive plasticity will often evolve in response to spatial or temporal variability in the risk of predation (reviewed in Benard, 2004; Ghalambor et al., 2007). Indeed, many behavioural, morphological and life history traits exhibit predictable plastic responses to predator cues (Benard, 2004). Given that nest predation is the primary cause of nest failure for most birds (Martin, 1993) and the potential that these warblers could disperse to islands with or without corvids, the observed plasticity in nest height of Catalina Island warblers is consistent with the spatial variation in predation risk imposed by corvids for ground nesting (McIntosh & Peckarsky, 1999; Peluc et al., 2008; Sih et al., 1998). Yet, despite the seemingly adaptive benefits of shifting nest height upwards after experiencing nest predation, we observed that some individuals continued to nest on the ground or nest lower following nest failure (Appendix, Fig. A1). How do we explain this variation? One plausible hypothesis is that, in the absence of jays, warblers reduce density- or frequency-dependent nest predation by exhibiting variation in nest placement (Martin, 1988, 1996). Previous work has found orange-crowned warblers occur at unusually high population densities on Catalina Island and experience density-dependent nest predation between years (Sofaer et al., 2014; Yoon et al., 2012). A common mechanism underlying this density dependence is the ability of nest predators to develop search images for nests that are found in the same location (Martin, 1988, 1996). For example, experimental increases in the overlap of nests using the same substrate result in higher nest predation (Martin, 1988, 1996; Schmidt & Whelan, 1999). Because Catalina Island warblers can plastically adjust their nest construction in response to nest height, they are able to take full advantage of the vertical range of nest heights from ground to canopy and can potentially prevent predators from being able to search for nests at any specific height.

Our study documents an impressive degree of behavioural plasticity in nest construction as a function of nest height and is contrary to the general expectation of a stereotypical nest structure or substrate (Hansell, 2000). We argue the lack of avian predators on Catalina Island favours this off-ground nesting behaviour and is an example of hierarchical plasticity in response to the absence of a top predator. Yet we also observed considerable variation in nest height among individuals, suggesting behavioural plasticity in nest construction could reduce density-dependent nest predation from the existing predator community. The degree to which the observed levels of plasticity are unique to this subspecies of orange-crowned warbler or generally common among ground-nesting species remains to be determined and will depend on additional studies of ground-nesting species in the presence and absence of avian predators.

Author Contributions

S.C.H. and R.G.C. contributed equally to this work. S.C.H. assembled the data, conducted the analyses with R.G.C. and co-wrote the manuscript with R.G.C. J.C.M. assisted with framework for the manuscript and analyses. C.K.G. and T.S.S. initiated, led and secured funding for the orange-crowned warbler project on Santa Catalina Island. C.K.G. conceptualized the idea for this study and provided valuable feedback. All authors edited various versions of the manuscript.

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Data Availability

All data and R code used for this publication will be made available in Dryad Digital Repository: doi.org/10.5061/dryad.5mkkwh777, and Github: https://github.com/RGCheek/OCWA_nest_analyses.

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Appendix

Table A1
Summary of redundancy analysis of 100 deconstructed Catalina Island orange-crowned warbler nests

	RDA1	PC1
Eigenvalues and their importance		
Eigenvalue	0.289	2.037
Proportion explained	0.058	0.407
Cumulative proportion	0.058	0.465
Biplot for constraining factors		
Nest height (m)	−1	—
Species scores		
Nest weight (g)	−0.659	−1.566
% Twigs	−0.725	−0.950
% Grasses	0.323	1.978
% Bark and leaves	0.343	−0.911
% Other	−0.320	−0.984

Nest height (m) was the predictor variable, and nest characteristics (nest weight (g); percentage of twigs, grasses, bark and leaves, and ‘Other’) were the response.

Table A2
Summary of redundancy analysis of 30 deconstructed Santa Catalina orange-crowned warbler nests built by 24 females

	RDA1	RDA2	PC1
Eigenvalues and their importance			
Eigenvalue	0.132	0.039	2.252
Proportion explained	0.026	0.008	0.451
Cumulative proportion	0.026	0.034	0.485
Biplot for constraining factors			
Nest height (m)	0.994	0.107	—
Attempt number	0.060	0.998	—
Species scores			
Nest weight (g)	0.332	−0.090	1.354
% Twigs	0.273	0.202	0.961
% Grasses	−0.011	0.116	−1.631
% Bark and leaves	−0.347	−0.110	0.786
% Other	0.299	−0.208	0.849

Nest height (m) and attempt number were the predictor variables, and nest characteristics (nest weight (g); percentage of twigs, grasses, bark and leaves, and ‘Other’) were the response.

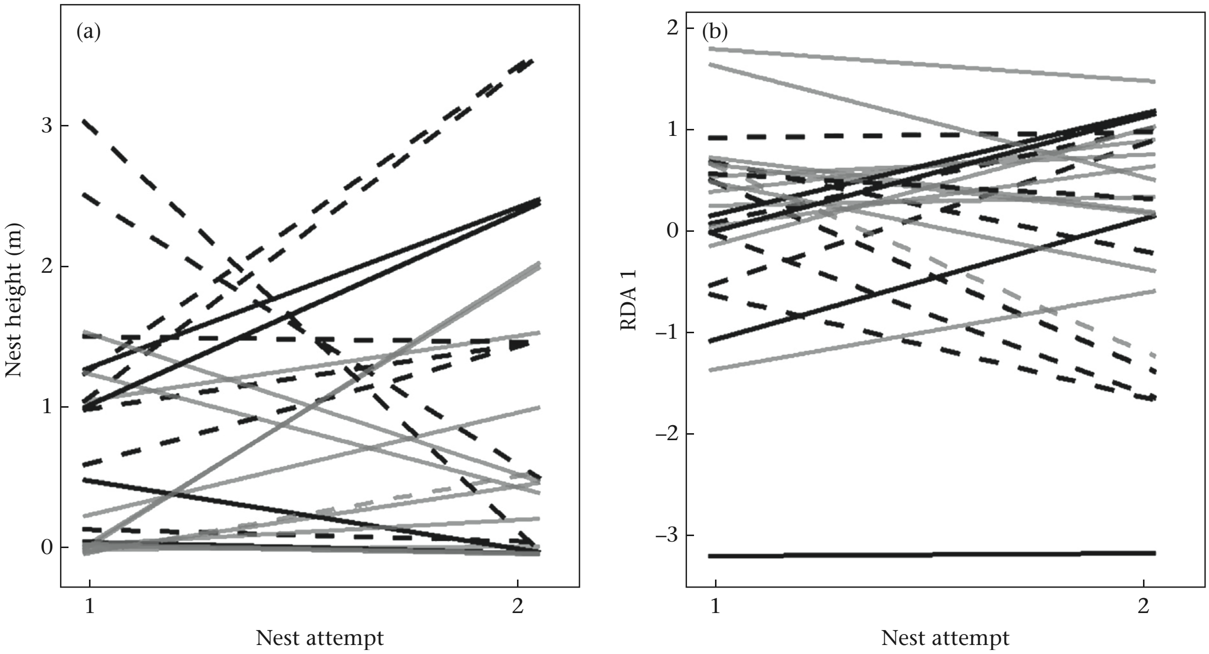

Figure A1. Reaction norms showing the change in (a) nest height and (b) construction relative to nest attempt between two consecutive nests built by the same female (lines $N = 23$). Solid grey lines represent females that fledged both nests ($N = 4$), and dashed grey lines represent females that fledged their first nest but failed their second nest ($N = 1$). Solid black lines represent females that failed both their nests ($N = 10$), and dashed black lines represent females that failed their first nest but fledged their second nest ($N = 8$).