NEST SITE SELECTION OF THE ENDEMIC "DUSKY" ORANGE-CROWNED WARBLER (*VERMIVORA CELATA SORDIDA*) ON SANTA CATALINA ISLAND

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Abstract—The *sordida* subspecies of orange-crowned warbler (*Vermivora celata*) often nests off-ground, unlike mainland populations. Here, we quantitatively describe nest site selection during one breeding season in two contrasting habitats, xeric and mesic, to better understand adaptive nest site selection. As expected, the Catalina Island orange-crowned warbler exhibited a high level of plasticity in nest site location with larger variation in nest heights when compared with mainland subspecies. We found that only canopy cover above nests was statistically different between the xeric and mesic habitats, being lower in the xeric habitat. There was also a wider variety of substrates utilized in the mesic habitat, which was likely related to differences in substrate diversity. There was a significant preference for a northeast orientation of nests and nest entrances in the mesic habitat, but a preference for nest entrances to be orientated west on the xeric plot. Nest and nest entrance orientation were highly correlated with the aspect of the slope on which the nest was situated.

INTRODUCTION

Various selection pressures act on nest site choice and have led to the evolution of a diverse array of nest structures, ranging in size, shape, nest construction materials, attachment of the nest to the chosen substrate, and nest location (Hansell 2000). Birds living in a heterogeneous environment have a variety of choices for potential nest placement, but these options may be limited by types of predators present (Remeš, 2005), interspecific or intraspecific competition for these sites (Svärdson 1949; Liebezeit and George 2002), or purely logistical restrictions such as sufficient physical support for large nests built by species with large body size (Hansell 2000). For example, birds may choose certain nest sites to avoid predators (e.g., Clark and Shutler 1999; Martin et al. 2000; Holway 1991; Weidinger 2002) or to allow a greater ability to see approaching predators (e.g., Götmark et al. 1995). Sites may also be chosen to provide a favorable microclimate for offspring development (see review

by Webb 1987). Consequently, nest site selection is often highly conserved in most species, such that populations occupying different environments will select similar nest sites (Baicich and Harrison 1997). For example, birds may choose a very specific orientation for the nest (e.g., Finch 1983; Hoekman et al. 2002; Burton 2006) or nest entrance (Facemire et al. 1990).

An example of a group that exhibits a stereotypical nest site choice is the genus Vermivora. In North America, the majority of these warblers nest on or close to the ground (Baicich and Harrison 1997). An exception to this pattern is found on Santa Catalina Island, California, where the endemic "dusky" orange-crowned warbler (*Vermivora celata sordida*) breeds and nests in a wide range of sites (H. Montag, personal observation). The dusky orange-crowned warbler is endemic to the California Channel Islands, which represent the southern edge of the species' breeding range. Dusky orange-crowned warblers have a mean body mass of 9.4 g (S.E. = 0.8g; $n = 106$) with

the males of this subspecies being significantly larger than the females (5%–6%; n = 106; Sogge et al. 1994). Both initial and replacement nests are initiated between February and June (H. Montag, personal observation). The female lays two to four eggs, two to three days after nest completion, and incubation starts on the day that the last (Sogge et al. 1994) or penultimate egg (H. Montag, personal observation) is laid. Only the female incubates, usually for 12 days, and all eggs hatch within 24 hr of each other. Nestling period is 11–13 days (Sogge et al. 1994).

On Santa Catalina Island, *V. celata sordida* inhabits a wide variety of ecosystem types, and populations of this species are especially dense, with around five breeding pairs per ha (H. Montag, personal observation). The endemic subspecies experiences very little interspecific competition for nesting locations, due to the fact that there are few other nesting passerines which utilize the same nesting substrates (mainly Hutton's vireo, *Vireo huttoni unitti*; spotted towhee, *Pipilo maculatus clementae*; chipping sparrow, *Spizella passerina arizonae*; and Pacific slope flycatcher, *Empidonax difficilis*) and so is not competitively excluded from specific nesting sites, as has been shown in other studies (Svärdson 1949). This provides us with an opportunity to study nest site choice in a situation where a wide variety of nest sites are available and choice is not limited by competition. In this study, we measured characteristics of dusky orange-crowned warbler nests and nest sites over one breeding season in a mesic and a xeric habitat. Our aim was to quantitatively describe the nesting site of the endemic orange-crowned warbler population on Santa Catalina Island, and to explore whether warblers would take advantage of the wide variety of nest sites available, or whether choice of nest site characteristics would be constrained due to selection pressures other than competition.

MATERIALS AND METHODS

Study Plots and Species

The study was undertaken on Santa Catalina Island, Los Angeles County, California, USA (33°22'30"N, 118°25'56"W) from March to May 2006. The study area was in Bulrush Canyon, a large east-west oriented valley located near the southwest coast of the island. The fieldwork was conducted on two plots, one mesic in the structure of its habitat and one xeric. The mesic plot was situated in the bottom of Bulrush Canyon, on a north-facing slope, where the habitat consists of creek beds (often dry), scrub oak (*Quercus pacifica*) and toyon (*Heteromeles arbutifolia*) dominated woodland, lemonade-berry (*Rhus integrifolia*), and large "meadow" areas composed of grasses and forbs. Average elevation for nest sites on this plot was 73.95 ± 3.1 m above sea level (n = 42). In comparison, the xeric plot included a south-facing slope and a ridge top. The vegetation was less diverse and was dominated by coastal sage (*Artemesia californica*) and prickly pear cactus (*Opuntia* ssp.). The average elevation for nest sites on this plot was 86.13 m (S.E. = 3.4 m; n = 14). Each study plot covered 500 x 300 m, and was gridded with flagging every 25 m and assigned a letter/number to facilitate mapping of territories and nests.

Nest Measurements

We searched for nests from 6 a.m. to 1–3 p.m. each day following methods in Martin and Geupel (1993). Bird behavior and vocalizations were closely observed and plots were methodically searched. A total of 56 orange-crowned warbler nests were found, 42 on the mesic plot and 14 on the xeric plot. Subsequent to failing or fledging, we collected detailed quantitative descriptions of nests and nest sites. This was done from day 25 to 30 (after clutch completion) to standardize the timing of measurements for each nest, as nest site characteristics can change over time (Burhams and Thompson 1998). We took the following measurements using a variation of the BBird protocol (Martin et. al. 1997): nest height, substrate, number and diameter of support branches, nest and nest entrance orientation, aspect, concealment, canopy cover, nest dimensions, and volume.

Nest height was measured from the base of the exterior of the nest to the ground below. For six nests that were inaccessible, nest height was visually estimated. Nests with height = 0 cm were categorized as "ground" nests, while nests with height > 0 cm were categorized as "off-ground" nests. For all off-ground nests, we recorded the species of plant(s) that the nest was placed in. Grass, twigs, and lichen were not identified to species. In addition, we recorded the status of the substrate

(alive or dead), the number of branches supporting the nest that were accessible or intact, and the diameter of the largest support branch. Substrate availability data were not collected for either site.

Orientation for nests and nest entrances were only measured for off-ground nests ($n = 42$). Nest orientation was assessed by directing a compass from the center of the nest substrate towards the nest and recording the bearing. The nest entrance was determined to be the most direct gap in the vegetation to the nest, also taking into account any flattened surface on the rim (indicating where adults perch in order to feed nestlings) and personal observations of the adults' flight patterns. For 34 nests with a measurable entrance, orientation of the entrance was measured in a manner similar to orientation of the nest. We also measured the orientation of both nest and nest entrance relative to downhill in order to explore any preference, as has been found in other studies (e.g., Roseberry and Klimstra 1970), that may aid in adult predator avoidance through ease of escape from the nest. Aspect for the 42 off-ground nests was measured by standing at the nest site, directing a compass downhill from that point and taking a bearing. Seven of these readings were omitted from the analysis due to a recording error. The angle between the orientation of the nest or nest entrance and the aspect of the slope was then calculated (i.e., 0° would be directly downhill, 90° would be at a right angle from downslope, and 180° would be upslope).

Concealment was measured as the percentage of the nest that was covered by vegetation. Mean lateral concealment was calculated by visually estimating concealment from 1 m away from the nest in each cardinal direction, then taking the average of these four measurements. Concealment was also assessed from above and from below (for elevated nests). Canopy cover was assessed by using a 35mm Fisheye Camera with 170° lens (Lomography, New York) to take a picture of the vegetation above the nest sites. The film was developed and converted into an electronic format using a negative scanner. Canopy cover was then calculated using Gap Light Analyzer software (Version 2.0, Simon Fraser University, Burnaby, BC, and the Institute of Ecosystem Studies, Millbrook, NY).

The dimensions of the nest were calculated as follows: outer height (from rim of the nest to base of the exterior), nest cup depth (from rim of the nest to base of inner cup), outer diameter (the diameter of the widest exterior part of the nest) and inner diameter (the diameter of the inner cup). Volume was calculated assuming a regular ellipsoid with equal width and depth, using the following equation (adapted from Lombardo 1994):

$$\text{Nest volume} = \frac{4/3\pi(w/2)h(d/2)}{2}$$

where both w (width) and d (depth) are equal to outer nest diameter, and h (height) is outer nest height.

SPSS 14.0 software (SPSS Inc, Chicago, IL) was used to analyze data. We used chi-square contingency tests to compare frequencies of substrate types and dead vegetation used for nests between the mesic and xeric plots. A chi-square contingency test was also used to compare the frequencies with which nests were observed off the ground between the two habitats.

Because the orientation data are considered to be circular data, we used Oriana 2.0 (Kovach Computing Services, Anglesey, Wales) to obtain circular graphs and mean vectors for nest and nest entrance orientation. Rao's spacing U-test was run on orientation data to compare distributions of orientations between mesic and xeric plots and to assess non-random preference for orienting nests or nest entrances in a particular direction. Rao's spacing test has been shown to be the most powerful statistical test for circular data and it is especially useful for polymodal distributions and with small sample sizes (Bergin 1991). Oriana does not give exact P values for this test, so we only report these values incrementally (e.g., $P>.05$, $P>.1$). Nests located in the center of the substrate were omitted from analyses of nest orientation on the substrate, as they had no particular bearing. We used a Watson-Williams F test to compare the orientation of nest entrances between mesic and xeric plots, as Oriana utilizes this test to compare two or more samples to explore if their mean angles differ significantly.

To test whether there was a bias to orient nests or nest entrances downhill, we used chi-square tests to compare the frequencies of nests/nest entrances oriented downhill versus upslope. A t-test was used to compare the mean angle between nest orientation and downhill between the two habitats, and a circular-circular correlation was used to examine

the relationship between nest site aspect and nest entrance orientation.

Two factor analysis of covariance was used to test the effects of habitat type (mesic/xeric) and nest height (on-/off-ground) on mean nest height, number of support branches, diameter of largest support branch, concealment, canopy cover, nest volume, and nest cup depth. For response variables that were only measured for off-ground nests, we used single factor analysis of covariance to compare means between xeric and mesic habitats. Means are reported with ±1 standard deviation.

RESULTS

We located orange-crowned warbler nests in 12 different vegetation substrates, with lemonade-berry being the most common overall (Table 1). The types of substrates used differed significantly between the two plots (χ^2=10.72, df=4, P=0.03),

with lemonade-berry, grass and trees being utilized more commonly on the mesic plot, and sagebrush being used predominantly on the xeric plot. However, we did not measure availability of these plants on each plot, and so conclusions in terms of preference are not quantifiable. Use of dead plant material was common, with 46% (n = 35) of nests placed in dead vegetation (Table 1). Between the mesic and xeric plots, there was no significant difference in the use of dead vegetation as the nesting substrate (χ^2=0.4, df=1, P=0.53) or in the number or width of branches supporting the nest (Table 2). Although canopy cover was higher for nests on the mesic plot than on the xeric plot (Table 2), there was no significant difference in nest concealment from above, below, or laterally (Table 2). Ground nests showed both higher lateral concealment and concealment from above than elevated nests (Table 2).

Means and standard deviations of nest height and nest characteristics are presented in Table 2. Of

Table 1. Numbers of orange-crowned warbler nests found in different substrates in two study plots on Santa Catalina Island, California. Nests that were placed in more than one substrate species are recorded in multiple substrate categories.

Substrate	Status	Mesic	Xeric
Lemonade-berry (*Rhus integrifolia*)	Live	15	4
	Dead	3	2
Coastal sagebrush (*Artemesia californica*)	Live	2	4
	Dead	2	3
Harding grass (*Phalaris aquatica*)	Live	3	–
	Dead	4	–
Narrow leaved bedstraw (*Galium angustifolium*)	Live	–	1
	Dead	–	1
California ivy (*Hedera helix*)	Live	1	–
	Dead	1	–
Honeysuckle (*Lonicera spp*)	Live	–	–
	Dead	2	–
Oak (*Quercus pacifica*)	Live	1	–
	Dead	6	–
Willow (*Salix spp*)	Live	1	–
	Dead	1	–
Toyon (*Heteromeles arbutifolia*)	Live	2	1
	Dead	–	–
Grass	Live	–	–
	Dead	1	–
Twigs	Live	–	–
	Dead	1	–
Lichen	Live	1	–
	Dead	–	–

Table 2. Means and standard deviations of nest site characteristics for on- and off-ground nests of dusky orange-crowned warblers on two study plots on Santa Catalina Island, California. Also presented are results of ANCOVA tests comparing nest site characteristics between ground and off-ground nests and between mesic and xeric habitats.

Nest-site characteristic	On-ground nest average	Off-ground nest average	Mesic plot average	Xeric plot average	ANCOVA Test	
					On-/off-ground nests	Mesic/xeric
Nest height (cm)	N/A	1 ± 0.8 $n=41$	1.1 ± 1 $n=32$	0.7 ± 0.4 $n=9$	–	$F_{1,54}=1.14$ $P=0.29$
Nest volume (cm³)	374 ± 305 $N=13$	706 ± 380 $n=35$	676 ± 359 $n=35$	609 ± 239 $n=13$	$F_{1,46}=5.8$ $P=0.02$	$F_{1,45}=0.48$ $P=0.49$
Nest cup depth (cm)	3.7 ± 0.4 $N=13$	3.9 ± 0.5 $n=35$	3.8 ± 0.8 $n=35$	4 ± 0.1 $n=13$	$F_{1,46}=1.07$ $P=0.31$	$F_{1,45}=0.91$ $P=0.35$
No. support branches	N/A	13.5 ± 11.9 $n=29$	15 ± 14 $n=21$	9.5 ± 4.6 $n=8$	–	$F_{1,27}=1.27$ $P=0.27$
Diameter of largest support branch (cm)	N/A	1.2 ± 1.7 $n=29$	1.3 ± 1.7 $n=21$	1.1 ± 1.6 $n=8$	–	$F_{1,27}=0.12$ $P=0.73$
Mean lateral concealment (%)	98 ± 4 $n=13$	79 ± 20 $n=29$	78 ± 5 $n=30$	84 ± 5 $n=12$	$F_{1,40}=12.3$ $P=0.001$	$F_{1,39}=0.11$ $P=0.74$
Concealment from above (%)	90 ± 14 $n=13$	66 ± 26 $n=29$	67 ± 5 $n=30$	59 ± 13 $n=12$	$F_{1,40}=9.77$ $P=0.003$	$F_{1,39}=0.07$ $P=0.79$
Concealment from below (%)	N/A	65 ± 31 $N=29$	72 ± 7 $n=21$	51 ± 10 $n=8$	–	$F_{1,27}=1.68$ $P=0.21$
Canopy cover (%)	86 ± 11 $N=10$	86 ± 14 $N=32$	90 ± 2 $n=31$	74 ± 8 $n=11$	$F_{1,39}=0.05$ $P=0.82$	$F_{1,40}=7.27$ $P=0.01$

the 56 nests found, a significantly larger number of nests were elevated (73%) than were placed on the ground ($\chi^2=12.07$, df=1, P=0.001). There was no significant difference in the proportion of nests placed on- and off-ground between the mesic and xeric plots ($\chi^2=0.76$, df=1, P=0.38). Nest cup depth was not significantly different between ground and off-ground nests or between habitats (Table 2). There was also no significant difference in nest volume between habitats. However, nests elevated off the ground were significantly larger in volume than those on the ground (Table 2).

For both plots combined, 22 of the 42 off-ground nests (55%) were placed in the center of the substrate. Of the remaining 19 nests, the mean vector of nest orientation was $41\pm77°$ (NE; $n=19$), with no significant difference in orientation between the two study plots (Rao's spacing test, U=33, P>0.5 $n=19$). Nest entrance orientation was

significantly different between the mesic and xeric plots (Watson-Williams F=5.74, P=0.023, $n=34$), with mean nest entrance orientation vectors of $40\pm103°$ (NE; $n=24$) on the mesic plot, and $281\pm104°$ (W; $n=10$) for the xeric plot. For the mesic plot, Rao's spacing test indicated a significant preference in orienting nest entrances to the northeast (U=165, P<0.05, $n=24$; Fig. 1). For the xeric plot, Rao's spacing test indicated a significant preference to orient nest entrances to the west (U=172, P<0.05, $n=10$; Fig. 1).

When looking at both plots combined, the mean angle of the nest orientation in the substrate from downhill was $41\pm42°$ ($n=15$, range 0–140°) and mean orientation of nest entrance from downhill was $71.9\pm53°$ ($n=29$, range 10–180°). Since both of these figures are less than 90°, they suggest a preference to orient nests and nest entrances downhill. The chi-square tests found this preference
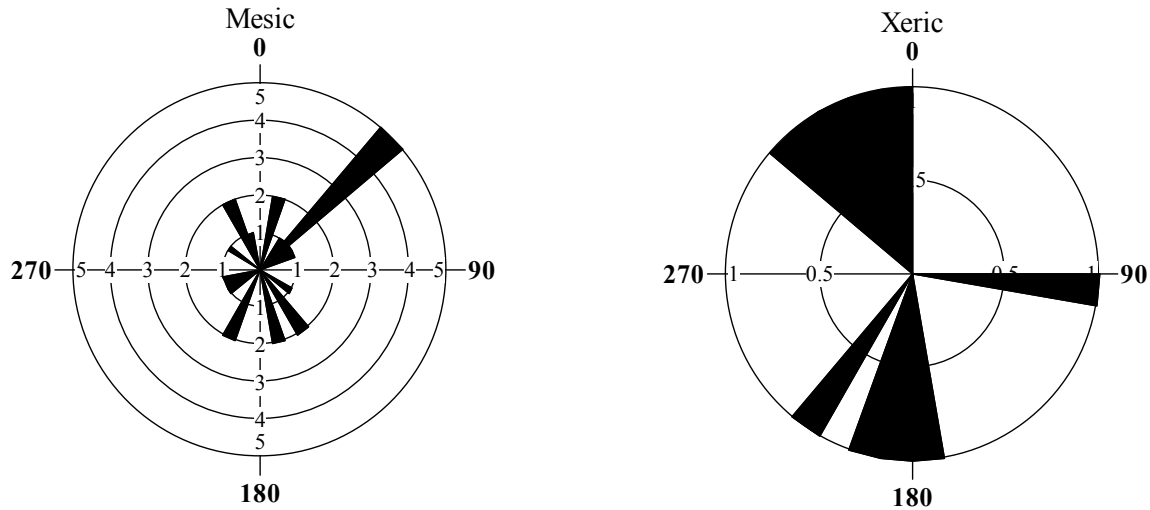
Figure 1. Circular histograms showing orientation of nest entrance for orange-crowned warblers in mesic and xeric habitats on Santa Catalina Island, California. Numbers inside the circles represent numbers of nests. Numbers on the outside represent compass bearing, with 0° indicating nest entrances oriented to the north.

significant for both nests (χ^2=8.1, df=1, P=0.01; Fig. 2) and nest entrances (χ^2=4.17, df=1, P=0.04; Fig. 2). Orientation of nests on substrate relative to downhill did not differ significantly between xeric and mesic plots (t=1.06, df=26, P=0.3). The mean aspect of all nests was 11.9 ± 83.3º (N; n = 35),

likely attributable to most of the nests being observed on the mesic plot, which was situated on a north-facing slope. Aspect of the nest site and direction of nest entrance were significantly positively correlated (with a circular-circular correlation r = 0.15, n = 29, P<0.05).
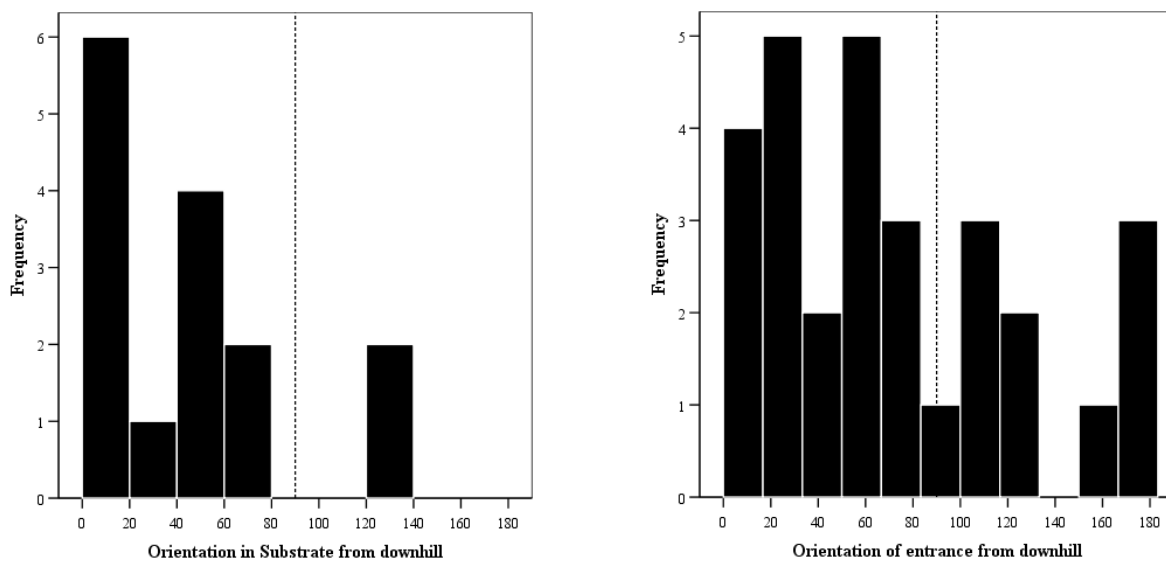

Figure 2. Orientation of both nests (left figure) and nest entrances (right figure) relative to downhill for orange-crowned warblers on Santa Catalina Island, California. Dotted lines represent flat ground at 90º; nests and nest entrances to the left of this line are oriented downhill.

DISCUSSION AND CONCLUSIONS

Dusky orange-crowned warblers on Santa Catalina Island utilize an array of nesting sites. Warblers appeared to utilize the nesting substrates most commonly found on their respective habitats, with coastal sage being most commonly used on the xeric plot and lemonade-berry being predominantly used on the mesic plot. Although no quantitative analysis of vegetation abundance was performed, personal observations by H. Montag were that the most widespread shrub on the xeric plot was coastal sage brush, whereas lemonade-berry was more common on the mesic plot. Thus, nest site selection may be purely due to availability, or it may be related to the 'potential nest site' hypothesis (Martin and Roper 1988), where birds may place nests at a site where there are many other similar sites nearby, to reduce predator search efficiency. Further study of the vegetation surrounding the nest site is needed to explore this. The greater array of nesting substrates on the mesic plot is probably due to the increased availability of different plants on this site (H. Montag, personal observation), although again, this needs to be quantitatively assessed. Off-ground nests tended to be larger, which may be explained by structural necessity, as off-ground nests may need more supportive material (such as twigs). This would need further investigation into nesting materials utilized. Although canopy cover on the xeric plot was lower, possibly due to the vegetation on this plot being comprised primarily of shrub-like species, nest concealment from any direction was not different from the mesic plot. The widespread utilization of dead vegetation as a nesting substrate may increase the crypsis of the nest as orange-crowned warbler nests are composed of predominantly dead plant material.

We observed most nests to be elevated off the ground, despite elevated nests being less concealed than ground nests. These results differ greatly from accounts of other orange-crowned warbler subspecies, which place their nests on or close to the ground (Sogge et al. 1994; Baicich and Harrison 1997). There has been only one study which describes off-ground nests in a mainland population (Zyskowski 1993), in which only of 3 of 131 (2.3%) nests found were above ground, ranging in height from 2 to 3.2 m. On Santa Catalina Island, 73% of nests were placed off-ground and the average height

for elevated nests was 1 m. The larger variation in nest heights on Catalina compared to mainland populations may be due to the process of ecological release; there are only seven other cup-nesting passerines on Catalina and therefore little competition for nest sites. Alternatively, nest predation alone, or in combination with ecological release, may explain the diversity of nest sites. Several snake and mammal species, but no bird species, are suspected of depredating warbler nests: gopher snake (*Pituophis melanoleucus*), Santa Catalina Island fox (*Urocyon littoralis catalinae*), Santa Catalina Island deermouse (*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. These potential nest predators preferentially depredate ground nests, and the probability of nest predation declines with increasing nest height on Catalina (Peluc et al. 2008). Interestingly, there are no jays on Catalina, which are thought to prey on predominantly off-ground nests, but warblers still respond to the perceived presence of jays by shifting their nest sites to the ground (Peluc et al. 2008).

Most nests were placed centrally in the substrate, which may impede predators by maximizing vegetation obstruction. Of the remaining nests, there was a significant preference for nests to be orientated to the northeast, or downhill in relation to the nest site aspect. Nest entrances were orientated northeast on the mesic plot, but west on the xeric and these too corresponded with the aspect of the slope, although this may be due to differences in the general aspects of the plots. Preference for nest entrance has been found in other studies (Austin 1974; Facemire et al. 1990), as well as actual nest orientation (Hartman and Oring 2003; Burton 2006). Reasons for this preference may be due to microclimatic factors or that most nests were found on a north-facing slope. This can be seen in the relationship between nest orientation and nest entrance orientation in relation to aspect; dusky orange-crowned warblers place nests in the section of the substrate which corresponds with the downhill direction of the slope. An explanation for this may be in terms of an escape strategy for the adult birds. It was noted that when flushing birds from the nest (either to target

net nests or nest check) the adults always flew downslope. It is assumed that this is due to the easiest and fastest route from the nest in order to avoid adult predation.

This study provides the first detailed description of the nest site location of a subspecies which is very poorly understood. Further analysis of nest locations and predation will be carried out to assess the relationship between choice of nest site and its impact on reproductive success. Future research may compare these characteristics to the nests and nest sites of other orange-crowned warbler subspecies, which are found in a vast array of different habitats, including coniferous, riparian, mixed woodland, burn areas, etc. and in elevations ranging from sea level to 2350 m (Sogge et al. 1994).

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