On the Nest Site Characteristics of the 'Dusky' Orange-Crowned Warbler (*Vermivora celata sordida*) Endemic to Santa Catalina Island

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DECLARATION BY CANDIDATE

This thesis is a presentation of my original research work. Wherever contributions of others are involved, every effort is made to indicate this clearly, with due reference to the literature, and acknowledgement of collaborative research and discussions.

The work was done under the guidance of Dr. Ruedi Nager at the University of Glasgow.

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ABSTRACT

This study focuses on the nest site of a poorly known endemic subspecies of orange-crowned warbler (*Vermivora celata sordida*). The research took place during 2006 on Santa Catalina Island, part of the Channel Island archipelago in Southern California. As one of the first detailed descriptions of the nest site characteristics of this subspecies, this study has revealed that nest placement is highly variable, particularly when compared to mainland populations. Nest height on Catalina ranges from ground to 5m, whereas mainland subspecies nest predominately on or close to the ground. This research also provides an extremely comprehensive analysis of materials used in nest construction and reveals surprising plasticity in the types and amounts of materials used.

Measurements of the nest site uncovered a significant preference to place the nest in the North-East part of the substrate, which was highly correlated with the slope of the terrain. There were no relationships between nest site characteristics and nest success in terms of fledge/fail, although 2006 was an extremely poor year in terms of reproductive success, with a Mayfield estimate of 0.17. It was found, however, that nests under a less dense canopy were active for a longer number of days, as were nests which had a higher level of concealment from below. This is an interesting outcome, as the concealment of a nest from below is not a measurement which is considered in most studies of nest sites. There was very little difference in nest site characteristics between the xeric and mesic ecotypes, apart from the lower canopy cover above nests found on the xeric plot. Interestingly, nesting success was higher in the xeric habitat when compared with the mesic.

Detailed microclimatic measurements were obtained for both nesting sites, before incubation, and for random points. It was found that nests were placed at a location in the substrate which provided lower maximum temperatures when compared to random points within the same substrate. Temperature within the nest was higher than just outside, indicating that the nest structure has an insulative function. Furthermore, it was found that grasses and dense plant matter incorporated into the nest structure provided a higher level of insulation. Nests which experienced higher maximum temperatures were active for a longer number of days, which may have been related to canopy cover, as mentioned above. Two nests were particularly interesting, as warmer temperatures within the nest were experienced throughout the night, but cooler temperatures during the day, when compared with just outside the nest.

This study has revealed several interesting characteristics of the nesting site of this poorly understood subspecies and provides a platform for possible future research in this area.

CHAPTER 1: GENERAL INTRODUCTION

The selection of a sedentary site in order to protect young during development is a strategy which has evolved in various taxa. The term ‘selection’ suggests the choosing of a site which differs in its characteristics to other random sites. Various studies have revealed non-random selection occurring in turtle species (eg. Wilson, 1998), snakes (eg. Burger & Zappalorti, 1986), lizards (eg. Shine & Harlow, 1996) and spiders (Morse, 1985). Perhaps the most widely studied, however, is in birds. Most avian life history traits require that for each reproductive effort, both eggs and altricial nestlings must remain in the confines of the nesting site until fledging. This is a crucial time in terms of a breeding bird’s reproductive success, which may require a large amount of investment by the adult birds in terms of meeting the energy requirements of the offspring and where both adults and developing young are at risk from various forms of predation. With many factors influencing reproductive success, an individual should choose a nest site which optimises both offspring and adult survival. Very few studies have looked at nest site selection and adult survival, although it has been shown that nest site characteristics may influence the fitness of the attending birds (eg. Amat & Masero, 2004; Miller et al., 2007). Choice of the nesting site is often attributed to the female bird, however there is some evidence that the male may also have a part to play in this (Meanley. 1971; Oliarnyk & Robertson, 1996; Graber et al., 2006).

The most common cause of nest failure is predation (Ricklefs, 1969) and various studies have revealed that the choice of nesting site can greatly affect the chance of discovery by predators (e.g. Martin & Roper, 1988; Martin, 1998; Clark & Shutler, 1999; Martin et al., 2000; but see Peak, 2003; Holway, 1991). Different habitats may also experience different predation pressures, nest site availability and resource abundance (Petit & Petit, 1996). A good understanding of the role of nest placement and the function of the vegetation around the nest may be particularly important where significant vegetation change due to deforestation or invasive flora occurs, especially as nest site choice may be constrained by availability of suitable vegetation within the territory (Pribil, 1998).

A nesting site may protect the adult and developing young through its concealment (e.g. Holway, 1991; Flaspohler et al., 2000; Remeš, 2005; but see Holway, 1991), its inaccessibility (Martin, 1995) or by allowing the adult birds to see approaching predators (Gotmark et al, 1995; Yanes et al, 1996; Wiebe & Martin, 1998). The ‘nest patch’ surrounding the nest site may also play a role in nest protection, but utilizing areas with many potential nest sites, thus reducing the search efficiency of the predators (Martin & Roper, 1988). Another pressure affecting nest site choice and nesting success may be brood parasitism. Successful nests can be well concealed or distanced far from the perches of brood parasites (e.g. Larison et al, 1998; Moskat & Honza, 2000).

Microclimate is an often overlooked factor when considering choice of nest site. Birds must maintain a narrow range of optimal developmental temperatures within the nest against the fluctuating climatic conditions outside and extreme variations in this may affect hatchability (reviewed in Webb, 1987) or fledgling performance later in the developmental stage (Gorman & Nager, 2004). Extremes of humidity at the nest can also be detrimental to the development of the embryos, either through excessive or insufficient water loss through the shell of the egg (Rahn et al, 1977; Walsberg & Schmidt, 1992). Choosing a site which provides an optimal climate is beneficial to the developing offspring, but can also reduce energetic costs to the breeding parents through reducing the need to maintain egg temperatures and allowing longer recesses off the nest for foraging (Williams 1996; Reid et al. 2002; Tinbergen & Williams 2002). So microclimate at the nest site can have a role to play in affecting the reproductive success of both the adults and the young.

The choice of nest placement can have an effect on the microclimate of the nest; it is known that birds in arid climates may position the nest to provide favourable conditions throughout the day (Walsberg & King, 1978; Walsberg, 1981). Nest height can affect temperatures through convection and heat stored in the ground (Conway & Martin, 2000). Both the positioning of the nest in the substrate and the structure of the nest itself may have a role in regulating the thermal balance of the developing young. Nesting material can have an insulative role, with certain materials acting as more efficient insulators than others (Hilton et al, 2004). The macro environment of the nest patch can also affect the conditions experienced by the nest through the type of habitat, slope, orientation or altitude (Martin, 1998; Martin & Roper, 1988; Rauter & Reyer, 2000).

Exploring nest site preference is a difficult task, especially when linking this to reproductive success, as any correlations found will depend on the availability of preferred nest sites (Pribil, 1998). So, if a certain nest site provides optimal reproductive success and that site is abundant, all birds will favour those sites and so no correlation will be found. One way to explore this further is to look at preference of certain nest site features to assess if certain features are being selected. Chosen sites can also be compared with possible, but unchosen sites in the same territory. Other problems may arise when predation is extremely high, and so a simple comparison of nest site features and nest success is impossible. One route around this, an option suggested in this study, is to measure nest success by the number of days it is active rather than whether it fails or fledges.

This study seeks to explore the hypothesis that nest sites are selected to optimize reproductive success both in terms of the protection a site offers from predation and the microclimatic effects it has on the developing offspring.

<u>Study species</u>— The orange-crowned warbler (*Vermivora celata*) ranges throughout the Western United States, Mexico and Canada. The poorly known subspecies, *V. c. sordida,* is endemic to the Channel Islands and is especially dense on Santa Catalina Island. This provides a good study population, as large numbers of nests can be found in one breeding season. Although this population seems to be flourishing, it is currently in decline on other Islands (Sillett, pers. comm.). The orange-crowned warbler is a medium sized wood warbler (9.4±0.8g) with the males of *V. c. sordida* being slightly larger (5-6%; *n*=106) than the females (Sogge et al., 1994). Nests are initiated during a variable period (from February through to June in 2005 and April to June in 2006, pers. obs.) and territories cover a variety of different habitats exposing them to a large diversity of different environmental conditions. This provides an opportunity to explore varying habitats and predation pressures on a single species. The nest is an open cup of varying sizes and nesting material differs immensely, including *Quercus* sp. (twigs, leaves and inflorescences), *Toxicodendron* sp. leaves, *Salvia* sp., grass and animal hair. The female lays 2-4 eggs, 2-3 days after nest completion and incubation starts on the last (Sogge et al., 1994) or penultimate egg (pers. obs.). Only the female incubates, usually for 12 days, and eggs hatch over a 24 -hour period. Nestling period is 11-13 days (Sogge et al., 1994). Unlike the mainland subspecies that nest solely on or near the ground, *V. c. sordida* nests can be built up to 8m from the ground (pers. obs.). This offers the opportunity to examine differences in nest sites, predation and microclimate in ground compared with off-ground nests. Various climatic measurements taken at these two heights reveal a significant difference (Table 1); temperature is higher on the ground, wind speed is lower, wind chill is higher, as is humidity, heat index and dew point. Birds may reflect this in their choice of nest site or nesting material.

Climatic measurement	Mean values		*t*-test	
	On ground	Off ground	*t*	P
Temperature (ºC)	16.87	15.41	12.03 df=117	0.001
Maximum Wind Speed	1.09	3.85	12.05 df=117	0.001
Average Wind Speed	0.5	1.92	13.8 df=117	0.001
Wind Chill (ºC)	16.75	15.27	12.29 df=116	0.001
Relative Humidity	62.94	58.31	12.23 df=117	0.001
Heat Index	16.26	14.58	11.11 df=117	0.001
Dew Point (ºC)	9.05	6.56	15.23 df=117	0.001

Table 1: At 06:00, 10:00, 12:00 and 14:00 each day (when possible), climatic readings were taken in the area that the observer was present at that time. A Kestrel 3000 Environmental Meter was used to take measurements both on the ground and at 1.5m, whilst rotating 360º over a 1min period. The table shows a significant difference between on and off ground readings for all climatic measurements. 'Heat Index' is a measurement which takes into account the effects of Humidity and Air Temperature. 'Dew point' is the temperature at which water vapour condenses into dew.

<u>*Study site*</u> —The field site, Santa Catalina Island (33°22’30”N, 118°25’56”W), is part of the Channel Island archipelago in Southern California. The location of the island is shown in Figure 1.

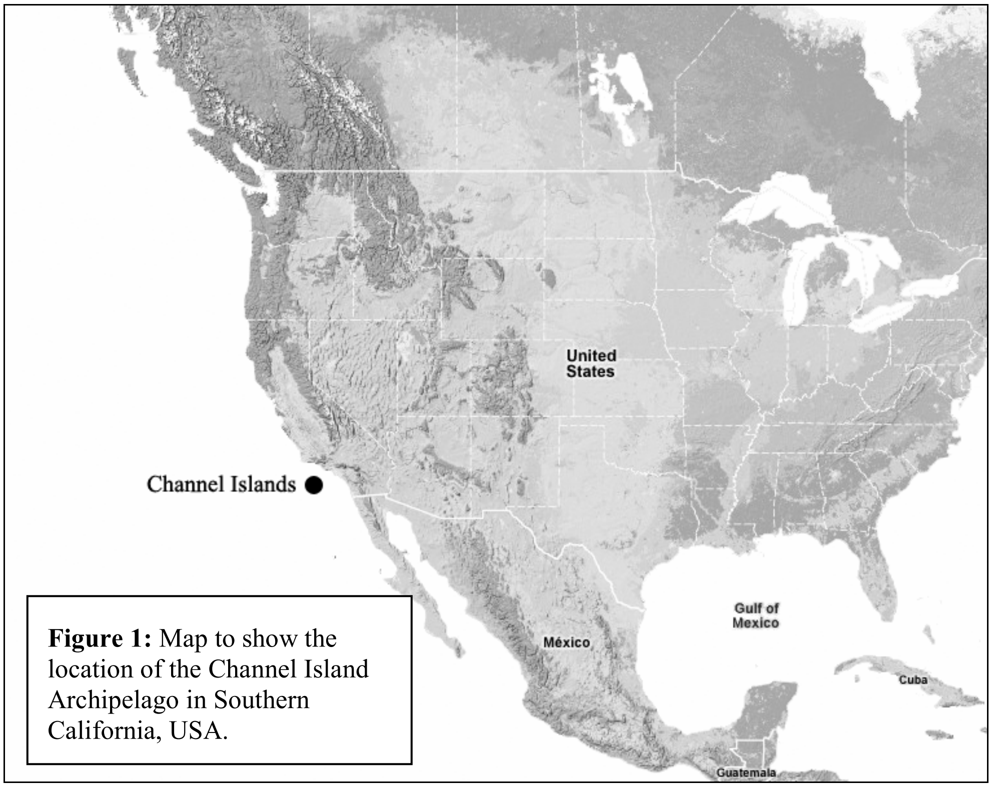

Figure 1: Map to show the location of the Channel Island Archipelago in Southern California, USA.

The study included two plots in Bulrush Canyon, a large valley than runs East to West in the South-East of the Island (Figure 2).

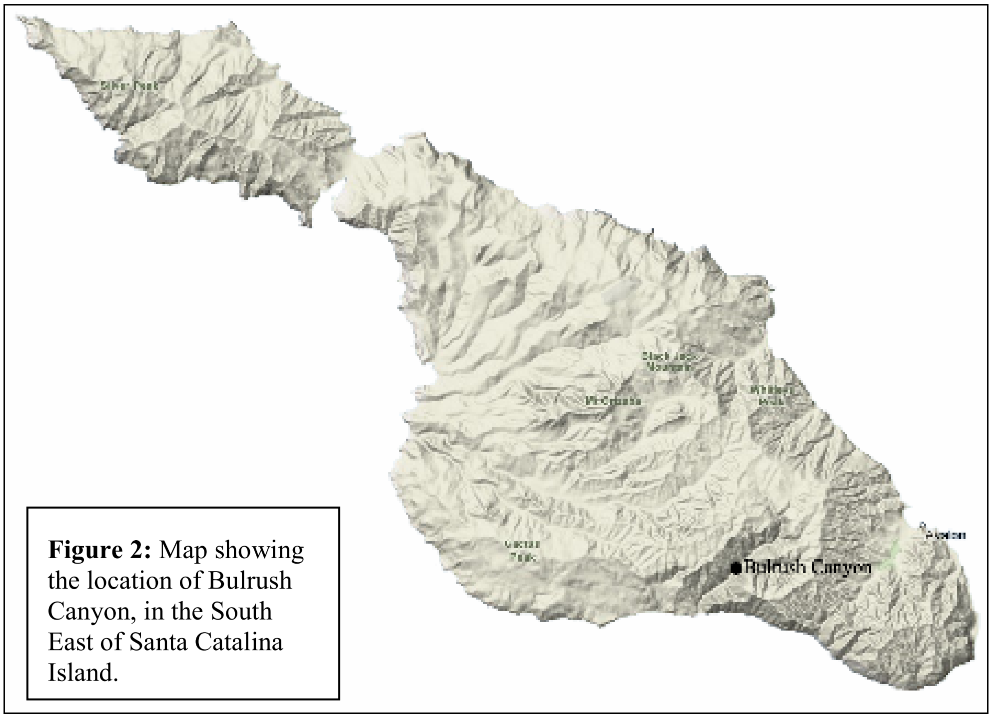

Figure 2: Map showing the location of Bulrush Canyon, in the South East of Santa Catalina Island.

Bulrush canyon, study site 1 (BRC1 hereafter) was selected to encompass the mesic environment at the base of the Canyon, where vegetation consists of scrub oak (*Quercus pacifica*) and toyon (*Heteromeles arbutifolia*) forest, lemonade-berry leaf (*Rhus integrifolia*) shrubs and various forbs and grasses. Bulrush canyon, study site 3 (BRC3 hereafter) was situated at a higher elevation, on a South-facing slope and is characteristic of a xeric sage-scrub habitat with mainly coastal sagebrush (*Artemesia californica*) and prickly-pear cactus (*Opuntia phaecacantha*). These two plots differ in vegetation as well as climate and so offer a good opportunity to examine differences in nest site, microclimate and nesting success in two distinct habitat types.

The climate on Catalina varies greatly throughout the breeding season, with greater variation in temperature at the beginning of the season and higher average temperature later (Figure 3). In 2006 the breeding season was relatively short, especially when compared with 2005 when breeding was initiated in February and ended in June (pers. obs.). On BRC1 temperatures both on and off the ground became more stable about half-way into the breeding season. Humidity off ground reflected changes in temperature and also became more stable at around the same time. On ground humidity, however, remained greatly variable throughout the field season. Surprisingly, humidity on the ground tended to reach the zero-point more often, whereas off ground humidity remained fairly high (Figure 3). Temperature on BRC3 remained more stable through the breeding season. Humidity was, again, fairly high off ground (Figure 3). These measurements for both sites may be reflective of the amount of fog that was present during the breeding season (pers. obs. and see humidity Table 2).

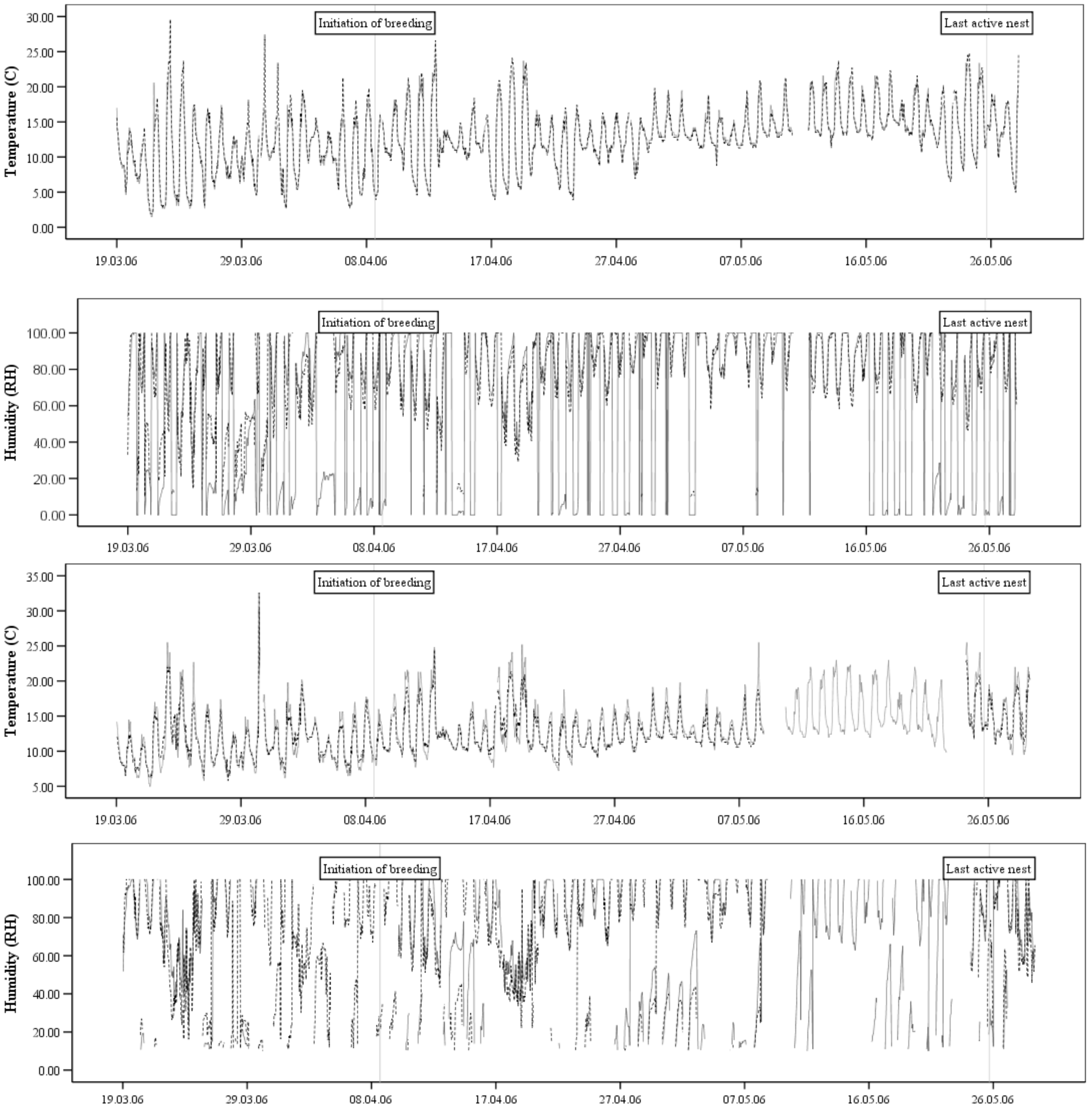

Figure 3: Shows temperature and humidity taken on BRC1 (top two graphs) and BRC3 (bottom two graphs) from 19.03 – 28.05.06. Off ground loggers (dotted lines) were placed 1.5m high, on ground loggers (solid lines) were placed at ground level. Temperature and humidity was recorded by leaving the data loggers in the shade and under a plastic 'umbrella' to protect them from rain. The loggers were set to record every 10mins throughout the day and night. Gaps in data are due to removal of loggers to download data, or logger malfunction. Initiation of breeding is defined by the first nest found at building stage and end of breeding was the end of the field season, so unfortunately was not the true end of breeding. There were, however, only 4 nests still active**.** See Appendix 2 for larger graphs.

Rain is also extremely variable between years and follows a cyclic pattern of very wet "El Niño" years and dry "El Niña" years. This is especially evident on Santa Catalina Island (Yoon, 2007 unpubl. data). Differences in climate (during the breeding season only) between years can also be seen on Table 2. Although 2006 was generally a very dry year, with a total of 3.7mm of rain in comparison to 21.82mm in 2005 (Catalina Island Conservancy website: www.catalinaconservancy.org), when considering the breeding season alone it was fairly wet and humid (Table 2).

Year	Average Wind Speed (m/h)	Average Temperature (°C)	Average Humidity (%)	Total Precipitation (mm)
2007	8.5	14.6	60	4.57
2006	7.96	11.35	78.66	19.3
2005	7.8	13.83	68.33	16.26
2004	7.5	15.37	68	4.57

Table 2: Shows climatic measurements between March-May (the main part of the breeding season) from 2004-2007. Data is taken from the Western Region Climate Centre (www.wrcc.dri.edu). 2006 was particularly cold and although it was a dry year, when looking at the breeding season alone, it was relatively wet and humid.

Initiation of breeding may be related to rainfall, as has been shown in other species (e.g. Zann et al., 1995). In 2006 the beginning of nest building commenced soon after a very heavy period of rain and the end of breeding was at a point in the season where there was very little rain (Figure 4).

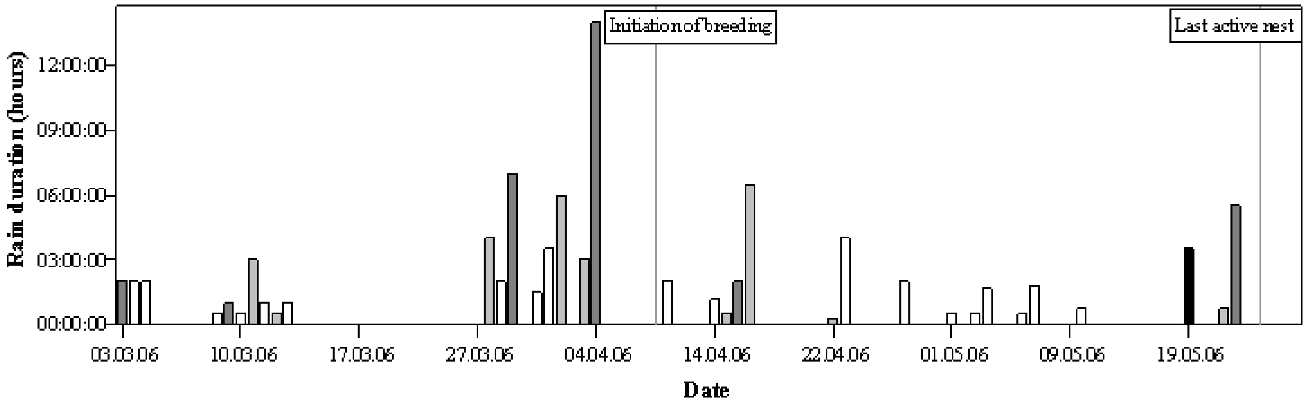

Figure 4: Shows rainfall through the breeding season in 2006. Rainfall was recorded when it was observed, noting the duration and rain "type". White bars represent fine drizzle; light grey represent intermediate; dark grey represent heavy rain; black represents heavy downpours. Rain duration is recorded in hours.

CHAPTER 2: HIGH LEVELS OF PLASTICITY IN THE STRUCTURE AND PLACEMENT OF NESTS

ABSTRACT

The *sordida* subspecies of orange-crowned warbler (*Vermivora celata*) is known to differ in its choice of nests sites from the mainland populations. Here, I quantitatively describe in detail the sites of nests found during one breeding season. The Catalina Island orange-crowned warbler displayed a significant preference for a North-East orientation of both nest and nest entrance and these were highly correlated with the aspect of the slope on which the nest was situated. There were also a variety of relationships between nest size, height, substrate and concealment. The study highlighted the surprising plasticity in material types used for nest construction and revealed correlations between the location of a nest within a nest substrate and materials used to build the nest.

How nest sites differ depending on habitat type is a component in understanding nest site selection. Here we found that only canopy cover was statistically different between the xeric and mesic ecotypes examined, it being significantly lower above nests in the xeric habitat.

INTRODUCTION

Many taxa utilise nest sites either for breeding or as dormitories or roosts and these sites can vary from being simple to very complex structures. Birds are particularly interesting as the majority of species undergo a sedentary period due to incubation and many require further use of a nesting site due to altricial development of the young. A nest can have a variety of functions, including to protect eggs, young or adults from predators, to attract a mate, to provide a favourable microclimate (Hansell, 2000) or to protect against avian brood parasites (Moskát & Honza, 2000).

Choosing a good nest site is an important component of breeding ecology as it may greatly affect an individual's reproductive success (e.g. Martin & Roper, 1988; Martin et al., 2000; Liebezeit & George, 2002; but see Bisson & Stutchbury, 2000). Birds living in a heterogeneous environment have a variety of choices for potential nest placement, but these options may be limited due to types of predators present (Remeš, 2005), interspecific or intraspecific competition for these sites (Martin, 1998; Liebezeit & George, 2002), or purely logistical restrictions, such as sufficient physical support for large nests built by species with large body size (Hansell, 2000). Different ecotypes may represent a diverse array of conditions and these can be expressed in the choice of dissimilar nest sites for birds occupying different environments either between or within populations (e.g. Martin 1998; Martin, 2001). An example of this is found in elevational variations in habitat type, where habitat at a lower altitude may experience more moisture and higher quality soils resulting in a higher and diverse range of species. Habitat at a higher elevation often becomes drier, rockier and sparser, resulting in a more xeric habitat type (Martin, 2001). This variation in habitat could potentially lead to variation in nesting sites of the same species.

The various pressures affecting nest site choice have resulted in the evolution of a hugely 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). Nest sites are often chosen due to various selective pressures and many populations of species have evolved particular nest site characteristics, such as a specific height, for example the majority of *Vermivora* sp. of warblers nest on or close to the ground in North America (Baicich & Harrison, 1997). Birds may also chose a specific orientation for the nest (e.g. Finch, 1983; Hoekman et al., 2002; Burton, 2006) or nest entrance (Facemire et al., 1990). Other considerations may be the concealment of the nest (Holway, 1991; Weidinger, 2002), the ability to see approaching predators (e.g. Götmark et al., 1995) or the density/size of supporting branches (e.g. Murphey, 1983). These various characteristics have been considered in many studies of nest sites and have more recently been compiled to form a standard protocol for the measurement of nest sites (Martin et al, 1997).

Nest construction materials may be selected to increases the crypsis of the nest or to secure the nest in the desired position (Hansell, 2000). Other nest materials may serve to insulate the nest (Hilton et al., 2004) or to protect against parasites and pathogens (Clark & Mason, 1985). However, very little work has been done on the variation in the composition of the materials used to build nests nests within populations.

The aim of this chapter was to quantitatively describe the nest structure and the nesting site of the endemic orange-crowned warbler (*Vermivora celata sordida*) population on Catalina Island, California. This subspecies is particularly useful to study due to the fact that it is extremely densely populated and inhabits a wide variety of ecosystem types on the island. It also experiences very little intraspecific competition for nesting sites and so is not limited to a specific habitat type, as has been shown in other studies of the same species (Martin, 1998). This allows the study of how environmental factors affect nest site choice, without the effects of competition. A comparison between a mesic and xeric habitat was used to explore how macroenvironment relates to nest placement and structure.

METHODS

The study was undertaken on Santa Catalina Island, Los Angeles County, California, U.S.A (33°22'30"N, 118°25'56"W) from March to May 2006 and is a part of a long term study of this orange-crowned warbler population. Santa Catalina Island is part of the Channel Island archipelago. The climate is Mediterranean and varies greatly throughout the year, with cool wet months at the start of the breeding season becoming dry and relatively hot during the summer.

The orange-crowned warbler inhabits the Western United States, Mexico and Canada. The Channel Islands are at the Southern edge of its breeding range and this population is recognised as its own *sordida* subspecies. The subspecies is endemic to the Channel Islands and is especially dense on Catalina. It is a medium sized warbler (mean body mass is 9.4±0.8g) with the males of this subspecies being significantly larger (5-6%; *n*=106) than the females (Sogge et al., 1994). Both initial and replacement nests are initiated over a variable period (from February through to June in 2005 and April to June in 2006, pers. obs.). The female lays 2-4 eggs, 2-3 days after nest completion and incubation starts on the last (Sogge et al., 1994) or penultimate egg (pers. obs.). Only the female incubates, usually for 12 days, and all eggs hatch within 24 hours of each other. Nestling period is 11-13 days (Sogge et al., 1994).

<u>*Study site*</u>— The study site, Bulrush Canyon (BRC), is a large valley which runs East to West from the South-West coast of the Island. The fieldwork was conducted on two plots, BRC1 and BRC3, which differ in altitude, aridity, vegetation composition and diversity. BRC1 is situated in the base 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, shrub-like plants such as lemonade-berry leaf (*Rhus integrifloria*) and large 'meadow' areas composed of grasses and forbs. These habitat types are characteristic of a mesic system. Average elevation for nest sites on this plot was 73.95±3.1 m a.s.l. (*n*=42). BRC3 is a xeric ecosystem, situated on a South facing slope at a higher altitude. The vegetation is less diverse and is more characteristic of sage scrub. The area is dominated mainly by coastal sage (*Artemesia californica*) and prickly pear cactus (*Opuntia phaecacantha*). The average elevation for nest sites on this plot was 86.13±3.4 m a.s.l. (*n*=14). Each study plot covered 500x300m and was gridded with flagging every 25 m and assigned a letter/number in order to draw accurate maps of territories and nests.

<u>*Nest surveying*</u>— Nest searching was conducted from 6am to 1-3pm each day using methods outlined in Martin & Guepel (1993). Bird behaviour and vocalisations were closely observed and plots were

methodically searched. Nests were marked with flagging, which was tied to vegetation at a distance of 7-10m. Every two days, usually close to midday when activity is lowest, nests were visited to check status. The stage of the nest, number of eggs/nestlings and other behavioural observations were recorded onto nest cards. In 2006, a total of 56 orange-crowned warbler nests were found, 42 on BRC1 and 14 on BRC3. Subsequent to failing or fledging, detailed quantitative descriptions of nests and nest sites were obtained. Nest dimensions, height, orientation and various substrate measurements were taken using the BBird protocol (Martin et al., 1997).

Nest site measurements— Nest height was measured from the base of the exterior of the nest to the ground below. This measurement was acquired for all nests found. Of these, 6 nests were inaccessible or still active at the end of the study and height was estimated. Nesting substrate was determined as the species of plant(s) that the nest was placed in; this was measured in all off-ground nests which were accessible. Only 'primary' nesting substrates, which were integral to the support of the nest, were included. Small branches which were touching, but not supporting, the nests were excluded from the analysis. Substrate health; dead or alive, was also recorded. More detailed measurements were taken for the 42 nests which were accessible and intact on day 25, where day 25 was before the end of the field season. This time span was chosen to standardise measurements for each nest, as it is known that nest site characteristics can change over time (Burhams & Thompson Ш, 1998). A period of 25-30 days ensured that the nest had either failed or fledged as it encompasses both the incubation and the nestling period (Sogge et al., 1994).

The number and diameter of the branches directly supporting the nest were recorded for all off-ground nests. Vegetation height at nest, from the ground below the nest directly upwards to the highest point of the nest substrate, was measured. Nest orientation in the substrate was calculated using a compass directed from the centre of the nest substrate towards the actual nest, nests positioned in the centre of the substrate were excluded from this measurement, but noted. Orientation of nest entrance was determined by assessing the most direct gap in the vegetation to the nest, any flattened surface on the rim (indicating adults perching in order to feed nestlings) and personal observations of the adults' flight patterns to and from the nest. With most nests there was only one obvious flight path from the nest. Aspect was measured by standing at the nest site, directing a compass downhill from that point and taking a bearing. To examine nest site orientation in relation to aspect of the slope, the angle between the orientation of the nest or nest entrance and the aspect of the slope was calculated (i.e. 90° would be at a right angle from downslope and 180° would be upslope). This additional measurement, "angle from downhill", was then used in the analysis for the orientation in the substrate and of the nest entrance.

Concealment was calculated by ocular estimation; the observer stood at each cardinal direction, at eye-level and 1 m away from the nest and assessed the percentage of the nest that was obscured by vegetation to the nearest 5%. This was also repeated, when possible, directly above the nest, looking down (concealment from above) and directly below the nest, looking up (concealment from below). When nests were inaccessible due to height or terrain, mirror poles were used to evaluate these measurements. Concealment from cardinal directions and from above was measured for all nests and concealment from below measured for all off-ground nests. All above measurements were conducted by the same observer (HM) to reduce bias and ensure consistency in estimations.

At 25-30 days after clutch completion a Lomography 35mm Fisheye Camera (with 170º lens) was used to take a picture of the vegetation above the nest sites. This was done by laying the camera horizontally at the spot that the nest had been, with the top of the camera pointing North. The film was developed and converted into an electronic format using a negative scanner. An accurate measure of ‘Canopy Openness’, the percentage of sky seen from the nest site, was then calculated using Gap Light Analysis (GLA) software (obtainable from Simon Fraser University, Institute of Ecosystem Studies, www.ecostudies.org/gla/). This data was used to gain a measurement of total vegetation and canopy density above the nest, ‘canopy cover’, whereas concealment from above, as outlined previously, was used to give a measurement of vegetation density within a metre of the nest.

Nest measurements— Nest dimensions were calculated to the closest 0.5cm as follows: outer height (from rim of the nest to base of the exterior), inner height (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). These measurements were obtained for all nests which were intact and accessible after fledge/fail and were taken as soon as possible, rather than at day 25-30, as many nests were destroyed by predators or weather. Nest volume was subsequently recorded using the equation for the volume of an ellipsoid as an indicator of nest size. A regular ellipsoid was assumed, with equal width and depth, as adapted from Lombardo (1994):

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

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

Collected nests were securely wrapped in Clingfilm and stored in a box containing mothballs to kill any insects present. Once in a laboratory, nests were weighed using electronic scales to the nearest 0.001g. Outer nest dimensions and nest weight correlated extremely closely with nest volume (all correlations $rs>0.45$ and $P<0.001$), so nest volume was used as an indicator of nest size. Nest volume was also known for a higher number of nests than nest weight. The nest was gently pried apart until a quarter of the material was separated; both from the outer cup and the nest lining (this was then weighed to ensure that it was equal to 25% of the original weight). Using forceps, the nesting material was divided into type of material and weighed separately. Material was then categorised into 8 types; plant stem, bark, grass, leaf, twig, dense plant matter, root or vine-like and other (as modified from Hansell, 2000). Common bedstraw (*Galium aperini*), wild cucumber stems (*Marah macrocarpus*) and a grass species which has extremely long, curly leaves were all treated as having 'vine-like' properties as they were very characteristic of vines and were used to hold nests together in the same way. All materials treated as 'other' were either very small or found in very small quantities and so it was assumed that they served little purpose in terms of nest construction. Large, dense clumps of material were classed under one category as they were of similar size, shape and quality. All materials found and their classifications can be seen in Appendix 1.

Statistical analysis— Sample sizes are as follows:- (i) 56 nest were found, of which height was measured for all. (ii) I measured nest dimensions for 48 nests (3 were inaccessible, 4 were still active by the end of the season and 1 was destroyed before collection). Substrate was also noted for the 35 nests which were off-ground. (iii) I obtained more detailed measurements at day 25-30 for 42 nests (29 off-ground and 13 ground); number and diameter of support branches were measured for all accessible off-ground nests (*n*=29) and concealment calculated for all 42 nests (cover from below was recorded for 29 off-ground nests). I measured orientation from the centre of the substrate to the nest site (19 nests measured, 23 were placed in the centre of the substrate) and where a distinct nest entrance could be seen, the orientation of this was also measured (34 nests had a measureable entrance, 8 did not). Aspect was also measured in 35 nests (7 nests had no valid measurement due to a recording error) and from this, 'angle from downhill' (see description above) was calculated for nests (*n*=15) and nest entrances (*n*=29). A total of 45 nests were collected for further analysis of nesting materials and weight.

SPSS 14.0 software was used to analyze data. Spearman's rank coefficient was used to measure the strength of all correlations, including ordinal data. Contingency tests were used to compare frequencies. Where Levene's test for equality of variance showed significantly unequal variances, the non-parametric Man-Whitney U-test was used. Circular data was examined using Oriana 2.0 (available from Kovach Computing Services www.kovcomp.co.uk/oriana/) to obtain circular graphs and mean vectors. Rao's Spacing U-test was run on orientation data to assess non-random preference, unfortunately Oriana does not give exact P values for this test. 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). Means are given with ±1 standard deviation.

RESULTS

Nest-site attributes and study plots— The orange-crowned warbler placed its nest in a wide variety of substrates, when considering all off-ground nests, with a total of 17 vegetation types being used on BRC1 (*n*=26) and 7 on BRC3 (*n*=9), as seen in Figure 5. Dead plant material was a common nest substrate, with 46% (*n*=35) nests placed in dead vegetation. There was no significant difference between BRC1 and BRC3 when looking at use of dead vegetation in the nesting substrate (χ^2=0.4, df=1, P=0.53). Overall, lemonade-berry was the most common nest substrate (Figure 5). Although the substrate of ground nests was not included in the analysis (as ground nests, by definition, do not require a substrate), the vegetation in which they were placed was recorded. Only 13 nests were in any kind of measurable substrate (others were destroyed or were in the ground or dead leaves) and 77% of these were in dead vegetation, 15% in grass and 7.7% in forbs.

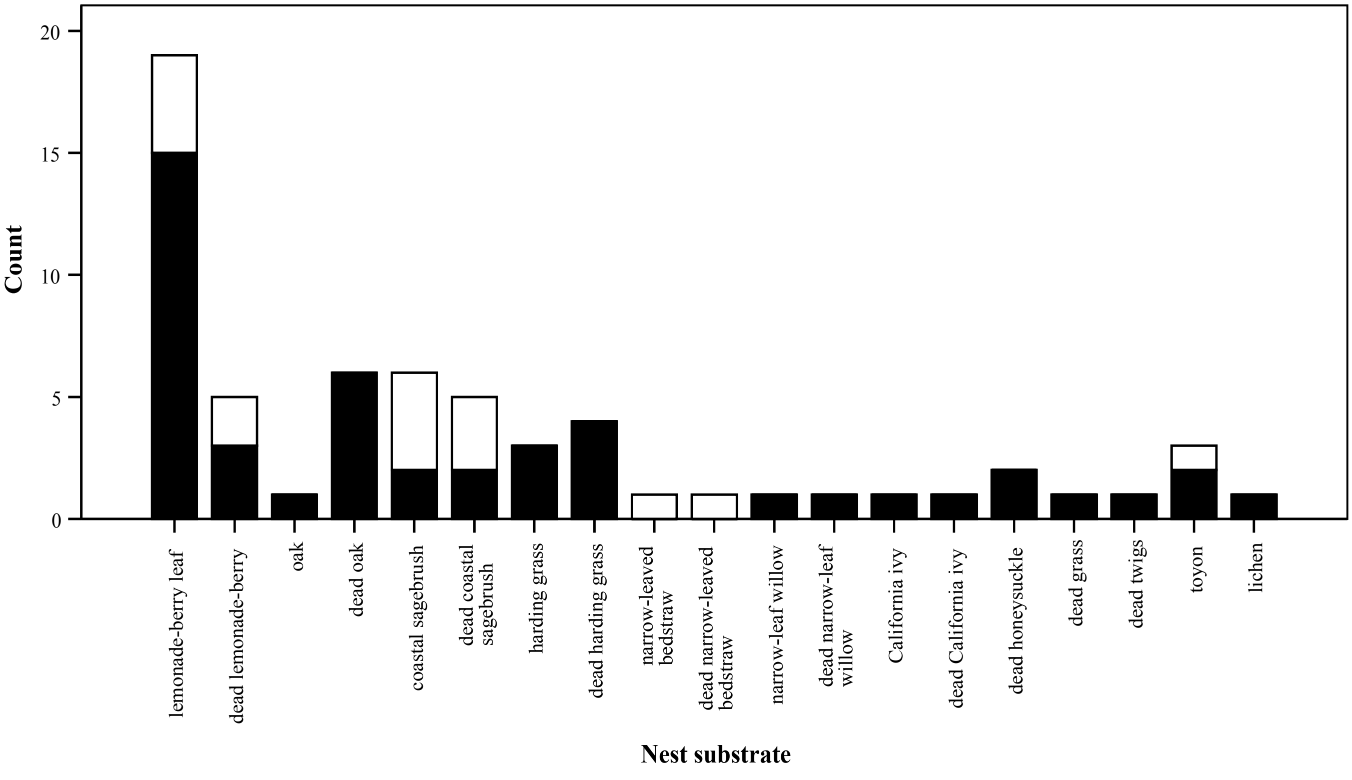

Figure 5: Histogram shows frequency of nesting substrates of all off-ground nests on BRC1 (filled bars *n*=26) and BRC3 (open bars *n*=9). Sums of frequencies are higher than the total sample size as nests can be built in more than one vegetation substrate. Dead grass, twigs and lichen were not identified to species (apart from the more obvious harding grass, *Phalaris aquatica).*

There was much variation in nest substrate use between sites (Figure 5), although there was no statistical difference in primary nesting substrate when comparing plots ($\chi^2=11.2$; df=4; P=0.02). Average height of the nest substrate was 1.38±0.55 m (range 0.48 m – 3 m; *n*=29), there was no significant difference in nest substrate height when comparing BRC1 to BRC3 (*t*=1.67, df=27, P=0.11).

Of the 56 nests found, a disproportionally larger number of nests were placed off the ground than were placed on the ground (73 % and 27 %, respectively; $\chi^2=12.07$, df=1, P=0.001). There was no significant difference in the proportion of off ground nests between BRC1 and BRC3 ($\chi^2=0.76$, df=1, P=0.38). There was also no significant difference in nest volume when comparing plots, nests off the ground, however, were significantly larger in volume than those on the ground (Table 3).

	ANCOVA Test	
Nest-site characteristic	On/Off ground	BRC1/BRC3
Nest height		$F_{1,39}=1.14$ P=0.29
Nest volume	$F_{1,44}=5.8$ P=0.02	$F_{1,45}=0.48$ P=0.49
Nest cup depth	$F_{1,46}=1.07$ P=0.31	$F_{1,45}=0.91$ P=0.35
No. support branches	–	$F_{1,27}=1.27$ P=0.27
Diameter support branches	–	$F_{1,27}=0.12$ P=0.73
Mean lateral concealment (N, S, E & W)	$F_{1,40}=12.3$ P=0.001	$F_{1,39}=0.11$ P=0.74
Concealment from above	$F_{1,40}=9.77$ P=0.003	$F_{1,39}=0.07$ P=0.79
Concealment from below	–	$F_{1,27}=1.68$ P=0.21
% Canopy cover	$F_{1,39}=0.05$ P=0.82	$F_{1,40}=7.27$ P=0.01

Table 3: Shows ANOVA tests for nest site characteristics on and off the ground and on BRC1 and BRC3. No significant relationships were found when examining height vs. plot.

Inner nest height was used as a measurement of inner cup size as this was more variable (mean 4cm, variance 0.26cm, *n*=48) than inner nest diameter (mean 5cm, variance 0.2cm, *n*=48). It was also assumed that females can alter the depth of the cup, but that the width is determined by the size of the bird. Nest cup depth was not significantly different when comparing between nests on and off the ground and when comparing between study plots (Table 3). Number of support branches did not differ between sites (13.52±11.91 (range 4–50; *n*=29), nor did the diameter of the largest support branch (1.24±1.65cm (range 0.1–6.5; *n*=29, Table 3). There was larger variation in the number of support branches used in BRC1 (Levene's test for equality of variances, F=5.78, P=0.05), although a non-parametric test also revealed the same non-significant difference in number of support branches between plots (U=79.5, P=0.83).

Lateral concealment did not differ between the four cardinal directions ($F_{3,39}$=0.32, P=0.81). Hence a mean of these measures was used as an indicator of lateral concealment. Ground nests showed a higher lateral concealment (98±4%, *n*=13) than off-ground nests (79±20%, *n*=29), but did not differ between study plots (Table 3). There was less cover from below when compared to lateral concealment (paired-*t*=2.34, df=28, P=0.03) and, similarly, from above (paired-*t*=2.97, df=41, P=0.005). Concealment from above also did not differ between sites, although ground nests had a higher level of cover (mean 90±14%, *n*=13) than off ground nests (mean 66±26%, *n*=29, Table 3). There was no difference in cover from below when comparing BRC3 to BRC1 (Table 3). Canopy cover was higher for nests on BRC1 (89±9%, *n*=31) than for nests on BRC3 (77±19%, *n*=11, Table 3). The variation in canopy cover was higher on BRC3 than on BRC1 (Levene's test for equality of variances, F=15.41, P=0.001), and a non-parametric test revealed an only marginally significant difference in canopy cover between study plots (U=112, P=0.09).

Nest orientation was not significantly different between the two study plots (U=33, P=0.36, *n*=19). When measuring nest orientation on both plots combined, it was found that 55% (*n*=42) of nests were placed in the centre of the substrate, these nests were omitted when considering nest direction as they had no particular bearing. Mean vector of nest orientation was 41±77° (*n*=19). I divided nest bearings into four groups according to cardinal directions (NE=0-89°; SE=90-179°; SW=180-269°; NW=270-359°). It was found that there was a strong bias to place the nest in the NE of the substrate, as shown in Figure 6.

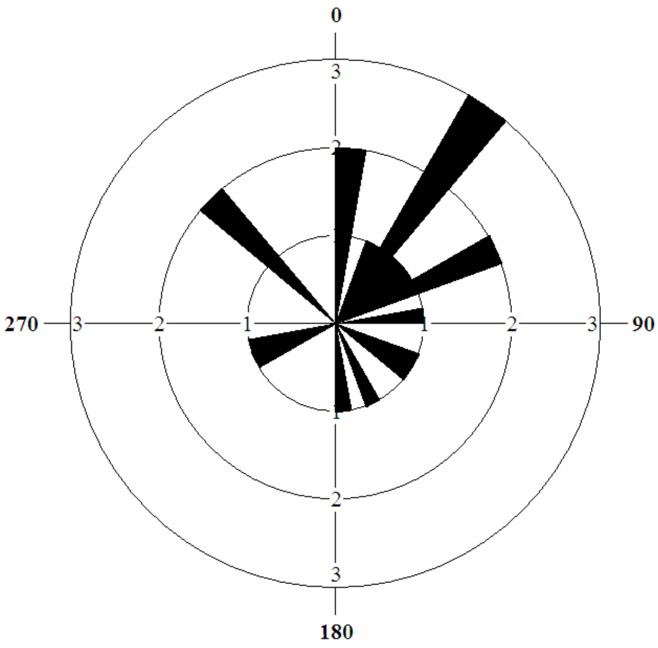

Figure 6: Circular histogram shows nest orientation in substrate. Numbers inside the circles represent numbers of nests. Numbers on the outside represent degrees, up to 360°.
A significant preference to place the nest in the North-East part of the substrate emerges (χ^2=11.53, df=3, P=0.01, *n*=19).

Nest entrance orientation, however, was significantly different when comparing BRC1 to BRC3 (U=56.5, P=0.02, *n*=34). Mean nest entrance orientation vector on BRC1 was 40±103º (*n*=24) and there was a significant preference to orientate the entrance to the NE. Mean nest entrance orientation vector on BRC3 is 281±104º (*n*=10) and there is a preference to orientate entrances to the West rather than the East (Figure 7).

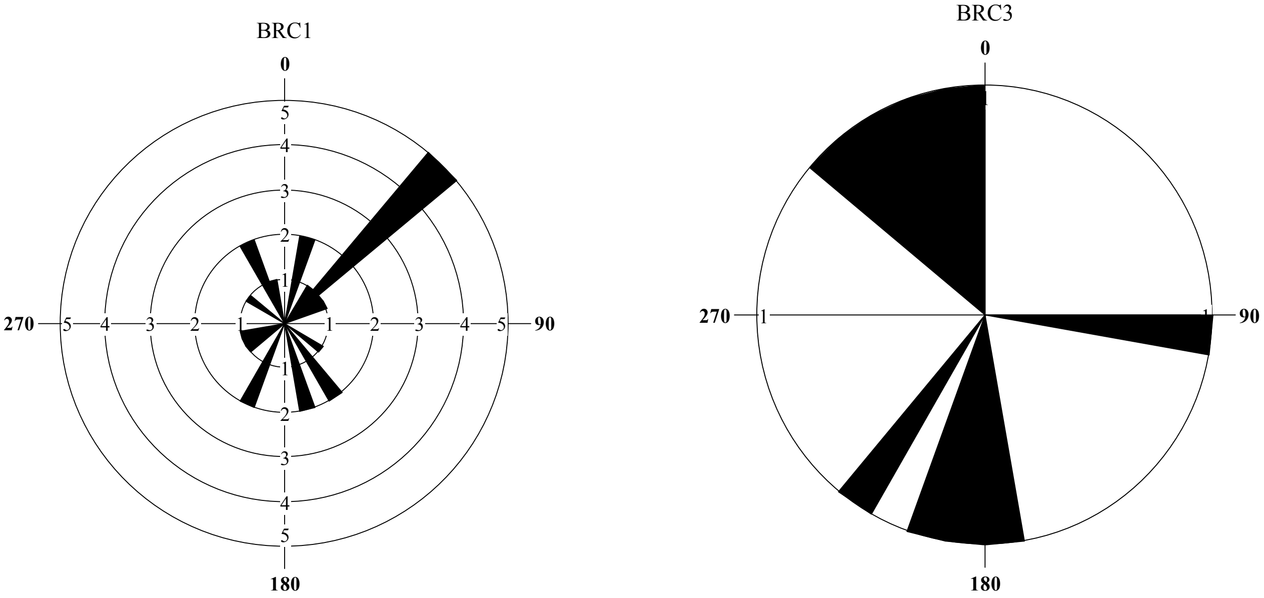

Figure 7: Circular histograms show a significant preference to orientate nest entrance to the North-East on BRC1 (U=165, P<0.05, *n*=24) and to the West rather than the East on BRC3 (U=172, P<0.05, *n*=10).

Most nests found were placed on a North facing slope, which was likely due to the fact that BRC1 was situated on a North facing slope. Aspect was not measured for all nests due to a mistake in the recording procedure (see methods), so sample sizes are smaller. 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).

The orientation of both the nest and nest entrance were compared with the slope by calculating the ‘orientation from downhill’. Downhill was measured as anything with a slope of below 90º and anything above this was classed as uphill. There was no significant difference between plots when looking at nest orientation from downhill (t=1.06, df=26, P=0.3). When looking at both plots combined, the mean angle of the nest orientation in the substrate from downhill was 41± 42º (*n*=15, range 0-140º) and mean orientation of nest entrance from downhill was 71.9± 53º (*n*=29, range 10-180º). Both of these figures are less than 90º and so represent a downhill orientation. A statistical analysis also shows that there was a significant preference to orientate both nests and nest entrances downhill (Figure 8).

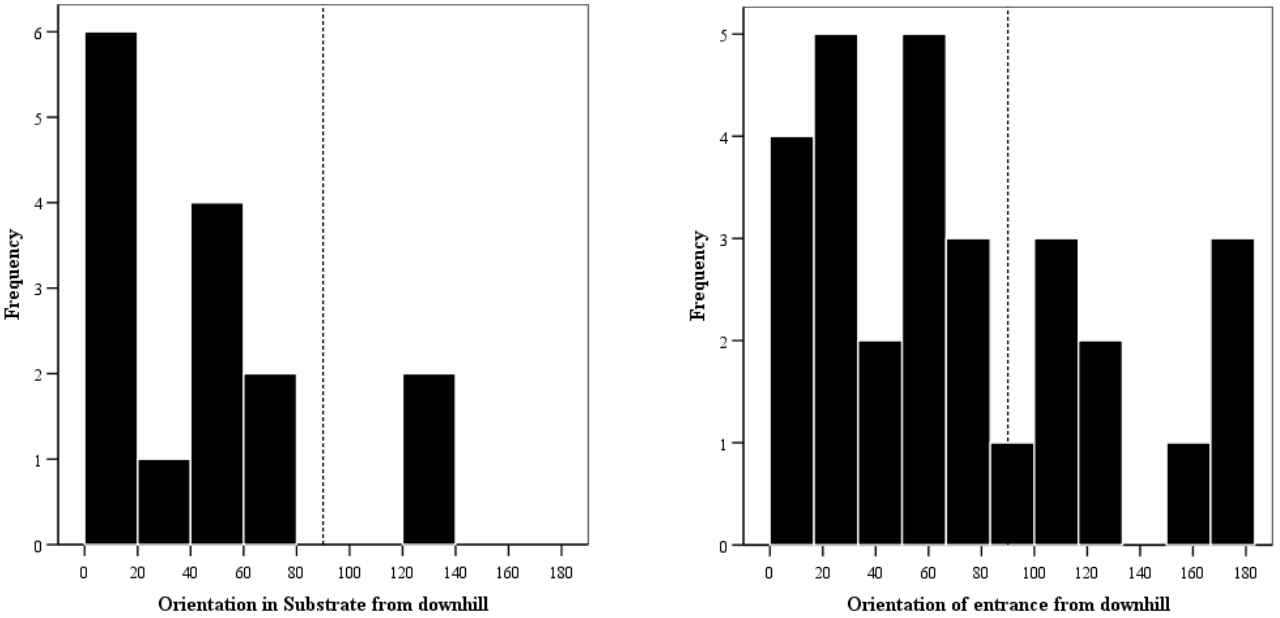

Figure 8: Graphs show orientation of both nests and nest entrances in relation to the slope. Dotted lines represent flat ground (90º) and so any nests below this line are downhill orientated and any above the line are uphill. There was significant preference to place both nests (χ^2=8.1, df=1, P=0.01) and nest entrances (χ^2=4.17, df=1, P=0.04) with a downhill orientation. Missing data is due to the fact that aspect was not recorded for all nests (see methods).

Relationships of nest-site characteristics— Few nest site attributes were inter-related, as is highlighted in Table 4. When looking solely at nests built off the ground, it can be seen that those built higher up in the vegetation had significantly fewer but larger support branches than nests lower down. Larger nests were, not surprisingly, more exposed. More concealed nests tended to have support branches of a smaller diameter.

	Nest volume	# support branches	Diam. of support branches	Mean lateral concealment	Concealment from above	Concealment from below	Canopy cover
Nest height	P=0.49 r_s=0.31 *n*=35	P=0.01 r_s=-0.6 *n*=29	P=0.01 r_s=0.55 *n*=29	P=0.32 r_s=-0.38 *n*=29	P=0.49 r_s=-0.34 *n*=29	P=0.07 r_s=-0.45 *n*=29	P=0.99 r_s=0.06 *n*=32
Nest volume	–	P=0.99 r_s=-0.15 *n*=29	P=0.99 r_s=0.26 *n*=29	P=0.04 r_s=-0.51 *n*=29	P=0.049 r_s=-0.49 *n*=29	P=0.28 r_s=-0.39 *n*=29	P=0.99 r_s=0.11 *n*=29
# support branches	–	–	P=0.04 r_s=-0.51 n=29	P=0.14 r_s=0.44 *n*=29	P=0.99 r_s=0.21 *n*=29	P=0.33 r_s=0.37 *n*=29	P=0.99 r_s=-0.1 *n*=27
Diam. of support branches	–	–	–	P=0.07 r_s=-0.49 *n*=29	P=0.35 r_s=-0.36 *n*=29	P=0.28 r_s=-0.38 *n*=29	P=0.99 r_s=-0.05 *n*=27
Mean lateral concealment	–	–	–	–	P=0.99 r_s=0.19 *n*=29	P=0.07 r_s=0.49 *n*=29	P=0.99 r_s=-0.07 *n*=27
Concealment from above	–	–	–	–	–	P=0.91 r_s=0.29 *n*=29	P=0.63 r_s=0.33 *n*=27
Concealment from below	–	–	–	–	–	–	P=0.99 r_s=-0.08 *n*=27

Table 4: Correlations (Spearmans rank) between various measurements. All P values have undergone a Bonferroni correction, where the P value has been multiplied by 7 (the number of variables tested). Mean % concealment is calculated using concealment from N,S,E & W. Diameter of support branches is that of the largest support branch.

Nest structure — Nest weight varied greatly, with a mean of 21.6±10.3g (range 5–48.2g, *n*=45). It was found that nests were constructed by loosely weaving stems, grass or bark strips and piling up smaller materials such as leaves. A total of 67 different nesting materials were used in the construction of 45 examined nests. The most commonly utilised materials were strips of honeysuckle bark (in 84% of nests), oak twigs (71%), oak leaves (69%), grass stems (53%) and a species of grass which produces very long and curly leaves (47%). On BRC1, a total of 59 materials were utilised (*n*=34) and on BRC3, a total of 40 (*n*=11). Materials which were found solely on BRC1 included; long black hairs (possibly human), rootlets, clumps of material from creek beds, prickly pear cactus skeletons, wild cucumber leaves or stems, maidenhair fern (*Adiantum jordanii*), feathers and moss. Those materials found only on BRC3 included; leaf skeletons and fox/cat hairs. Once divided into material types, it can be seen that higher nests were composed of more twigs, whereas lower nests were comprised of a significantly higher percentage of plant stems and lower amounts of twigs. Nests with more support branches were compromised of more plant stems and tended to have less twigs. Nests with larger support branches tended to contain less plant stems (Table 5). Canopy cover was excluded from the table as all P values were greater than 0.24. When looking at on and off ground nests, a significantly higher percentage of twigs and bark were utilised in off ground nests. A comparison of study plots revealed that more twigs were exploited on BRC1 (Table 5).

Nest-site characteristic	% weight							
	plant stem	bark	grass	leaf	twig	dense plant matter	root/ vine-like	other
Nest height	r_s=-0.3 P=0.04	r_s=0.21 P=0.18	r_s=0.07 P=0.66	r_s=-0.1 P=0.51	r_s=0.52 P=0.001	r_s=0.11 P=0.49	r_s=-0.13 P=0.38	r_s=-0.19 P=0.22
# support branches	r_s=0.68 P=0.001	r_s=-0.15 P=0.45	r_s=0.29 P=0.14	r_s=-0.16 P=0.43	r_s=-0.37 P=0.06	r_s=-0.15 P=0.47	r_s=0.05 P=0.81	r_s=0.29 P=0.14
Diameter of support branches	r_s=-0.34 P=0.08	r_s=-0.22 P=0.26	r_s=-0.31 P=0.12	r_s=0.05 P=0.82	r_s=0.26 P=0.2	r_s=-0.02 P=0.94	r_s=0.12 P=0.55	r_s=-0.32 P=0.1
Nest weight	r_s=-0.46 P=0.001	r_s=0.31 P=0.04	r_s=-0.13 P=0.39	r_s=0.01 P=0.96	r_s=0.57 P=0.001	r_s=0.21 P=0.16	r_s=-0.22 P=0.15	r_s=-0.26 P=0.08
On/off ground	*t*=0.87 df=9.89 P=0.41	*t*=2.15 df=26.82 P=0.04	*t*=0.77 df=12.59 P=0.46	*t*=0.85 df=13.24 P=0.41	*t*=4.26 df=41.23 P=0.001	*t*=0.59 df=14.57 P=0.56	*t*=1.07 df=12.97 P=0.31	*t*=0.96 df=42.03 P=0.34
Study plot (BRC1/BRC3)	*t*=1.12 df=17 P=0.28	*t*=0.56 df=14.32 P=0.59	*t*=1.1 df=20.749 P=0.28	*t*=0.65 df=13.46 P=0.53	*t*=2.33 df=28.44 P=0.03	*t*=0.5 df=16.68 P=0.62	*t*=1.16 df=17.29 P=0.26	*t*=1.05 df=10.59 P=0.32

Table 5: Shows relationships between height of the nest and the nesting material types used. Statistical tests were separated; Spearmans rank correlation was used for all off-ground nests (*n*=35 for nest height, *n*=27 for support branches) and *t*-test for differences between on ground (*n*=10) and off ground (*n*=35) nests and BRC1 (*n*=34) and BRC3 (*n*=11).

93% of all nests collected (*n*=45) had a distinctive structural layer (the outer cup) and a layer of lining of very different material. 2 nests were made from the same materials both in the cup and the lining, so it was impossible to separate these two structures. The material in the outer cup was used for all of the previous analysis, but it is also interesting to consider the lining. 96% (*n*=43) nests were lined with bark strips, most (76%, *n*=34) had utilised fine strips of honeysuckle (*Lonicera hispidula*) bark and this was similar for BRC1 (79%, *n*=27) and BRC3 (64%, *n*=7) (χ^2=1.52, df=1, P=0.22). 20% (*n*=42) of nests utilised animal hair in the cup lining, those which could be identified were fox or cat, bison and human strands. Feathers were found in only two nests and one of these may have possibly been those shed by the nestling or adult.

DISCUSSION

It can be seen that the population of orange-crowned warbler on Catalina Island utilises a vast array of nesting sites and materials. Most nests were built off the ground and there were distinct relationships between nest characteristics. There was also a significant preference for nest and nest entrance to be orientated to the Northeast on BRC1, or downhill in relation to the nest site aspect. The comparison of the two sites, BRC1 and BRC3, did not reveal a significant difference in nest structure or nest placement. Nests on BRC1 were placed under a denser canopy and utilised a higher percentage of twigs in the outer cup.

These results are very distinct and differ greatly from accounts of other orange-crowned warbler subspecies. Nests of other subspecies are placed on or close to the ground (Sogge et al, 1994; Baich & Harrison, 1997). There has been only one study which describes off-ground nests in a mainland population, where a total of 3 nests of 131 found were placed 2-3.2m off the ground (Zyskowski, 1993). In this study, only 27% of nests were placed on the ground. The larger variation in sites used for nesting on Catalina compared to mainland populations may be due to the process of ecological release that the species seems to have undergone on the island; there are only 7 other cup nesting passerines on Catalina and so there is little competition for nest sites. On Catalina there is also an absence of Island scrub jays (*Aphelocoma insularis*), a particularly aggressive nest predator on Santa Cruz Island. The perceived presence of jays has been shown to affect orange-crowned warbler nest placement on Catalina (Peluc, *In Press*). Further study may reveal a difference in nest placement between the two islands, particularly in terms of nest height.

The orange-crowned warbler utilises nesting substrates which are most commonly found on the two plots. The most common shrub on BRC3 is coastal sage brush whereas lemonade-berry leaf is more common on BRC1 (pers. obs.), although a quantitative analysis of vegetation abundance is needed. This may be purely due to availability, or it may be related to the ‘potential nest site’ hypothesis (Martin & 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 wider vegetation surrounding the nest site is needed to explore this. The greater array of nesting substrates on BRC1 is probably due to the increased availability of different plants on this site (pers. obs.), although again, this needs to be quantitatively assessed. The widespread utilisation 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. No green vegetation is used although it is available, particularly on BRC1.

High nests were bigger and less concealed, whereas low nests were smaller and very concealed. High nests had larger but fewer support branches, although this correlation was not found with nest size. The relationship between nest height, size and concealment appears to be purely logistical; higher nests have less support branches at an increased diameter, probably due to the properties of this layer of vegetation which is composed of large shrubs and trees. A larger nest may, consequently, be more exposed than a smaller nest in terms of % cover as there is a greater nest mass to conceal. High nests are also in a vegetation layer which is less dense. Similarly, the differences between on and off ground nests can also be explained logistically; ground nests are smaller as they need less support and have higher concealment due to the properties of the vegetation layer. The lower % canopy cover on BRC3 may be due to the fact that the vegetation on this site is mainly shrub-like. The lack of a correlation between overhead concealment and canopy cover may be due to the nest being less concealed from a metre away, but situated under a dense canopy and also ascribable to the fact that the fisheye is taking 180º of cover over the nest. The lower nest concealment from below and above in comparison to lateral concealment may be linked to the predator types present and this will be investigated further in Chapter 3.

There is an issue of observer bias in that more conspicuous nests tend to be found more easily. This was overcome through detailed territory mapping, which ensured that all known pairs could be followed until nests were found. If a mapped pair did not have an associated nest, more effort could be put in to find this (usually more hidden) nest.

Most nests were placed centrally in the substrate, which may impede predators. This will be further explored in Chapter 3. There is a preference to place nests and nest entrances to the North-East on BRC1. Preference for nest entrance has been found in other studies (Austin, 1974; Facemire et al, 1990), as well as actual nest orientation (Hartman & Oring, 2003; Burton, 2006). Much of this has been linked to microclimate; this is explored further in Chapter 4. Another reason for this preference may be in 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; 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 theory may be explored by further analysis of the above trend and nest success (see Chapter 3). The trend to orientate the nest entrance downhill was not found on BRC3 and hence orientation may have a microclimatic explanation. This will be explored further in Chapter 4.

The orange-crowned warbler on Catalina shows surprising plasticity in the nesting materials utilised. No other studies have been carried out to explore nest construction in similar detail, so it is difficult to draw any conclusions on the unusualness of this. The wide-spread use of honeysuckle bark is interesting, as this is not a particularly wide-spread plant, especially on BRC3. Many birds observed collecting material were acquiring it from dead honeysuckle (pers. obs.) and the bark can be stripped in various sizes (some as long as 50cm). Utilization of twigs and bark in high nests is probably necessary in terms of construction of the cup. The fact that there were more twigs used on BRC1 may be reflective of the higher number of trees found there and also the fact that nests tended to be higher.

This study provides an extremely detailed study of the nest site of a subspecies which is very poorly understood. It also offers an insight into the plasticity and uses of various nesting materials as well as providing a new technique to quantify these. Future research may compare these descriptions 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 2,350 (Sogge et al., 1994).

It was found that there was little variation between the mesic and xeric habitats, although this may have been affected by the fact that 2006 was a particularly dry year and so BRC1 was not as moist as previous years, thus possibly affecting the vegetation composition. Further research spanning several breeding seasons may uncover differences between these two habitats depending on climatic conditions.

CHAPTER 3: THE EFFECTS OF NEST PLACEMENT ON NESTING SUCCESS

ABSTRACT

Understanding how nest site selection interacts with nesting success is an integral part to understanding the ecology and population dynamics of a species and key to conservation planning. This is especially important when considering endemic and declining populations such as the Channel Island subspecies of orange-crowned warbler. Here we examined how nest site characteristics are related to nesting success and found that nests with higher concealment from below and under a less dense canopy were active for longer, although the study indicates that these relationships are strong in a mesic habitat but less important in a xeric ecosystem.

INTRODUCTION

Avian incubation and altricial development of nestlings requires that both eggs and dependent nestlings must remain within the confines of the nesting site until fledging. This sedentary period, within the nest, can be a time of high risk of reproductive failure through either predation or adverse climatic conditions (Ricklefs, 1969). Thus, nest sites should be selected which increase the chance of survival for both the adult bird and the young. Few studies have looked al parental survival and nest site choice (Miller et al., 2007), and it is possible that there may be some degree of trade off where the optimal nest site for parental and offspring survival conflict. It is known in the temperate zone that adults are less risk adverse in terms of their own survival when compared with tropical species and may jeapordize their own survival over that of their offspring (Ghalambor & Martin, 2001).

Reproductive success may be enhanced by sites with a favorable microclimate (Walsberg & King, 1978; Walsberg, 1981), sites which reduce the risk of brood parasitism (Moskát & Honza, 2000) or to protect against the most common cause of nest failure; predation (Ricklefs, 1969). It has been found that nest location can greatly affect predation risks (e.g. Martin & Roper, 1988; Martin, 1998; Clark & Shutler, 1999; Martin et al., 2000). Birds may select certain nest sites which aid in protection from predators. This can be considered in terms of the 'nest concealment' or 'nest inaccessibility' hypothesis (Filliater et al., 1994), which postulate that successful nests may be directly concealed from predators (e.g. Martin & Roper, 1988; Flaspohler et al., 2000; Remeš, 2005 [a]; but see Holway, 1991; Peak, 2003) or positioned at a site which is inaccessible to predators (Martin, 1995), respectively. Density of vegetation at the nest patch may also conceal the movement of the parents to and from the nest (Peterson & Best, 1985; but see Gottfried & Thompson, 1978) or prevent olfactory cues reaching predators which may be attracted by scent at the nest site (Whelan et al., 1994). Nests may be placed in areas of vegetation with a high amount of potential nest sites, thus decreasing the efficiency of predators that actively search for nests (Martin & Roper, 1988). The importance of all the above considerations may vary depending on the type of predator present (Remeš, 2005[b]).

These selection pressures can also be applied to the parents' survival, as predators may target any attending adult as well as the contents of the nest. So additional factors affecting nest site selection may be the ability of the adult birds to detect approaching predators (Götmark et al., 1995; Yanes et al., 1996; Pribil, 1998; Wiebe & Martin, 1998) and the availability of an unobstructed flight path away from the nest (Bekoff et al., 1987). These may be affected by the vegetation directly at the nest itself, or the orientation on the nest in the substrate and in relation to the landscape (as discussed in Chapter 2). Interestingly, the nest concealment factor, previously discussed, works contradictory to this and so may result in a trade off between the nest being well hidden and the ability of the adults to see approaching predators.

This study focuses on nest survival of orange-crowned warbler *Vermivora celata* in relation to the structure and location of their nest. Nest location may be restricted to a species due to interspecific or intraspecific competition, or due to availability of nesting sites in various habitat types (Martin, 1998; Hansell, 2000). I therefore studied nest survival in the *V. c. sordida* subspecies endemic to the Chanel Islands, California, where its nesting habits are not restricted by the presence of jays, which are known to affect the nest location in this species (Peluc, *In Press*, see also Chapter 2). Orange-crowned warblers on the Channel Islands occur in a range of habitats; from mesic and xeric habitat types. This population is therefore interesting as it can utilize a wider range of nest sites than other populations, and nest survival in relation to nest location can be studied in different habitat types. I used extensive techniques to quantitatively describe nest site characteristics and regular monitoring of nests to obtain accurate records of nest survival. Specifically, I will address nest survival in relation to the characteristics of the nest in terms of [1] the microenvironment of the nest site, [2] the positioning within the substrate, [3] the structure of the nest itself, [4] the habitat type (mesic or xeric habitat and [5] the timing of breeding.

METHODS

This study was carried out in 2006 on Santa Catalina Island, California, U.S.A (33°22’30”N, 118°25’56”W) and focused on its endemic subspecies of orange-crowned warbler, *Vermivora celata sordida*. This population differs from the other subspecies in its nesting ecology as nest sites range from on the ground to around 8m high (pers. obs.) whereas on the mainland this species nests mainly on the ground or up to 2 ft (Zyskowski, 1993; Baicich & Harrison, 1997). Nesting is initiated in late February to early April and extends until June. 2-4 eggs are laid per clutch and the female incubates for around 12 days. Hatching occurs within a 24hour period and the nestlings remain in the nest for 11-13 days before fledging (Sogge et al. 1994). Nesting success varies greatly over years. In 2005 nesting success was very high and several pairs invested in a second brood, which has only been recorded once on the mainland (Sogge et al., 1994).

<u>Study site</u>— Bulrush Canyon is situated in the South-West of the Island and runs East to West. Two 500 x 300 m plots were selected and gridded with flagging every 25 m. BRC1 is situated in the base of the canyon on a North facing slope where the habitat is moist, although the creeks are often dry in the summer months. This site consists of areas of scrub oak (*Quercus pacifica*) and toyon (*Heteromeles arbutifolia*) woodland, lemonade-berry (*Rhus integrifloria*) shrubs with grass-dominated ‘meadows’. This habitat can be described as ‘mesic’ in its composition. BRC3 is at a higher altitude and on a more xeric, South-facing slope. This area consists mainly of coastal sage (*Artemesia californica*) and prickly pear cactus (*Opuntia phaecacantha*) with very little tree cover.

<u>Nest surveying</u>— In the pre-laying period, plots were visited on alternate days (usually both plots were visited on the same day) and nest searching took place from 6am to 1-3pm. This was started before the initiation of nest building, in order to locate early nests and to cover the onset of nest building. Bird behaviour was closely observed and the site methodically searched. Located nests were flagged 7-10m away and a concise description of the nest site was written on the flagging.

Once a nest site was marked, it was visited every two days and the status of the nest was recorded onto nest cards, including no. eggs/nestlings and descriptions of nest appearance or adult/fledgling behaviour subsequent to nesting completion. This was carried out during the middle of the day, when possible, when parental activity is lowest. Observer effects on nest success were kept to a minimum during visits by watching for activity at a distance, when possible, and rubbing sage into the hands if vegetation surrounding the nest or eggs/nestlings needed to be touched. Failure was assumed if the nest was found empty and evidence of disturbance, egg shells or feathers were noted. In this way, a very accurate date for nest failure could be obtained within ±1 day.

Nests were visited every day from day 11-13 during incubation and day 11-13 during the nestling period to obtain exact dates for hatching and fledging. Hatching date was established once all nestlings had emerged from the egg (excluding unfertilised or damaged eggs) and fledging date when young were no longer in the nest and at least one individual had successfully fledged. To ensure that nestlings had fledged rather than been depredated, the territory was visited every day to locate fledglings or begging calls. A compact, flattened nest with a small amount of feces on the rim also indicated successful fledging. All nests had an incubation period of 12 days, apart from one, which had an incubation period of 14 days (*n*=28). This data was obtained from nests where the exact dates of clutch completion and hatching were known. Nestling period was calculated for nests which were successful and where the exact hatching date was known. Average nestling period was 12±1 days (range 11-14, *n*=9), where the day of hatching is counted as day 0. These figures were used as a guideline to calculate clutch completion and hatch day for the remaining nests where these dates were not known (*n*=21). This was assumed to be relatively accurate as incubation and nestling period did not vary greatly between nests (as shown above).

Nest success was quantified in two ways; whether the nest fledged/failed (*n*=53) and also the number of the days that the nest was active prior to fledge/fail (*n*=41). Number of active days was calculated from the clutch completion date (day 0) until the day that the nest was first observed to be no longer active. Where the clutch completion day was not known, but hatching date was, number of active days was estimated assuming a 12 day incubation period (as mentioned above).

Nest site measurements were recorded 25-30 days after clutch completion to guarantee that nests were no longer active. This ensured that all nests were measured at a standardised time relative to their timing of breeding and at the soonest date subsequent to fledge/fail, rather than successful nests being measured consistently later than failed ones. Detailed descriptions of the nest itself, the position of the nest and the vegetation surrounding it were recorded using BBird guidelines (Martin et al., 1997), with an additional measurement; concealment from below the nest.

Nest measurements— Nests were measured in the same way as outlined in Chapter 2, although only nests where nest fate was known were included. Nests where the number of days for which they were active was known are also included, as sample sizes were different. Measurements and sample sizes are as follows:

- Nest height. Obtained for all nests found where nest fate was known (n=53). For those which were inaccessible, height was visually estimated (n=3). Of these, number of active days was known for 40 nests.

- Nest substrate. All plant species which were a component of the support of off ground nests (*n*=35). Of these, number of active days was known for 36 nests.
- Number and diameter of support branches. For all off-ground nests that were accessible and still intact (*n*=29). Of these, number of active days was known for 21 nests.
- Nest dimensions. Inner and outer height and diameter (*n*=48). Of these, number of active days was known for 36 nests.
- Nest volume. Using the equation for a regular ellipsoid, as modified from Lombardo (1994).

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

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

- Nest concealment. From all cardinal directions and from above (*n*=42) and from below for all off ground nests (*n*=29). Of these, number of active days was known for 33 nests (lateral concealment) and 21 (cover from below).
- Nest and nest entrance orientation. Nests placed centrally in the substrate were noted (*n*=23), 23 of which number of active days was known. Those which had a particular orientation (*n*=19; 15 of which number of active days was known) and those which had an obvious nest entrance (*n*=34; 26 of which number of active days was known) were measured. Nest entrances were recorded when there was a clear flight path to and from the nest in the vegetation. This was also supported by checking the nest for flattened perching ‘platforms’ and by observing birds, when possible.
- Nest site aspect. Measured as the bearing from the nest directly downhill (*n*=35; 26 of which number of active days was known). Several nests were omitted from this measurement due to a recording error (*n*=7). From this measurement, orientation of the nest within the substrate (*n*=15; 11 of which number of active days was known) and of the nest entrance (*n*=30; 23 of which number of active days was known) from downhill were calculated and recorded as “angle from downhill”.
- Canopy cover. A Lomography 35mm camera with Fisheye lens (170°) was used to take a photograph of the overhead vegetation and the picture analyzed using Gap Light Analysis (GLA) software (obtainable from Simon Fraser University, Institute of Ecosystem Studies, www.ecostudies.org/gla/) to obtain a measure of % canopy cover (*n*=41). Of these, number of active days was known for 31 nests.

Predator type— I was able to distinguish between snakes and mammals/birds as nest predators during incubation. A nest was determined to be depredated by a snake when the nest lining was completely intact and there were no eggshells in the nest (n=7). Nests which failed during incubation and eggshells were present were determined to be depredated by a mammal or bird (n=9). Missing nests are due to errors in recording nest condition subsequent to failure. Although it is known that snakes prey on nestlings, it is difficult to ascertain if the lining was ripped up by the predator or the nestling. Additionally, if the adult bird was also preyed on and feathers were found by the nest, a depredation by a mammal or bird was assumed. Sample sizes are low due to the fact that analysis was restricted to nests depredated during incubation and nests where the observer had noted the presence/absence of shells.

Statistical Analysis— Data was analysed using SPSS 14.0 software. Correlations were explored using Spearman's rank coefficient as this is suitable for all data including ordinal data sets. A t-test was used to test significant differences between two data sets.

RESULTS

Nest searching was initiated at the beginning of March, but the first nest found, at building stage, was on the 9th June on BRC1. This was a relatively late start, especially when compared with 2005, when birds were already initiating incubation at the beginning of March (per obs.). The first nest found on BRC3 was on the 12th June, slightly later.

A total of 56 nests were found at various stages, as shown in Table 6. There was no significant difference in nests found at various stages between plots. When nests were divided into early and late (using the median clutch completion date), it was found that there was no significant different in stages of nests found early or late in the season (Table 6).

Nesting stage	Number of nests found on each plot		Number of nests found early/late in season	
	BRC1	BRC3	Early	Late
Building	15	5	13	4
Laying	5	0	2	3
Incubation	18	8	15	2
Hatching	1	1	1	1
Nestling	3	0	2	0

Table 6: Illustrated number of nests found at each stage on both BRC1 and BRC3. There is no significant difference between plots (χ^2=3.8, df=4; P=0.43) or between early/late in the season (χ^2=6.17, df=4; P=0.17).

To test if newly initiated nests were located equally likely on BRC1/BRC3 and early/late in the season, days before or after the clutch completion date which the nest was found was calculated. There was no significant difference between both plot and time in the season (Table 7).

	Number of days on each plot		Number of days early/late in season	
	BRC1	BRC3	Early	Late
Mean days before/after clutch completion date that nest was found	-0.12±7.1 days *n*=33	1.3±7.1 days *n*=10	0.7±7.4 days *n*=33	-1.4±5.72 days *n*=10

Table 7: Shows mean days before or after clutch completion that a nest was found. A negative number indicates that nests were found prior to clutch completion, a positive one indicates after. There was no significant difference between plots (*t*=0.56, df=41, P=0.58) or time in the season (*t*=0.82, df=41, P=0.42).

A total of 53 orange-crowned warbler nests were found where nest fate was known, of which 11 fledged successfully and 42 failed. When assessing nest success per territory (for BRC1 only), it can be seen that 2006 was a relatively unsuccessful year; 2007, probably due to the severe drought, was extremely unsuccessful (Table 8).

	Number of nests found	Nest success	Number fledged
2007	5	0	0
2006	42	0.35	1.05
2005	106	0.74	2.47
2004	73	0.64	1.61
2003	104	0.73	1.72

Table 8: Number of nests found in each year (for BRC1 alone) and the nest success and number fledged per territory.

Nesting success was significantly higher on BRC3 (χ^2=8.97; df=1; P=<0.01), where 4 nests fledged at least one young (28.6%, *n*=14). On BRC1, 7 were successful (18%, *n*=39). There was, however, no significant difference between plots when considering the stage of failure (Table 9).

	Number failed on each plot		Significance of difference between plots
Nesting stage	BRC1	BRC3	
Building	1	0	-
Laying	0	2	-
Incubation	14	4	P=0.9
Hatching	0	0	-
Nestling	17	4	P=0.42

Table 9: Number of nests which failed on each plot and the stage of failure. There is no significant difference between BRC1 and BRC1.

Temporal patterns in nest failure— There was no significant pattern in when nests were initiated and nest fate (Wald χ^2=1.04, df=1, P=0.31), as seen in Figure 9. This variable, therefore, was omitted in further considerations.

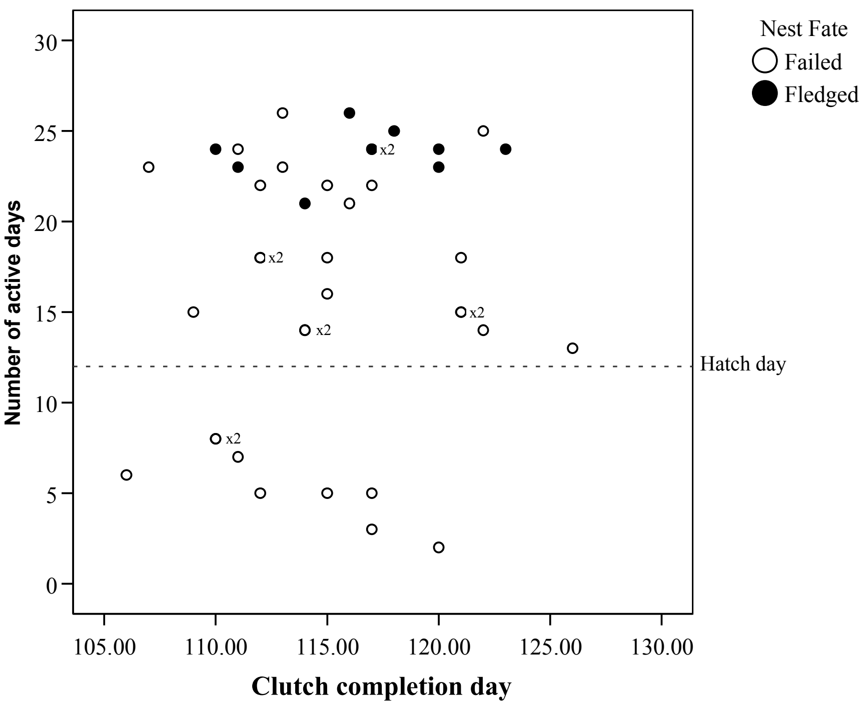

Figure 9: Scatterplot shows temporal spacing of fledged and failed nests. Clutch completion date is used as an indicator of timing of breeding and is given as day of the year. Number of active days is taken from clutch completion day. Sample sizes are smaller due to the fact that in some cases the clutch completion day was not known. This occurred if a nest was found and failed during incubation or nestling stage (*n*=10), if a nest failed before clutch completion (*n*=3) or if the nest was still active at the end of the field season (*n*= 3).

All circles which fall at the same point are noted with x2. (None differ in their nest fate). Hatch day is shown as day 12.

There also appears to be two distinct data groups, where nests failed either after hatch day or a few days before, whereas none failed during the period encompassing hatch day (Figure 9).
When examining the difference in clutch completion day with plot, it was found that this was not statistically significant ($F_{1,38}$=1.4, P=0.24), as was number of active days ($F_{1,14}$=0.25, P=0.62).

<u>*Nest characteristics and success*</u>— When considering nests that fledged successfully and nests which failed, it was found that they did not differ in any significant way in their nest site and nest characteristics (all P values>0.15). If, however, number of active days is used as a measure of nest success, several significant relationships emerged. Nests which were more obscured from below were active for a longer period of time. (Table 10, Figure 10). Nests placed under a less dense canopy were more successful (Table 10, Figure 11).

Nests which were supported by more branches were also active for longer, although this was possibly due to a correlation with cover from below (without a Bonferroni correction, as in Table 4, Chapter 2, the correlation is significant; r_s=0.37, P=0.05, *n*=29).

	Nest height	# support branches	Diam. support branches	Nest volume	Lateral conceal-ment	Conceal-ment from below	Conceal-ment from above	Canopy cover
# active days both sites	F=0.3 df=1 P=0.6	F=6.04 df=1 P=0.02	F=0.7 df=1 P=0.42	-	F=0.01 df=1 P=0.91	F=5.23 df=1 P=0.04	F=0.13 df=1 P=0.72	F=5.08 df=1 P=0.03
Significant difference of covariate between plots	F=2.9 df=1 P=0.1	F=0.4 df=1 P=0.54	F=0.07 df=1 P=0.79	F=7.37 df=1 P=0.01	F=1.43 df=1 P=0.24	F=0.2 df=1 P=0.66	F=3.3 df=1 P=0.08	F=0.41 df=1 P=0.53
# active days BRC1	-	-	-	*rs*=-0.3 P=0.13 *n*=27	-	-	-	-
# active days BRC3	-	-	-	*rs*=0.52 P=0.15 *n*=9	-	-	-	-

Table 10: Shows relationships between number of days a nest is active and the characteristics of the nesting site. Where a significant difference in the covariate between plots was found, correlations were run for each plot separately. If plots were not significantly different, correlations were run for both plots together. Sample sizes are smaller as number of active days was known for only a limited number of nests (see methods).

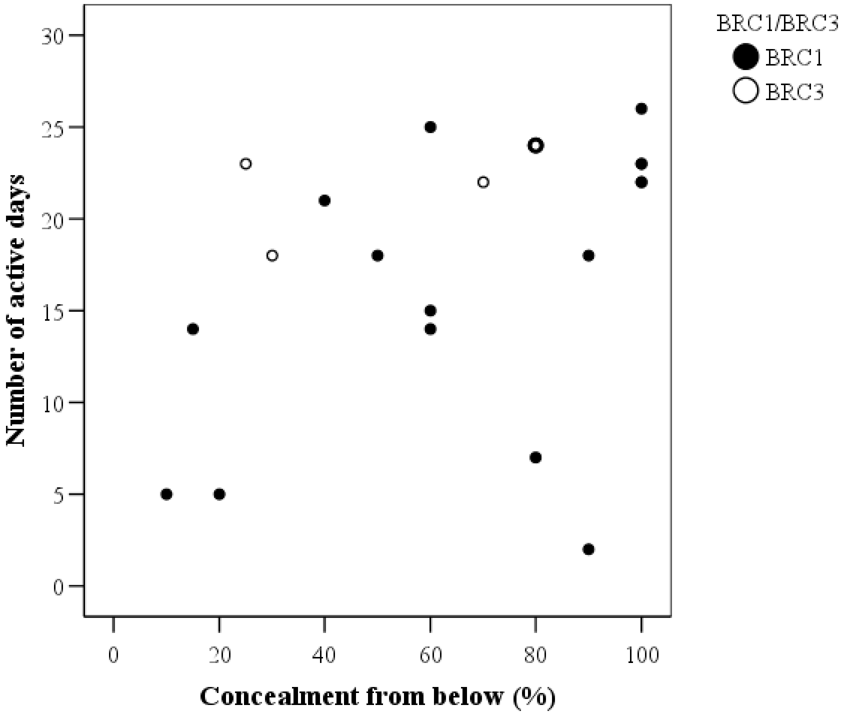

Figure 10: Shows significant positive correlation between cover below the nest and the number of days which it was active.

The thicker circle represents two overlaying dots from the same study site.

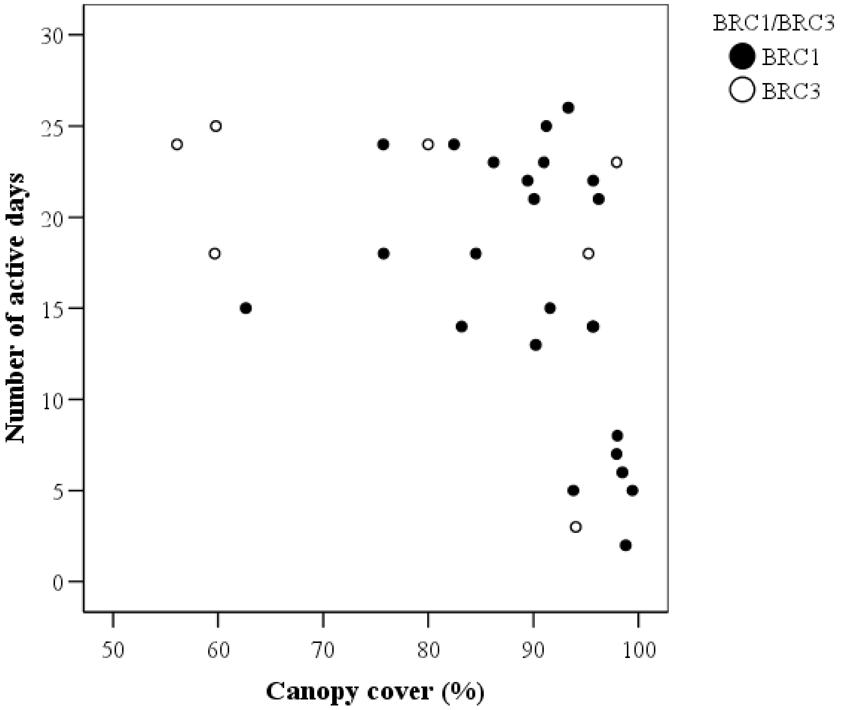

Figure 11: Shows significant negative correlation on BRC1 between the density of the canopy above the nest and the number of days it was active.

There was no significant effect of the interaction between nest height (on/off ground) and plot on the number of days active (F=2.83, df=1, P=0.1) and no different between plots (F=0.46, df=1, P=0.5), so these were not treated separately. It was found, however, that there was no significant difference in number of active days when looking at off and on ground nests (F=0.4, df=1, P=0.53). There is a significant interaction between plot and nest volume when considering number of days active (F=7.37, df=1, P=0.01). Nest volume was split into 'large nests' (those above the mean nest size) and 'small nests' (those below mean nest size) and these are shown in Figure 12.

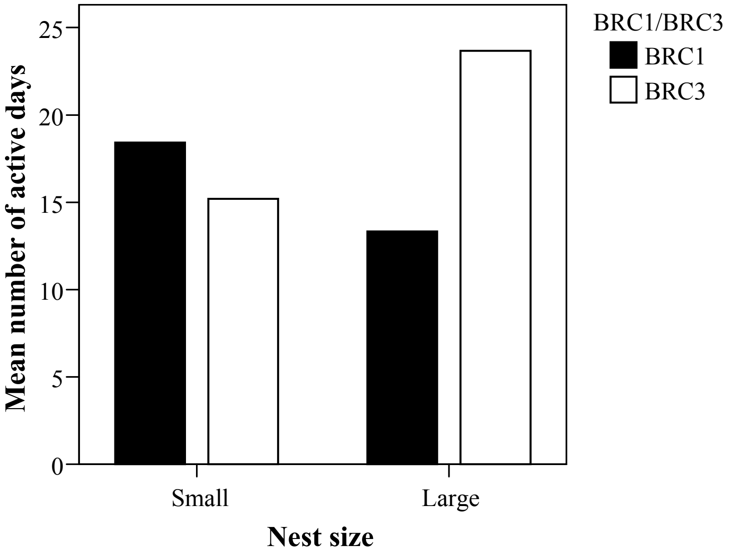

Figure 12: Graph shows nests divided into 'large' and 'small' depending on if they are above or below the mean nest volume of 616.13±388.64cm³ (range 117.23-1607.68, *n*=48).

There is a trend for small nests to be more successful on BRC1 (*t*=1.76, df=24, P=0.09) although this less statistically significant on BRC3 (*t*=0.11, df=4.35, P=0.11), possibly due to smaller sample sizes.

When looking at orientation of the nest in the substrate in relation to the slope ('angle from downhill' as discussed in Chapter 2), it can be seen that there was no correlation between this measurement and the number of days that the nest was active (r_s=-0.09, P=0.8, *n*=11). This was also evident when looking at orientation of the entrance (r_s=0.03, P=0.91, *n*=23).

I found no difference between successful and failed nests in the nesting substrates they occupied (lemonadeberry, grass, forb, sage, vine and tree; χ^2=0.7, df=5, P=0.98).

Nest Predators— Known and potential nest predators which are resident on Catalina are outlined in Table 11. The high number of snake depredations encountered in comparison with other species is likely due to the fact that snakes will spend a large amount of time in the nest after they have eaten the contents (per. obs.).

POSSIBLE PREDATORS		EVIDENCE FOR NEST PREDATION	NO. CASES
Introduced mammals:	Feral cat (*Felis felis*)	Feral cats are responsible for bird extinctions on various Islands (Nogales et al., 2004)	None observed
	Norway rat (*Rattus norvegicus*)	Known to depredate Island seabird nests (Drever & Harestad, 1998)	None observed
	Black rat (*Rattus rattus*)	Known to prey on colonial nesting birds (Martin et al., 2000)	None observed
Native species:	Beechey ground squirrel (*Spermophilus beecheyi nesioticus*)	Avian nest predator (Calkins et al. 1999)	None observed
	Santa Catalina Island deer mouse (*Peromyscus maniculatus catalinae*)	Peromyscus sp. are known avian nest predators (Bradley & Marzluff, 2003). Mouse droppings found in old orange-crowned warbler nests on Catalina, mice probably use old nests as dormitories (pers. obs.)	None observed
	San Diego gopher snake (*Pituophis melanoleucas*)	Known orange-crowned warbler egg predator on Catalina (pers. obs.)	4 cases (2004-2006) 2% (*n*=182)
	Southern Pacific rattlesnake (*Cyotalus viridis*)	Known orange-crowned warbler nestling predator on Catalina (pers. obs.)	2 cases (2004-2006) 1% (*n*=182)
	Santa Catalina Island fox (*Urocyon littoralis catalinae*)	Unspecified Island fox depredated nest with young (Sogge et al., 1994). Santa Cruz subspecies known to predate bird nests (Curry & Delaney, 2002).	None observed
	Common raven (*Corvus corax*)	Known to depredate passerine nests on Catalina (pers. obs.)	1 case (2004-2006) 1% (*n*=182)

Table 11: Potential predators of the orange-crowned warbler on Santa Catalina Island and supporting evidence. Number of cases include all instances where this has been observed as the cause of nest failure, also expressed as a percentage of all failed nests.

Although only one depredation was actually witnessed in 2006, by a gopher snake, some inferences about the type of predator can be made by examining the failed nest. Two types of predation events were distinguished and examined in terms of the nest site (Table 12). Snake-predation occurred in significantly lower nests. These nests were of a smaller size and were positioned at a site with higher concealment from above.

Nest site characteristic	Snake predation	Bird/mammal predation	*t*-test
Nest height (m)	0.17±0.34 (*n*=7)	0.78±0.6 (*n*=9)	*t*=2.4, P=0.03
# support branches	43 (*n*=1)	9±4 (*n*=6)	-
Diam. largest support branch (cm)	0.1 (*n*=1)	0.6±0.4 (*n*=6)	-
Nest volume (cm^3)	252±131 (*n*=7)	778±464 (*n*=8)	*t*=3.07, P=0.02
Mean lateral concealment (%)	98±4 (*n*=6)	83±18 (*n*=6)	*t*=2.02, P=0.1
Concealment from below (%)	100 (*n*=1)	63±38 (*n*=6)	-
Concealment from above (%)	96±7 (*n*=6)	55±29 (*n*=6)	*t*=3.31, P=0.02
Canopy cover (%)	92±4 (*n*=6)	94±11 (*n*=6)	*t*=0.34, P=0.74

Table 12: Shows means of nest site characteristics for nests depredated by snakes and birds/mammals. t-test results show significant differences. Statistics not done for sample sizes of 1.

When looking at each plot individually, it can be seen that a similar proportion of nests were predated through incubation by snakes; 42% (*n*=12) on BRC1 and 50% (*n*=4) on BRC3. This was not statistically different (Fishers exact test P=0.99).

DISCUSSION

This study reveals significant relationships between nest site characteristics and nest success. Nests which were more concealed from below were active for longer, an interesting outcome as this is a measurement which is often overlooked in nest site descriptions. Nests under a less dense canopy were also active for longer. Failure of lower nests was attributed to predation by snakes, whereas higher nests were more likely depredated by mammals or birds. There was no difference in nest survival or failure at the various stages of the breeding cycle, although there was an absence of nest failure during the hatch period, particularly during late incubation.

The primary cause of nest failure during this study was due to predation. Only one nest was built where no eggs were laid, which was attributed to abandonment by the female. There has been some evidence of failure due to inclement weather in previous years, although this is rare (*n*=2 out of 330 nests 2003-2007). Overall reproductive success in 2006 was relatively low, with 0.94 daily survival rate, in comparison to other years. This may be due to the especially productive year previously, which could have led to a higher density of both orange-crowned warblers and nest predators such as snakes in 2006. The small sample size of successful nests is problematic when looking at statistical significance between nest site characteristics and nest success, so a long-term study would be needed to explore this to a further degree. The evidence of higher nesting success on BRC3 is surprising as this xeric habitat would appear to be suboptimal for this warbler species. Nesting success may, however, be lower on BRC3 in very hot years as it provides less shelter for nest sites. It is possible that this dry area is not suitable habitat for many of the nest predators as well and so nest predation is lower. Although there is no quantitative data, it was noticed that less potential predators were observed on BRC3. Various snakes were commonly spotted on BRC1 (*n*=5), but never on BRC3. There may be a trade-off between selecting a sub-optimal habitat, with less food and nesting sites, but additionally experiencing less competition for territories and resources and fewer predators. A similar pattern has been seen in a study of habitat selection in prothonotary warblers in flooded and dry habitats (Petit & Petit, 1996). This hypothesis is further supported by the lack of any significant relationships between nest site characteristics and nest success on BRC3, as we would expect this in a habitat with reduces predation pressure.

A prior aim of this study was to examine the relationship of nest site characteristics and adult survival to explore any relationships and possible conflicts between optimal sites for adults compared with those for the offspring. It was found, however, that adult survival was high and it was difficult to determine if an adult was predated at the nest. In previous years, however, adult feathers have been found at failed nests and so it would be possible to explore this further.

Nests placed at a site where the canopy is relatively open were more successful in terms of number of days active. This may be due to predator density (i.e. predators may remain under the more dense canopy), nest crypsis (eggs are white and therefore less cryptic in a shadowed nest) or parental behaviour (eggs or nestlings in the cooler shade may require more parental attention for thermal reasons). Further research is needed to test these hypotheses. The positive correlation between cover from below and number of active days may be an expected pattern as we would predict the amount that the nest is obscured from below to be an important factor in nesting success in a population where aerial nest predators are few and most mammalian and reptilian nest predators remain on or close to the ground. This is particularly relevant when considering nest predators which search visually, but may also apply to those which may rely on olfactory cues, such as the reptilian predators on Catalina. Vegetation obscuring the nest may possibly act as a barrier to smell as well as sight (Whelan et al. 1994). In this study many inferences were made about predator types, although it is consistent with the idea that snakes would predate nests which are lower in the vegetation. The relationships between nest size/concealment and predator type may be merely an aspect of the nest site depending on its height; higher nests are bigger and less concealed. A negative correlation between size of support branches and number of active days emerges and this may be explained by the fact that larger branches can aid access to the nest by predators. Interestingly, larger nests were more successful on BRC3 and smaller ones on BRC1, which may also reflect predator types. It is possible that predators on BRC1 tend to be visually orientated and so small nests are harder to find, whereas predators on BRC3 may use olfactory cues and so larger nests may disguise these signals. Additional research on nest predators using complex filming methods, for example, would shed further light on predator types in relation to the various nest sites.

The lack of significant correlations between nest fledge/failure and nest site characteristics may be misleading. One interpretation may be that placement of the nest does not affect reproductive success, but this may be a false assumption. If there is an abundance of ‘good’ sites, then these will always be chosen and so no statistical correlation will be found between nest site attributes and nest success (as highlighted by Pribil, 1998).

The temporal patterns in predation reveal that nests very early or late in the season are more likely to fail. This may be due to predator abundance or it may be a density dependent relationship. It can be seen that there are more active nests in the middle of the season and this may be true for other species, so there may be a swamping effect on potential nest predators. Possibly poorer quality individuals breed early or late when there is less competition.

This study highlights the idea that nest placement in the vegetation can be an important factor in determining nesting success. This may be important for future conservation strategy, particularly as there is currently a large-scale project underway on Catalina to remove non-native flora.

An important finding of the study is the relationship between cover from below the nest and nest success. Most nest site quantifying techniques (including the BBird protocol, Martin et al., 1997) do not include this measurement in their descriptions and this study emphasises that this may be an important factor in determining nest success.

CHAPTER 4: A MICROCLIMATIC DESCRIPTION OF NEST SITES DURING THE PRE-INCUBATION STAGE: DOES NEST LOCATION AFFECT CLIMATIC CONDITIONS EXPERIENCED WITHIN THE NEST WITHOUT PARENTAL MANIPULATION?

ABSTRACT

Nest site selection in relation to microclimate is a poorly understood area and field studies are particularly scarce. Here, microclimate before incubation is measured, to eliminate any effects of parental behaviour and the results are explored in terms of the characteristics of the nest site. It was found that sites were chosen within the substrate which offered lower maximum temperatures than random sites within the same substrate. Lower nests were warmer throughout the night when compared with ambient temperatures. The structure of the nest itself had an insulative function, creating a warmer environment within the nest when compared with just outside it. Grasses and dense plant matter had the most effective insulative properties, whereas nests with higher amounts of root/vine-like materials had lower insulation. Interestingly, nests with higher maximum temperatures were active for a longer period, although this may be linked with characteristics of the nest site.

INTRODUCTION

During incubation birds have to provide optimal conditions for their eggs in order that offspring successfully develop. They are able to maintain optimal conditions during embryonic development within a relatively narrow range, despite fluctuations in the ambient conditions (Haftorn, 1988). In the maintenance of optimal embryo development conditions the incubating bird, the nest and the nest site form an important functional unit (Ar & Sidis, 2002) and all will contribute to the development conditions experienced by the embryo. The thermal environment will vary as a function of radiation (short wave length radiation from the sun and long wave length reflective radiation from the sky or surrounding vegetation), convectivity from wind, and the orientation of the nest which can influence a bird's overall heat balance (Rauter & Reyer, 2000; Wolf et al., 2002). Between-nest variation in these micro-climatic conditions is a possible, but often overlooked, contributor to the high intraspecific variation in incubation behaviour (Conway & Martin, 2000[a]). Therefore, optimal climatic conditions at the nesting site can have two effects; a reduction in the parental energy expenditure through less effort put in maintaining optimal incubation and brooding conditions and also providing optimal conditions for the developing embryo.

If the microclimatic conditions reach suboptimal conditions, the adult bird faces a trade-off between time spent incubating to maintain optimal conditions for embryonic development and foraging time to meet their own energy requirements (Webb, 1987; Williams, 1996). Such trade-offs between parental and offspring requirements for an optimal microclimate have been rarely considered. The effects of microclimate on the optimal development of avian embryos in the wild are important in understanding optimal nest site selection. This may be especially important in areas where there are considerable changes in local climate due to global climate change.

Maintaining an optimal developmental environment for offspring against a gradient with ambient condition influences the energetic, ecological and behavioural costs to the breeding parent (Williams 1996; Reid et al. 2002; Tinbergen & Williams 2002). Generally nest attentiveness decreases as ambient air temperature increases (e.g. White & Kinney, 1974). However, at very high temperatures, birds have been observed shading the nest and thus increasing nest attentiveness (Yom-Tov et al., 1978; Vleck, 1981; Ar & Sidis, 2002; Brown & Downs, 2003). The majority of research on nest site choice and microclimate has focused on species in environments that experience climatic extremes (e.g. high elevation or desert) although birds in a variety of other habitats can also experience high temperatures at the nest (Bennett et al., 1981). The incubating adults' energy budget can be supplemented and nest attentiveness increased in cases where individuals feed the mate at the nest (Martin & Ghalambor, 1999; Pearse et al., 2004) but this behaviour is not found in all species.
The effect of a suboptimal microclimate on the developing young is an area which has been widely studied in domestic chickens under laboratory conditions (e.g. Suarez et al., 1996; Leandro et al., 2004). There has been little work on passerines and very few field studies. There have been incidental reports of large drops in egg temperature in the field, which has not affected hatchability (Vleck, 1981; Morton & Pereyra, 1985; Sockman & Schwabl, 1998; Nuechterlein & Buitron, 2002). On the other hand, high ambient temperatures in the field can alter equilibrium egg temperature to lethal levels (Maclean, 1967; Webb & King, 1983; Webb, 1987) with detrimental effects on embryo development. Nest humidity can be equally as detrimental as both excessive as well as insufficient water loss interferes with normal embryonic development (Rahn et al., 1977; Walsberg & Schmidt, 1992). This is the result of temperature-dependent water loss from the eggs as well as the effects of the incubating parent (in reducing or increasing humidity at the nest) and also ambient humidity (Ar & Sidis, 2002).

Although the attending parent can have an influence on maintaining nest microclimatic conditions, there are times that the adult must fulfill its own energy requirements and so recesses off the nest are necessary. This results in a potential for the developing young to experience suboptimal conditions. Such fluctuations in conditions during early development can affect egg hatchability (reviewed in Webb, 1987) and offspring performance later in life (Gorman & Nager, 2004). An example of this can be seen in preliminary tests on unincubated eggs of the dusky flycatcher (*Epidonax* *oberholseri*), experiencing direct sunlight and shade conditions similar to a nest environment, but where the female was not attending, that did not develop successfully (Montag & Martin, unpub. data).

There are many components of the nesting site which may influence the thermal nest environment both at a large scale (macrohabitat) and at a local level (microhabitat). If site selection does influence the microclimate experienced by the developing young, and this is an important factor in the development of the young, then nest sites should be selected over random locations to optimise conditions. Macrohabitat may influence nest site selection in terms of microclimate, especially in species with ranges that cover a variety of habitats, e.g. mountainous areas. Temperature and humidity may vary with altitude or slope orientation and this can affect nest site microclimate (Martin, 1998; Martin & Roper, 1988; Rauter & Reyer, 2000). Nest height may affect rates of heating or cooling of the nest (Conway & Martin, 2000[b]) due to convection and radiative heat from the ground. Nest sites may be selected with an orientation that produces a favourable microclimate (Wiebe & Martin, 1998; Bekoff et al., 1987; Martin & Roper, 1988) or with exposure to sunlight at cooler times in the day and cover at the hottest (Walsberg & King, 1978; Walsberg, 1981). Relatively dense vegetation surrounding the nest site may provide a more favourable microclimate (Holway, 1991) and foliage cover may protect nests during periods of adverse weather, where there is heavy rainfall (Kelly, 1993). A good understanding of the function of the vegetation around the nest on the nest microclimate may be particularly important where significant vegetation change due to deforestation or invasive flora occurs, especially as nest site choice may be constrained by availability of suitable vegetation within the territory (Pribil, 1998). The nest itself can be a component of microclimatic conditions, as its size and shape may alter the conditions experienced within the nest (McGowan et al, 2004), or the materials used can have an insulative function (Hilton et al., 2004).

The aim of this study was to accurately describe the microclimate of the nest to assess the conditions experienced by the developing embryo. Both temperature and humidity was recorded as well as wind speed and temperature of the surrounding area. This was done for both nesting sites and also random sites. The nesting sites were monitored without the effects of parental behaviour to assess whether sites are specifically selected over random sites for the microclimate that they experience. Nest site characteristics were also quantified (as investigated in Chapter 2) and the relationship between nest site characteristics and microclimate was explored. The orange-crowned warbler is a good candidate species for such a study, as it breeds at high densities on Catalina Island and up to 150 nests can be found during one season (figure from 2005). The study required that nests were found pre-incubation and so a large number of nesting birds made this task easier. The orange-crowned warbler on Catalina, unlike the mainland subspecies, nests at a huge variety of heights, and so represents a large array of nesting sites. This also means that it is not restricted to one nest site type and so has more scope for nest site selection studies. Catalina Island provides an extremely variable climate; cool, wet weather early in the breeding season, compared to dry and hot at the end of the season. This enables a study of nest microclimate to encompass a wide array of ambient conditions.

METHODS

The study was carried out on Santa Catalina Island, part of the Channel Islands in California, USA (33º22'30"N, 118º25'56"W) and extended from early March to the end of May 2006. This research was conducted as part of a large, ongoing project looking at the ecology, behaviour, physiology and migration of the Catalina Island subspecies of orange-crowned warbler (*Vermivora celata sordida*). The climate on Catalina is described as Mediterranean and is extremely variable, being cool and wet during the early part of the year and becoming extremely dry and often very hot during the summer. This can be seen in the temperature logger readings, which were recorded throughout the field season (see Chapter 1: Introduction); range 1.5 – 32.6ºC (*n*=36,911).

The poorly known subspecies of orange-crowned warbler which is present on Catalina is endemic the Channel Islands and, although the population is declining (Sillett, pers.comm.), it is particularly dense on Catalina Island. The timing of the nesting season is variable and is initiated between late February-early April extending to May or June. The nest sites are very different to the mainland subspecies, which nest solely on or close to the ground (Sogge et al., 1994), with only a very few exceptions recorded (Zyskowski, 1993). On Catalina, 73% of the nests were off the ground in 2006 and nests have been observed up to 5m high (pers. obs. from 2004-2007). Nest building takes 3.2±0.2 days (*n*=19, range 2-5 days) and females lay a clutch of 2-4 eggs, starting up to 4 days after nest completion (Sogge et al., 1994). Nests are extremely variable in their size and composition, as well as their placement (described in Chapter 2).

<u>Study site</u>— A 0.15km² area study plot was established in Bulrush Canyon, a valley which runs East to West in the South-West of Catalina Island. The plot was situated at the base of the canyon on the North-facing slope. It is characteristic of a mesic habitat and is composed of small rivers (often dry in the summer months), patches of oak (*Quercus pacifica*) and toyon (*Heteromeles arbutifolia*) woodland with a shrub understory comprised of mainly lemonade-berry bush (*Rhus integrifolia*). There are also open areas of grasses and forbs. The plot was flagged every 25m to produce a grid so that accurate maps including nests and territories could be constructed.

<u>Nest surveying</u>— Nest searching was carried out on alternate days from 6am to 1-3pm. Active nests were monitored every 2 days and nest contents as well as adult behaviour was recorded. Nests which were found during the building or laying stage were subjected to detailed measurements of microclimate. A total of 56 nests were found in 2006.

Microclimate measurements— Nest microclimate was obtained for all nests found during building or laying (*n*=12). For these sites, random points were selected within the nesting substrate and within the birds' territory to test whether a specific part of the substrate is selected, or if a particular substrate is selected within the wider territory. Nests which were initiated by focal pairs for the ongoing study were not used in case breeding success was affected. Due to the fact that so few nests were found in the upper part of the study area (BRC3), nest microclimate was not measured on that site.

Nest site microclimate was obtained during the period of post building and pre-incubation, at least 1 day after building and 1 day before incubation. Hobo Data Loggers were used with probes attached, set to record every minute. Loggers were left at the nest for at least 24 hours, giving a total of 2,880 readings. The data logger was covered in camo-tape and rubbed with sage to prevent any olfactory cues that may attract predators, then secured beside the nest. A temperature probe was passed through the wall of the nest so that it lay just under the lining at the base of the inner cup. This resulted in temperature at the nest site, just outside the nest, and temperature within the nest to be recorded simultaneously in 10 nests. Two nests had temperature measurements from within the nest only due to a shortage of data loggers. Due to the fact that some nests (n=6) were found with one egg in them, logger readings were later checked for any peak where the female may have got on the nest. It was found that there was no parental activity, except during laying, and so a mean of the temperatures before and after this event was used. It was found that for most nests, the first 24 hrs of temperature recordings were better quality, as there was little or no parental activity and so this 24hr block was used in the analysis. A maximum and minimum temperature was obtained from the downloaded figures as well as a mean temperature.

Relative humidity (RH) was obtained by constructing hygrometers out of thin, hollow PVC tubing using a method outlined in Rahn et al., 1977. A 10cm section was cut and pierced with 300 equally spaced holes using a 20-guage hypodermic syringe. The tube was then filled with dry silica gel of 28-200Å mesh size and the ends sealed using silicone adhesive and sealant. A small egg incubator was set at 25°C with 100% RH (the water compartment of the incubator was filled entirely), at sea level (both the lab and field site were very close to seal level), resulting in a known water vapour pressure of 23.8 torr or 3.17kPa (Rahn et al., 1977) and the hygrometers placed inside. The incubator ensured the hygrometer was kept at a constant water vapour pressure and a thermometer was used to check the temperature twice a day. These were then weighed at 6-6.30am and 12.45-14.00pm using electronic scales accurate to 0.001g for at least 48 hours, thus calibrating the hygrometers under a known temperature and RH. The water vapour conductance of each hygrometer was then calculated using the following equation:

water vapour conductance = change in mass / water vapour pressure outside
(mg day^{-1} kPa^{-1}) (mg day^{-1}) (kPa)
(Ar et al., 1974)

The same equation was then used to convert measurements taken in the field (change in mass, with a known water vapour conductance) back into water vapour pressure outside. Between deployments the glue plugs of the hygrometer tubes were removed and the Silica gel carefully dried in an oven at 250ºC for 3-4hrs, then returned to the tubes and resealed. Hygrometers were wrapped in Clingfilm during every transitional stage to ensure that no water was absorbed or lost. It was found that the weight gain for the hygrometers was evident, but on a very small scale (<0.05g per day at 3.17kPa), so later in the season the tubes were perforated with 100 large holes (using a sewing needle) and recalibrated (Figure 13).

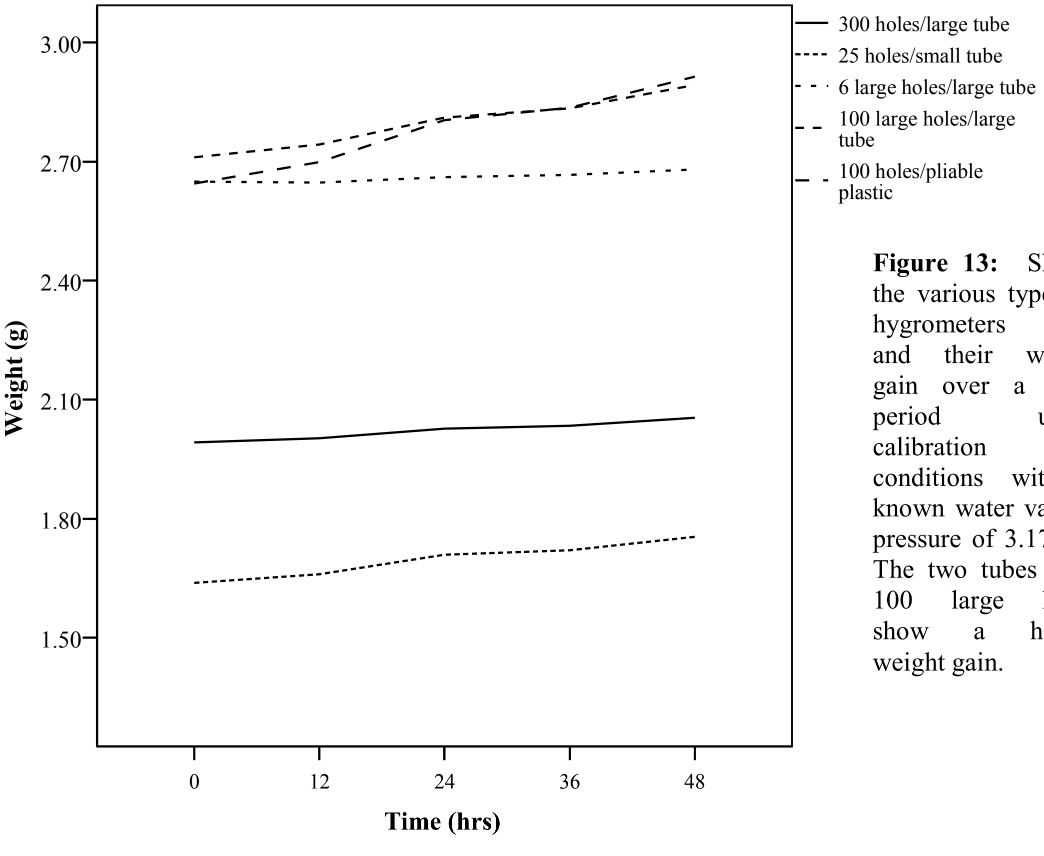

Figure 13: Shows the various types of hygrometers used and their weight gain over a 48hr period under calibration conditions with a known water vapour pressure of 3.17kPa. The two tubes with 100 large holes show a higher weight gain.

The hygrometers used in the field, with their respective conductance, are outlined in Table 13.

	Hygrometer no.	Vapour Conductance (mg day^{-1} kPa^{-1})
100 large holes/large tube	4	0.0101
100 large holes/large tube	2	0.0100
100 large holes/large tube	5	0.0080
100 large holes/large tube	3	0.0069
100 large holes/large tube	1	0.0061
25 holes/small tube	8	0.0055
25 holes/small tube	7	0.0054
25 holes/small tube	6	0.0054
100 holes/pliable plastic	14	0.0023

Table 13: Water vapour conductance of the 9 hygrometer tubes which were used in the field. The tubes with 100 large holes (conductance was measured for each one), were preferentially used, but the smaller tubes with 25 tubes were utilized if there was a shortage.

Both hygrometer tubes and logger probes were placed inside the nest (the hygrometer was also threaded through the nest wall) and the actual data logger placed next to the nest. All were secured using plastic ties and covered with a dead leaf to obscure them from view. A point within the nesting substrate was then selected using a table of random numbers which provided height (range 0-3.5m), distance (range 1-3.5m) and bearing (range 1-360º) from nest. A temperature logger and hygrometer were secured at this point in the same way. A random point within the territory was obtained from an equivalent random numbers table, but where figures for distance were increased (range 5-40m). If the location selected was outside the territory, the substrate or did not fall on a vegetated area, the next number on the list was selected. By selecting these two random points, two separate questions can be considered; do birds select a nest site with a particular microclimate from random possible sites within their territory? And do birds select, on a smaller scale, a particular site within a chosen substrate? Loggers and hygrometers were collected 48hrs later. Hygrometers were wrapped in Clingfilm to avoid further water absorption and weighed on return to the laboratory, less than 3 hrs later. Additional wind and temperature measurements were taken at the nest site and random points using a Digitron infrared temperature laser gun and Kestrel 3000 Environmental Meter. Temperature of the nest (or random point), of the vegetation directly above the nest and of the ground directly below the nest (if nest was <1.5m off the ground) was measured with the infrared sensor. These additional microclimate measurements ensured that a range of microclimatic measurements were taken; the air movement experienced at the nest site as well as any conductive heat from the ground or surrounding vegetation. This was carried out before the female began incubation, when the Loggers and Hygrometers were set out and again when they were collected, 48hrs later. This took place either at the beginning of the day (7.30-9.00am) or at the end of the field day (11.45-13.45pm).

<u>*Nest measurements*</u>— As the data loggers and hygrometers were set out, before incubation, a 35 mm Lomograpphy 170º Fisheye camera was placed at the nest site and also the random points, with the top of the camera pointing North, and a picture was taken of the overhead vegetation. This was then analysed using Gap Light Analyzer (GLA) software (obtained from Simon Fraser University, Institute of Ecosystem Studies, www.ecostudies.org/gla/). An exact measure of canopy cover was obtained from this to give an indicator of solar exposure. Unfortunately, there were some technical problems with the processing of the film and so this was obtained for all 12 nests, but only 9 of the random points.

25-30 days subsequent to clutch completion, descriptive measurements were taken of the nest and nest-site (see nest measurements below). This time-span was selected as a standardised period which ensured that nests had either fledged or failed. This method was employed as it was recognised that there is a possibility that vegetation may change between nest site selection and fledge/fail (Burhams & Thompson Ш, 1998). It was assumed that many of the nest measurements relevant to nest microclimate would not greatly change over time, such as height, orientation and nest dimensions. Although it is possible that nest concealment may alter over 25-30 days, it assumed that this would not be a significant change as 2006 was a particularly wet year and so the vegetation did not undergo the drying out and dying which is typical on Catalina through the summer.

Nest height was measured for all of the study nests (n=12). If the nest was still active at the end of the study, this was estimated (n=2). Nest orientation was assessed by measuring the bearing from the centre of the substrate to the nest site. If the nest was placed centrally in the substrate, and so had no particular orientation, this was noted. Nest entrance orientation was obtained by assessing the most open route to the nest and where the nest rim was flattened through the adults perching. Nest concealment, through ocular estimation, was the % of the nest which was concealed by vegetation from 1m away. This was taken at eye-level from each cardinal direction and also from above, looking down, and from below (where the nest height >1m). Nest dimensions were obtained by measuring the height and diameter of the inner cup and also the largest height and diameter of the outer layer of the nest to the nearest 0.5cm. The outer nest measurements were then put into the following equation for a regular ellipsoid to gain an indicator of nest volume (with the inner cup excluded):

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

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

adapted from Lombardo (1994)

The above measurements were taken for all nests which were inactive at day 25-30 (*n*=10). Subsequent to these measurements, the nest was removed, wrapped in Clingfilm and stored with mothballs to kill any insects. These were taken to a laboratory and weighed using electronic scales accurate to 0.001g. Nesting materials were measured using methods outlined in Chapter 2.

Ambient climatic measurements— Ambient climatic data was taken from measurements taken from data loggers which were left out throughout the breeding season, as described in Chapter 1.

Statistical analysis— SPSS 14.0 statistical software was used for data analysis. Correlations were tested using Spearman's rank coefficient. *t*-tests were used to test the difference between two independent samples and paired *t*-tests for related samples. Circular data was analysed using Oriana 2.0 (available from Kovach Computing Services www.kovcomp.co.uk/oriana/). Means are presented with a ±1 standard deviation.

RESULTS

Nests and random sites— Occupied nest sites were compared to a random site in the nesting substrate as well as a random site in the territory.

Height and canopy cover of nests was not significantly different from randomly chosen sites in the territory and the nest substrate (Table 14).

Site characteristics	Nest	Random in substrate	Random in territory	Mean
Height	0.95±0.82m 0-2.25m *n*=12	0.71±0.86m 0-2.83m *n*=12	1.55±1.17m 0-3.38m *n*=12	1.07±1m *n*=36
Canopy cover	88.24±11.17% 62.63-99.88% *n*=12	82.85±14.85% 47.8-95.88% *n*=9	83.61±8.31% 69-93.87% *n*=9	85.24±11.56% *n*=30

Table 14: Shows average height and canopy cover of nests (with ±SD) and the two random points chosen. Height was not significantly different between these three points ($F_{2,33}=2.45$, $P=0.1$) as was also seen with canopy cover ($F_{2,27}=0.67$, $P=0.52$). 3 values are missing in the sample sizes for canopy cover at each of the random points due to technical problems with processing the Fisheye pictures.

Temperature at the nest site (outside the nest) was compared with temperature at the two random points. Mean temperature at the occupied nest site was significantly lower than the random point within the same substrate. It was, however, not different to a random point within the birds' territory (Table 15). This was further explored in the differences in maximum temperatures; nests were placed in the substrate at a site with significantly cooler maximum temperatures (Table 15). Calibrated hygrometers tubes were used to measure water vapour pressure at the nest site and the two random sites. Water vapour pressure was relatively high for both occupied nest sites and for random points (Rahn et al., 1977, gave a range of 1.2-3.3kPa^{-1} for nest sites) and probably reflect the high humidity experienced during the breeding season (see General Introduction, Table 2). There was no significant difference in vapour pressures between the nest and random points (Table 15).

Air movement and heat from the ground and surrounding vegetation (wind speed and vegetation/ground temperature) varied between nest and random points. Average wind speed and temperature were not significantly different between the nest site and random points (Table 15), apart from temperature directly above the nest, which was higher at the random point in the nesting substrate when compared with the occupied nest site (Table 15).

		Means			Paired *t*-tests	
	Climatic measurements	Occupied nest site	Random point in substrate	Random point in territory	Occupied nest site/ Random point in substrate	Occupied nest site/ Random point in territory
Data logger temperatures	Mean temperature (ºC)	12.72±2.36 *n*=10	13.41±2.35 *n*=12	12.83±1.8 *n*=12	*t*=2.89 P=0.02 df=9	*t*=0.48 P=0.65 df=9
	Maximum temperature (ºC)	18.86±4.59 *n*=10	24.87±9.59 *n*=12	20.26±2.98 *n*=12	*t*=2.34 P=0.04 df=9	*t*=1.18 P=0.27 df=9
	Minimum temperature (ºC)	9.24±2.83 *n*=10	8.64±3.48 *n*=12	8.93±3.05 *n*=12	*t*=1.87 P=0.09 df=9	*t*=1.1 P=0.3 df=9
Hygrometer	Water vapour pressure (kPa)	2.89±2.15 *n*=11	2.91±1.93 *n*=11	3.22±2.32 *n*=11	*t*=0.11 P=0.91 df=10	*t*=0.64 P=0.54 df=10
Anemometer	Wind speed (Average)	0.06±0.28 *n*=21	0.04±0.2 *n*=21	0.39±0.77 *n*=21	*t*=0.25 P=0.81 df=20	*t*=1.75 P=0.1 df=20
Laser gun measurements	Nest Site Temperature (ºC)	17.83±3.96 *n*=21	18.73±4.09 *n*=21	17.27±4.02 *n*=21	*t*=1.52 P=0.14 df=20	*t*=0.59 P=0.56 df=20
	Temp Above Nest (ºC)	17.37±4.25 *n*=21	18.45±4.35 *n*=21	16.98±3.97 *n*=21	*t*=2.05 P=0.05 df=20	*t*=0.54 P=0.6 df=20
	Ground Temp (ºC)	19.14±4.05 *n*=10	18.69±3.99 *n*=11	18.18±4.57 *n*=10	*t*=1.88 P=0.09 df=12	*t*=1.03 P=0.33 df=9

Table 15: Shows mean values and paired *t*-tests between nest site and random points. The sample size is larger for random points due to the fact that for 2 nests only nest temperature (inside the nest) was measured due to shortage of loggers. One measurement for the water vapour pressure is missing due to the fact that the nest was built prior to the Hygrometer calibrations. Sample sizes are smaller for ground temperature due to the fact that this was not measured if the nest or random point was high and so not affected by the temperature on the ground. 21 measurements were taken for wind speed and with the laser gun (nest site, above nest and ground temperature) as multiple measurements were taken of some nests (i.e. when starting and removing the data logger).

These results could suggest non-random preference for nest sites with a certain microclimate, or could merely reflect a preference for nest site characteristics which in turn affect the microclimate of the site. In order to explore this further, the relationships between nest site characteristics and the resulting microclimate can be tested. When looking at the microclimate of the nest site in relation to nest site attributes (nest height, nest volume, nest orientation, nest entrance orientation, nest concealment and canopy cover), all 6 P values were >0.1.

<u>Within nest patterns</u>— Data loggers were also placed within the nest as well as outside it. It is therefore possible to explore differences in the microclimate of these two locations in order to test if the structure of the nest affects the microclimate experienced by the eggs within it. It can be seen that mean temperature was significantly higher within the nest, when compared to just outside (Table 16). Maximum temperature did not differ, but minimum temperature within the nest was significantly higher (Table 16).

Climatic measurements	Mean inside nest	Mean outside nest	Paired tests
Mean temperature (ºC)	13.28±2.18 *n*=10	12.72±2.36 *n*=10	*t*=3.66 P=0.005 df=9
Maximum temperature (ºC)	19.19±5.79 *n*=10	18.86±4.59 *n*=10	*t*=0.34 P=0.74 df=9
Minimum temperature (ºC)	10.06±2.76 *n*=10	9.24±2.83 *n*=10	*t*=3.01 P=0.02 df=9
Temperature range (ºC)	9.12±5.57 *n*=10	9.63±4.25 *n*=10	*t*=0.43 P=0.68 df=9

Table 16: Shows means ±sd for microclimatic measurements within the structure of the nest and just outside it before incubation started. Paired *t*-tests within and outside the nest reveal significant differences in both mean temperature and minimum temperature.

The difference between the temperature outside the nest and temperature within the nest was obtained by subtracting the former from the latter (temperature differential). This figure was then used to explore its relationship with nest site characteristics. It was found that there were no significant correlations between the temperature differential and the nest site characteristics measured (all 6 P values were >0.23). The same procedure was carried out with minimum temperature, maximum temperature and temperature range. Again, no significant correlations were found (all 6 P values were >0.13)

<u>Daily variation in temperature</u>— The temperature differential (temperature inside the nest minus temperature outside the nest) over a 24 hour period was used to explore how the nest structure affects the temperature inside the nest. It was found, however, that there was no significant correlation between this figure and measures of nest structure such as volume, weight or outer dimensions (all 6 P values >0.74).

Temperatures recorded within the nest were separated into day and night. Exact times for sunrise and sunset were obtained for each nest from the U.S Naval Observatory and averages calculated. All nests were warmer inside the nest at night when compared with just outside. Interestingly, two nests (0615 and 0637) exhibited a pattern in the difference between nest and nest site temperature, in that temperature within the nest was warmer than the nest site during the night and cooler during the middle of the day (Table 17). Data logger readings were checked to ensure that the female did not get on the nest over the 24hr time period (there were no sharp peaks in temperature as seen during incubation).

Nest ID	Average daytime temperature inside nest (ºC)	Average daytime temperature outside nest (ºC)	Average nighttime temperature inside nest (ºC)	Average nighttime temperature outside nest (ºC)	Days before clutch completion that measurements were taken
0602	16.36	14.56	6.61	6.39	5
0608	11.77	11.34	10.26	10.06	6
0611	12.73	12.13	11.46	10.92	3
0615	12.31	12.48	9.95	7.29	2
0620	12.38	12.12	10.55	10.04	5
0632	15.77	14.52	9.07	8.28	3
0637	16.25	17.54	13.07	12.61	2
0642	15.12	14.85	12.12	11.54	Female abandoned
0647	17.20	16.60	14.23	13.47	2
0655	19.68	18.87	14.41	14.11	2

Table 17: Average daytime temperature inside the nest is not significantly different to outside (paired t-test, *t*=-1.75, df=9, P=0.11). Average nighttime temperature, however, is significantly higher inside the nest than outside (*t*=-3.01, df=9, P=0.01). Nests 0615 and 0637 exhibit lower daytime temperatures within the nest in comparison to outside and higher nighttime temperatures within the nest when compared to outside. The last column indicates how many days before the last egg was laid that the datalogger was placed at the nest. Incubation started, in all cases, on the last egg.

This can also be seen in Figure 14. Most nests remained at around the same temperature as just outside the nest through the night, but exhibited varying degrees of temperature differential through the daytime.

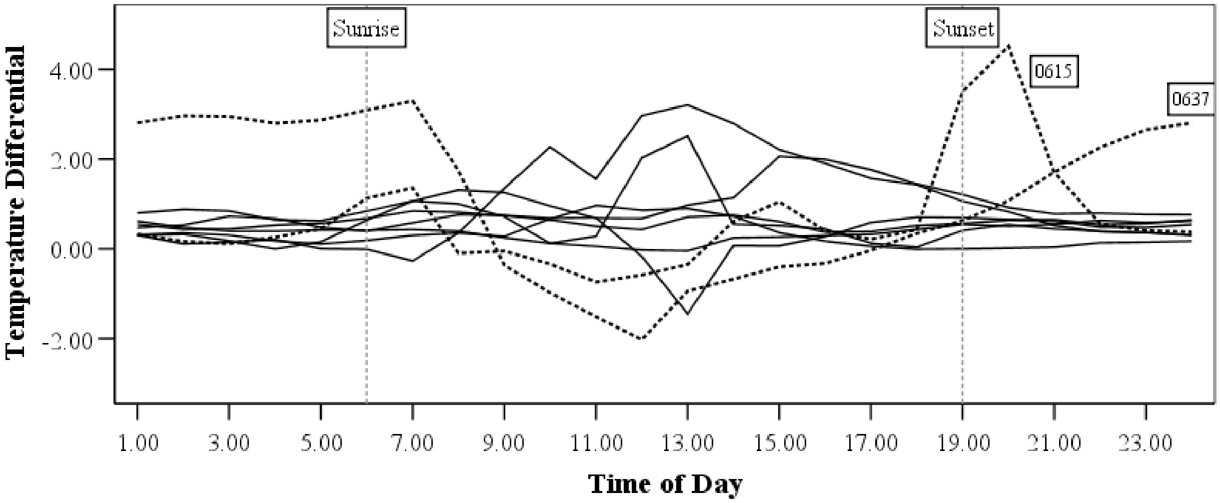

Figure 14: Temperature differential between inside and just outside the nest plotted over a 24hr period, with sunrise and sunset included. Positive values on the vertical axis reflect higher temperatures inside the nest than just outside the nest. The larger variations can be seen through the middle of the day, with very little difference at nighttime. The two nests, 0615 and 0637 (annotated), with warmer temperatures at night and cooler through the day, are indicated with dotted lines.

The difference between average temperature inside the nest and ambient temperature was calculated and correlated with various nest site characteristics. It was found that through the day, nests with lower canopy cover tended to be warmer in comparison to the ambient temperature (Table 18). During the night, lower nests were warmer when compared with ambient temperature, as were nests with more cover to the East (Table 18).

Temperature difference (Tn-Ta)	Mean, range, SD	Height	Canopy cover	Overhead cover	Cover from the North	Cover from the South	Cover from the East	Cover from the West	Nest volume
Day	0.14 -1.22–2.26 ±1.3	*rs*=-0.03 P=0.93 *n*=10	*rs*=-0.69 P=0.03 *n*=10	*rs*=-0.03 P=0.94 *n*=8	*rs*=-0.27 P=0.51 *n*=8	*rs*=-0.15 P=0.72 *n*=8	*rs*=-0.07 P=0.86 *n*=8	*rs*=-0.63 P=0.09 *n*=8	*rs*=-0.1 P=0.82 *n*=8
Night	0.97 -0.19–4.78 ±1.4	*rs*=-0.68 P=0.03 *n*=10	*rs*=-0.32 P=0.37 *n*=10	*rs*=0.59 P=0.12 *n*=8	*rs*=0.44 P=0.28 *n*=8	*rs*=0.68 P=0.06 *n*=8	*rs*=0.79 P=0.02 *n*=8	*rs*=0.01 P=1 *n*=8	*rs*=-0.64 P=0.09 *n*=8

Table 18: Shows temperature difference between Tn (temperature inside nest) and Ta (ambient temperature) in comparison to nest site characteristics. Some sample sizes are smaller due to the fact that there were still two active nests at the end of the field season.

Nest microclimate and nesting materials— The temperature differential between inside and outside in terms of average, minimum and maximum temperature, was compared with the percentage of type and size category of the materials used to construct the nest. This tested whether certain material types may have insulative properties. It was found that most correlations were non-significant (all 33 P values>0.26, *n*=9-11) apart from a relationship between the temperature differential and the use of grass, dense plant material and root/vine-like material in the nest structure. Nests which utilized more grass had a higher maximum temperature inside the nest than outside, as did those which had a higher percentage of dense plant matter. Nests with a higher amount of root/vine-like material had lower maximum temperatures inside the nest when compared with just outside. These relationships are shown in Figure 15. There was a relationship, in that nests with less root/vine-like material had significantly more grass (r_s=-0.5, P=0.01, *n*=45), therefore the fact that nests with higher amounts of root/vine-like were warmer was likely due to the fact that they had more grass incorporated into the structure.

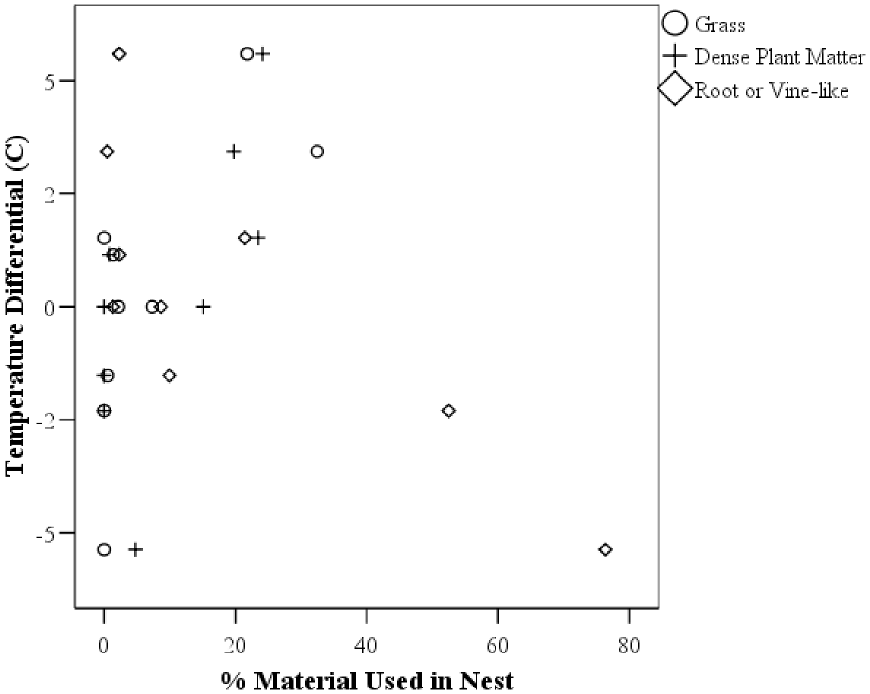

Figure 15: Shows the temperature differential in terms of maximum temperature inside and just outside the nest and significant correlations with grass (r_s=0.67, P=0.05, *n*=9), dense plant matter (r_s=0.73, P=0.03, *n*=9) and root or vine-like (r_s=-0.71, P=0.03, *n*=9).

A positive temperature differential indicates a higher maximum temperature inside the nest when compared to outside.

<u>Nest microclimate and reproductive success</u>— The correlation between number of days the nest was active and the microclimatic measurements was explored. It was found that all relationships were non-significant (P values were >0.06), except for the relationship between number of active days and maximum temperature and temperature range. Nests which experienced higher maximum temperatures were active for longer (r_s=0.66, P=0.04, *n*=10), as were nests which experienced a larger range of temperatures (r_s=0.69, P=0.03, *n*=10), although these two measures are clearly related.

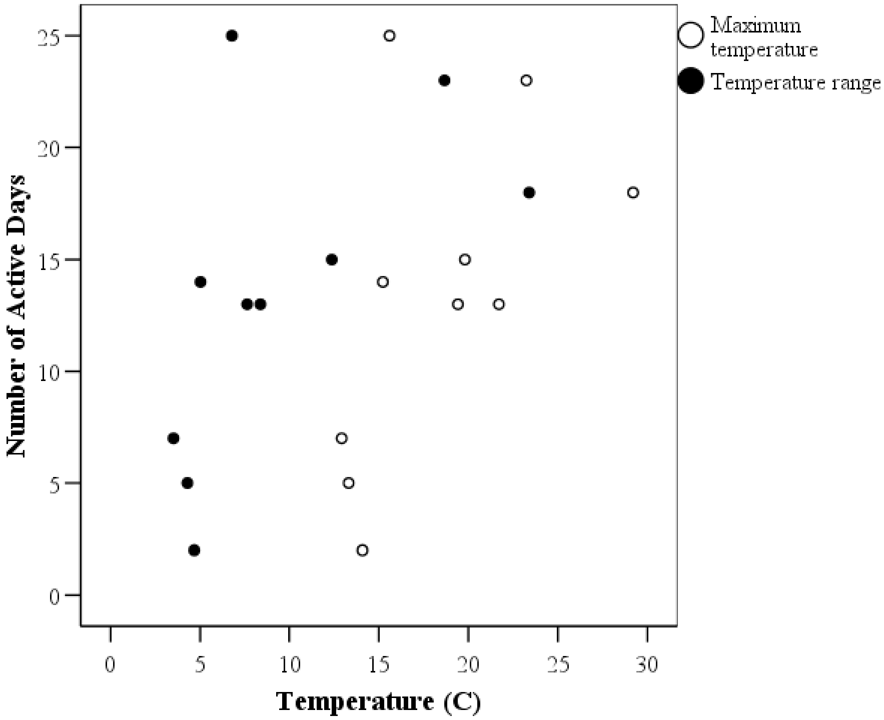

Figure 16: Shows maximum temperature and temperature range within the nest and the correlation with number of days which the nest was active.

These correlations can be seen in Figure 16. Relationships with nesting success in terms of fledge or failure could not be explored, as all nests where microclimate was measured failed.

DISCUSSION

The previous chapters have discussed the relationships between nest placement, structure and success and microclimate can now be added to these considerations. Although further study is needed to clarify whether nest sites are preferentially selected for the microclimate that they offer, several interesting patterns did emerge. It can be seen that nests are placed in a part of the substrate which is cooler than other random points in the same substrate. The nest structure clearly has some insulative role as temperatures within the nest are warmer than just outside. Where temperatures are separated into night and daytime, several relationships were revealed; lower nests, with higher cover to the east were warmer at night and nests with more canopy cover were cooler through the day. Interestingly, two nests exhibited a pattern where temperature inside the nest was warmer at night, in relation to just outside, and cooler through the day. Nests which experienced higher maximum temperatures, and so a larger temperature range, were active for a longer number of days.

It is possible that potential relationships were not picked up during 2006 due to the fact that it was a particularly cool and wet year. In the more representative hot years, there may be more selection occurring in relation to nest site characteristics and their subsequent effects on nest microclimate. The orange-crowned warblers on Catalina may experience different pressures depending on the particular climate of that year and so further, long term study is needed to explore this.

Surprisingly, only a small number of significant relationships between nest microclimate and nest site characteristics emerged. Canopy cover above the nest does affect the temperatures experienced during the day, probably due to the shading properties of the canopy. This has been seen in other species, which may preferentially chose nest sites under high/low canopy cover depending on the amount of sunlight (Riper III et al, 1993). Further research may look at nest placement and canopy cover during hot and cool years or an interesting experiment may be to manipulate canopy cover to either reduce or increase it and examine the effects on temperature and behaviour. Lower nests were warmer through the night, possible due to warmth stored in the ground during the day time. Hummingbirds are known to use this radiative heat and position nests at varying heights depending on the time of year (Horvath, 1964). This could also be tested on the orange-crowned warbler on Catalina by comparing nest height during hot and cool years. Nests which had lower cover to the East were warmer throughout the night, which may be due to sunrise, although the same relationship did not emerge during daytime temperatures. It is important to note that when carrying out large amounts of correlations, some significant relationships may emerge by chance. A larger sample size is needed to explore this in a more statistically robust way.

Nest structure has an important role to play in affecting the temperatures experienced by the young within the nest. Several studies have shown that birds manipulate certain nesting materials, such as feathers, for their insulative properties (Lombardo et al, 1995; McGowan et al, 2004). Dense plant matter and grasses had a higher insulative value, whereas root/vine-like materials were less protective in terms of temperature, possibly due to the absence of grasses and dense plant matter in nests with high amounts of root/vine-like materials. This has also been found in a study testing the density of nesting material and the insulative properties which relate to this. More dense materials (which grasses and dense plant matter are) had higher insulative properties, whereas less dense materials (which root/vine-like is) have lower insulative properties (Skowron & Kern, 1980). Another study on insulative properties of nesting materials found that grass had very low insulative properties, although this was in relation to materials which were not utilized in this study; wool, moss, down and feathers (Hilton et al, 2004). Interestingly, from chapter 2 it was found that neither dense plant material nor grasses were correlated with any nest site characteristics, although they were widely used. Therefore, these materials may not be utilized for their structural properties, but rather their insulative value.

Interestingly, nests which experienced higher maximum temperatures were active for a longer number of days. Chapter 3 revealed a negative correlation between canopy cover and number of active days and this can be then related to the significant relationship found in this chapter, as nests with lower canopy cover were warmer through the day. It is possible that a less dense canopy lets more sunlight in and so raises the temperature of the nest. This may enable the female to take longer off bouts and so reduces parental activity at the nest, which may, in turn, reduce the chances of predation, particularly during the egg and early nestling stage where the young require more temperature regulation.

All nests experienced higher temperatures within the nest at night when compared to just outside and lower temperature through the day were very interesting, as it is possible that these birds are selecting nest sites which provide shade through the day, but warmth at night, thus creating more favourable climatic conditions. Unfortunately, the sample size was too small to reveal if this was an anomaly or if this is a regular occurrence. Further study is needed to clarify this, particularly in climatically more representative years. There is a possibility that the female was on the nest during the night in these two cases, although there were no sharp rises in nest temperature that may indicate this. Videotaping nests during the night would confirm that this was not the case.

Overall, interesting relationships between nest characteristics and nest micro-climate emerged, but it is impossible to come to any conclusions about how microclimate affects nest site choice. Further experiments were planned to test how modifying microclimate affects the incubating bird and so how important a consideration it is, but it was not possible due to the abnormal weather conditions.

CHAPTER 5: CONCLUSIONS

This study has provided the most detailed description yet of the nest site of the poorly known subspecies of orange-crowned warbler population on Santa Catalina Island. Several interesting patterns emerged which highlight the fact that there is some degree of selection taking place when choosing nest sites. Nests were placed predominately in the North-East part of the nesting substrate which correlated with the direction of the slope. This could be related to ease of escape from predators, as birds tend to flush from the nest in a downhill direction (pers. obs.). An alternative hypothesis may be that North-East facing nests offer a more favourable microclimate, although this study shows that there are no significantly different climatic measurements for nests with this orientation. Nest site studies rarely explore nest site characteristics in this detail, and the fact that this study covers many angles allows certain possible explanations to be ruled out.

There were relationships between the placement of the nest and the number of days which it was active; nests with higher concealment beneath them and with a less dense canopy were active for a longer period of time. Although there were relationships between nest structure and placement, in that larger nests were higher and less concealed, this did not affect the nesting success. Nest sites were selected within the substrate with lower maximum temperatures than random sites within the same substrate. Low nests were warmer at night when compared with ambient temperatures. The nest structure also had an insulative role and minimum temperatures within the nest were higher than just outside. Grass and dense plant matter incorporated into the nest structure yielded the most effective insulation. Further exploration, in the same vein as that done by Hilton et al., 2004, could test insulative properties of specific materials.

The nest site characteristics of this subspecies of orange-crowned warbler have not yet been fully explored and this study provides a comprehensive account. It has revealed a huge variation in nest site characteristics, particularly in terms of nest height. It has been previously thought that nests of all three subspecies were very similar (Sogge et al., 1994), but this study indicates that this may not be so. Future research may consist of a comparison between subspecies or islands; it is known that nest sites differ greatly between Santa Catalina and Santa Cruz Island (pers. obs.), where nests tend to lower and more concealed. The Santa Catalina population probably represents a good example of ecological release, whereas on Santa Cruz there are a larger number of nesting passerines. The absence of Jays on Catalina also has a part to play in the choice of nest sites (Peluc, *In Press*).

This study also provides an extremely detailed account of the composition of the nest structure. I am unaware of any published work which has provided a similar amount of detail, although similar methods have been used in an ongoing study in Ecuador (Yanayacu Natural History Group). The orange-crowned warbler showed surprising plasticity in the types of materials which were utilized and it would be interesting to explore this in more detail. Further study may reveal the reason for this, in terms of proximity to certain materials, female preference, insulative purposes, cryptic reasons etc. Only canopy cover was significantly different when comparing nest sites between mesic and xeric habitats and this was possibly due to the difference in vegetation structure between the habitat types, as there was less tree cover on the xeric plot (pers. obs.). The absence of any difference in nest sites between plots was unexpected and may, again, relate to the ambient climatic characteristics of 2006; the xeric habitat did not experience particularly 'xeric' climatic conditions and so nest sites may have reflected this. Again, a cross-year comparison would enable this to be explored further, where wet, cool years could be compared with hot, dry years.

Due to the low nesting success in 2006, reproductive success in terms of fledging or failure was difficult to explore in relation to nest site characteristics. Using the number of days active as a measure of nesting success is not widely utilized in nest site studies (I am unaware of any, although the Mayfield method uses a similar approach, Mayfield, 1975) and may be a good measurement to explore nesting success in populations with very low nest survival. Although in terms of population study, reproductive success is a key measurement, for nest site studies the number of active days may be equally important. This takes into consideration the fact that a nest that is active for longer is more likely to be chanced upon by a predator. So poorly placed nests will be predated quickly, whereas those at a 'better' site will last longer. When solely failure or success is considered, those nests which were depredated on day 1 fare as well as those which were active until the day before they fledged.

The cause of nest failure was attributed to predation on Catalina, but only assumptions based on the state of the nest after the event can be used to speculate on predator type. Only snake predation has been witnessed on the island, although there are many other potential predators and future study may explore this further by using cameras at the nest. There was, however, a relationship between number of active days and cover from below and so we may deduce that potential predators are ground based. This is an important discovery, as many studies of nest site characteristics omit this measurement and it is not included in the BBird protocol (Martin, 1997). Future studies of off-ground nests, therefore, should possibly consider inclusion of this measurement.

When looking at nest site selection in terms of nesting success it is important to be aware of the fact that no significant relationships does not necessarily indicate that no selection is taking place. It is possible that optimal nest sites are available and so selected with every nesting attempt, which would result in no patterns emerging (Pribil, 1998). This is particularly relevant to this study population, as there appears to be little intraspecific competition for nest sites due to the fact that there are few other breeding passerines on Santa Catalina with similar nest sites.

Surprisingly few nest site characteristics were related to the microclimate experienced at the nests site. Nest sites were selected with lower maximum temperatures when compared to random sites in the same substrate. Lower nests were warmer at night and the material used in the nest structure had an insulative function, but there were no other apparent relationships. The fact that 2006 was a particularly cold, wet and humid year (See Table 2, Introduction page 8) may have affected the results, as high levels of solar radiation can be particularly damaging to developing embryos and so would be expected to be a factor in nest site choice during a 'hot' year. It would be particularly interesting to carry out the same study during a hotter, drier year and look at differences in nest site choice. Unfortunately, the hygrometers did not work as well as expected and so no accurate measures of humidity were obtained. It is possible that during 2006 humidity was not a particularly important factor, as it was a particularly wet season. During 2004, a particularly hot and dry year, two failed nests were found with unhatched eggs. Upon dissection, it was found that the nestlings inside were fully developed, but had not broken through the shell. Both nests were on very arid slopes and the lack of humidity may have affected hatchability, as has been found in other studies (Rahn et al., 1977). Further study of humidity during hotter, drier years may reveal some interesting patterns in nest site choice in regards to this.

The population of orange-crowned warbler on Santa Catalina Island is an extremely interesting one, particularly as part of a long term study. There appear to be yearly oscillations in reproductive success, climate, population density and vegetation type and it is probable that these are interrelated (pers. obs.). It is, therefore, possible that nest sites may vary in response to these differing pressures.

This study has revealed some degree of non-random nest site selection in this endemic subspecies and the relationships between these nest sites, structure, microclimate and survival. These add to the current understanding of nest site selection and further support the evidence that the choice of placement for a nest can have many implications. The fact that this population of orange-crowned warbler is successful in a wide variety of habitats and displays surprising plasticity in the nest sites it chooses implies that this particular population is less restricted in where it can nest. Other bird populations, however, may not exist under this kind of ecological release and intraspecific competition, climatic conditions, vegetation or predation pressures may play a part in determining where a bird can nest (Martin, 1998). An interesting comparison would be between the Catalina and Santa Cruz Island populations. On Santa Cruz, the orange-crowned warbler is much more restricted in its nesting sites; there are many more nesting passerines on the island, jay presence has an effect on the nesting site (Peluc, *In Press*) and damage by feral pigs has affected the vegetative ground cover. This population is much less successful, with lower reproductive success and a less dense population (pers. obs.).

Nesting sites can have a huge influence on the ecology of the species; birds with very specific nesting requirements, such as secondary cavity or cave nesters, will face more limitations in where they can nest and have consequent effects on the distribution or density of the species (eg. Brawn & Balda, 1988). Nest construction can also affect clutch size; the size and shape of the nest may affect the number of eggs laid. Large nests can support a larger number of eggs, as can nests with more support, such as cavities or Megapodes' mounds. The population on Catalina exhibits a clutch size on the lower end of the scale when compared with other *V. celata* subspecies (Sogge et al., give a range of 4-6). This may be explained by differences in nest height (ground nests may be able to support more eggs) or in terms of adult reproductive effort, as birds with higher survival rates (such as the short distance Channel Island migratory subspecies) may invest less in each reproductive effort than those species with lower survival and so a shorter number of breeding seasons (Ghalambor & Martin, 2001). This is currently being investigated by long-term researchers on Catalina. Many factors can influence the size and shape of nestrs and this can have various implications on the life history trait of the bird (Martin, 1988). Intense predation, for example, may select for nests of a smaller size to decrease conspicuousness and therefore, in turn, decreasing clutch size (Snow, 1978). A comparative study of populations with varying predation pressures may reveal such patterns.

MANAGEMENT IMPLICATIONS

The management efforts of the Catalina Island Conservancy on Santa Catalina Island have been extremely successful and in the last few years both pigs and goats, two extremely destructive species, have been eradicated completely. Feral cats are currently being neutered. There have also been several projects to eradicate invasive plant species, which is recently gaining strength, with a dedicated invasive plant team now in full time employment.

The other Channel Islands vary in terms of invasive species and current management practices, for example Santa Cruz Island has very recently eradicated feral pigs and it would be very interesting to find out what the implications will be for orange-crowned warbler nest site choice and reproductive success. It is possible that the high plasticity in nest site choice exhibited by the Catalina population means that changes in vegetation have little effect on nest sites, as the population is not restricted to just one type of nesting location. This plasticity, however, may not exist on other islands or there may be a 'time lag' between the eradication of invasive species and the ecological release in terms of nesting sites.

On Catalina it appears that the warblers preferentially nest in native plant species (χ^2=29.4, df=1, P=0.001), although this may be due to availability or the suitability of invasive species as nesting sites. A notable invasive which is often used as a nest site is harding grass which is found in large patches on BRC1. In these areas, however, there is very little else and so the choice of this grass for nesting may be through lack of any other suitable vegetation. Although this study did not reveal any differences in nest success when looking at nest substrates, the small number of nests found in non-native species makes it difficult to investigate if there is any variation in nesting success when looking at native vs introduced species. A multi-year approach, which would increase the sample size greatly, may reveal some patterns. One important consideration is the possible effects of invasive species on low vegetation cover. This study has shown that nests which are obscured by vegetation from below are active for longer and so any reduction in this vegetation layer may lead to lower nesting success.

In terms of management of invasive species which may predate nests (notably rats and cats), it is unclear what impact these mammals have on the orange-crowned warbler population. Further investigation involving the filming of nests would reveal the importance of these species as nest predators. From 2004-2007, around 5 females have been depredated at the nest and a pile of feathers (and occasionally the legs, particularly when banded) were observed close to the nest. This would suggest feline or canine predation, although further study is needed to clarify this.

An important factor, in terms of management of this species, is its susceptibility to drought (as outlined in Table 8, page 1) which has a considerable effect on nesting success and can even result in the forgoing of breeding altogether. This consideration is being explored in the research which is currently being undertaken on the island.

Overall, it appears that the presence of invasive species currently present on Catalina has a minor impact on the nesting of this species, although this may differ on other islands. It is, however, possible that that these invasive species may have a negative impact in other areas, such as food availability, territory quality or fledgling survival.

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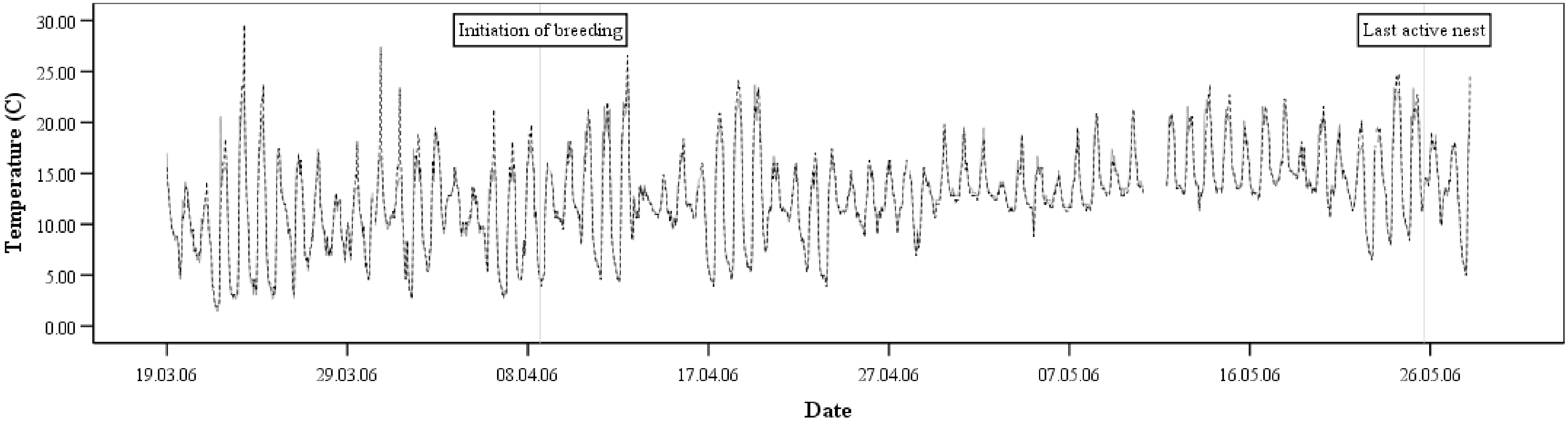
APPENDIX 1

Nest materials divided into ‘types’:

Wild cucumber	*Marah macrocarpus*
Honeysuckle	*Lonicera hispidula*
Toyon	*Heteromeles arbutifolia*
Horehound	*Marrubium vulgare*
Oak	*Quercus pacifica*
Common bedstraw	*Galium aperini*
Narrow-leaved bedstraw	*Galium angustifolium*
Catalina bedstraw	*Galium catalinense*
Coastal Sagebrush	*Artemisia californica*
Chickweed Mallow	*Malva parviflora*
Chamise	*Adenostoma fasciculatum*
Lemonade-berry leaf	*Rhus integrifolia*
California maidenhair	*Adiantum jordanii*
Mule fat	*Baccharis salicifolia*
“Red leaf” possibly Poison oak	*Toxicodendron diversilobum*
“Hair-like fibres” possibly fungi	

Plant Stem	**Bark**	**Grass**	**Leaf**	**Twig**	**Dense plant matter**	**Root or vine-like**	**Other**
Grass stem	Honeysuckle bark	Straight grass leaf	Toyon leaf	Oak twig	Lichen	Wild cucumber stem	Long black hairs
Sage stem	Dark bark		Oak leaf	Oak twig with leaves	Dead material from creek	Common bedstraw stem	Oak inflorescence
Grass stem with rootlets	Grey bark		Mallow leaf	Oak twig with Lichen	Opuntia skeleton	Red/Brown rootlet	Grass seed
Forb plant stem	Chamise bark		Lime leaf	Twig and lime leaf		Thick root	Spiral grass seed
Narrow-leaved bedstraw stem			Lime leaf with lichen	Mallow stem with leaf		Curly grass	Fox/Cat hair
Catalina bedstraw stem			Sage leaf	Mallow stem		Wild cucumber stem with vine tendrils	Horehound flower
Pretty, fine stems			Red Artichoke-like petal			Wild cucumber vine tendrils	Fluffy bud
Red plant stem			Lemonade-berry leaf				Leaf vein
Black stem			Oak leaf clump				Lime green plant bud
			Curly leaf				Mule fat fur
			Horehound leaf				Hair-like fibres
			Wild cucumber leaf				Lemonade-berry flower
			Red leaf				Catkin-like
			Fine orange leaf				Bedstraw flower
			Leaf skeletons				Feathers
			Bumpy leaf				
			Clump of Lemonade-berry leaves				
			Maidenhair leaf				
			Grey leaves				

APPENDIX 2


Initiation of breeding
Last active nest
Temperature (C)
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20.00
15.00
10.00
5.00
0.00
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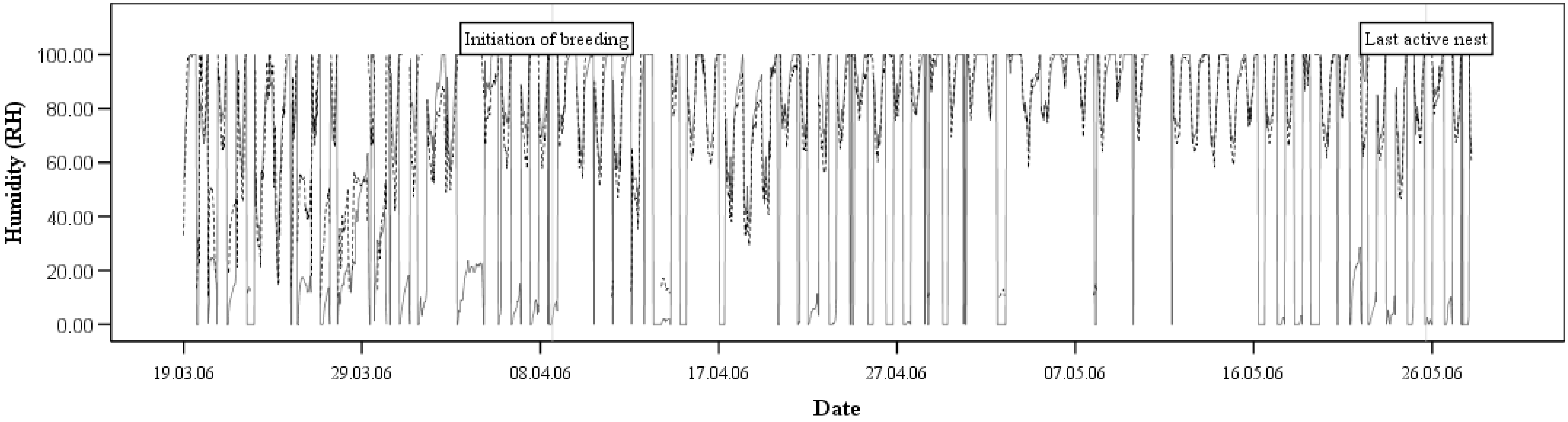
16.05.06
26.05.06
Date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Last active nest
Humidity (RH)
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40.00
20.00
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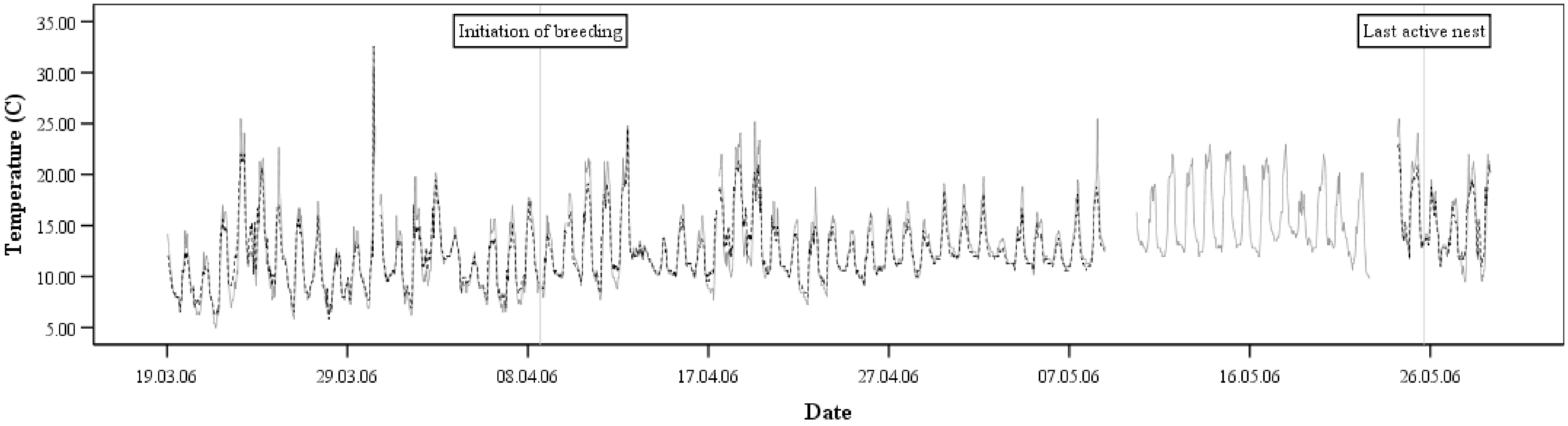

Initiation of breeding
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Temperature (C)
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25.00
20.00
15.00
10.00
5.00
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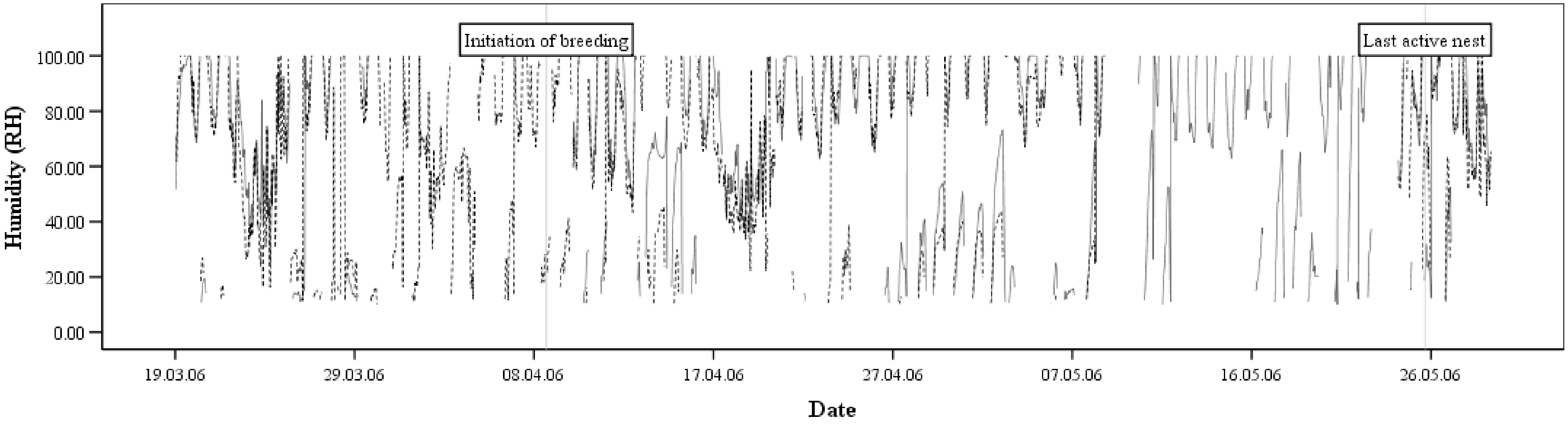
Date



Initiation of breeding
Last active nest
Humidity (RH)
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80.00
60.00
40.00
20.00
0.00
19.03.06
29.03.06
08.04.06
17.04.06
27.04.06
07.05.06
16.05.06
26.05.06
Date