DISSERTATION

HABITAT USE, TERRITORIALITY, AND PARENTAL BEHAVIOR OF ORANGE-CROWNED WARBLERS (*OREOTHLYPIS CELATA*)

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ABSTRACT

HABITAT USE, TERRITORIALITY, AND PARENTAL BEHAVIOR OF ORANGE-CROWNED WARBLERS (*OREOTHLYPIS CELATA*)

This study addresses three important correlates of fitness in the orange–crowned warbler (*Oreothlypis celata*): habitat use, territoriality, and parental behavior. The dissertation examines these fitness correlates by first modeling the spatial distribution of warbler abundance (Chapter 1), then examining geographic variation in male territorial behavior (Chapter 2), and finally examining differences in male–female parental behavior (Chapter 3). I expand on these chapters below.

The focus of the research in Chapter 1 is to understand how ecological factors shape the abundance and distribution of a species. The research methodology takes a habitat modeling approach using a Classification and Regression (CART) model. This model uses measures of territory size and remote-sensing data of vegetation to predict the abundance of a population of the *O. c. sordida* subspecies found on Santa Catalina Island, California. The findings provide evidence that the Normalized Difference Vegetation Index (NDVI) and percent oak coverage were the best model predictors of warbler territory density. A test of the model results using a large–scale distance sampling data set revealed that the density estimates from the CART model were comparable with those from the distance sampling analysis. The main conclusions drawn from this study are that

the habitat modeling approach based on the plot–based territory maps, accompanied by model evaluation using an independent dataset, can provide a useful tool to understand and predict species–habitat relationships.

The focus of Chapter 2 is to investigate how life history and competitive environments shape geographic variation in male territorial behavior, and how this is mediated by differential individual recognition strategies. To test these ideas, this chapter contrasts two populations of orange–crowned warblers in Alaska and California. Life history theory predicts that males with high residual reproductive value should avoid risk–taking behavior such as territorial aggression to minimize the costs to current reproduction. Intraspecific competition should also favor aggressive males that can acquire limited resources. This aggressive behavior can be modulated by familiarity with neighbors: reduced aggression to neighbors vs. strangers (dear enemy hypothesis). In a highly competitive environment, male aggression can be shaped either by "dear enemy" recognition or increased aggression towards neighbors to defend limited resources (nasty neighbor hypothesis). To test these competing hypotheses a simulated territory intrusion experiment using a taxidermic model coupled with neighbor–stranger songs to focal males from the two populations. Males from a population near the southern limit of its geographic range on Santa Catalina Island, California (*O. c. sordida*), had relatively higher adult survival but bred in higher density with lower food levels, compared to males from a population near the northern limit in Fairbanks, Alaska (*O. c. celata*). The main results of the study were that California males responded more aggressively towards conspecifics than Alaska males, where California males reacted more strongly to neighbors, and Alaska males reacted more strongly to strangers. These results suggest that high breeding densities and potential food limitation lead to elevated male–male aggression and intense territory defense against neighbors, regardless of their familiarity.

Finally, Chapter 3 examines how differences in food limitation, extra–pair paternity, and climate drive geographic variation in parental care provided by each sex in the two populations from Alaska and California. Four hypotheses were tested to explain variation in the amount and type of care provided by each sex: 1) food limitation favors high biparental care, 2) elevated male territory defense reduces male care, 3) high levels of extra–pair paternity should reduce male care, and 4) an environment with cold temperatures should favor high female brooding with high male provisioning or high provisioning effort by both sexes. The research approach to test these hypotheses includes videotaping nests to obtain the patterns of parental behavior during the nestling period, followed by measuring food availability, breeding density, extra–pair paternity, and ambient temperature. It was discovered that Alaska and California parents provided different types of biparental care: high female brooding with high male provisioning in Alaska vs. high male–female provisioning in California. However, these patterns were not directly explained by any of the ecological factors tested. The main conclusions drawn from this study are that more synthetic alternative hypotheses are needed. For example, a short breeding season with high food level in the Alaska population should allow a biparental strategy for nestling care with high female brooding and male provisioning effort to facilitate rapid nestling development, whereas a competitive environment with low food level and high breeding density in the California population should favor increased biparental strategy by both sexes to facilitate the probability of offspring recruitment in California. The studies in Chapter 2 and 3 recommend more comparative studies to better develop theory and provide empirical evidence for the factors that drive variation in the costs and benefits that shape parental care.

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ABSTRACT

Understanding how ecological factors shape the abundance and distribution of a species is central to ecology and conservation biology. Most habitat modeling studies have revealed a strong association between species abundance and resource availability. In this paper, we present a habitat modeling approach using a territory mapping survey to predict habitat–specific abundance of orange–crowned warblers (*Oreothlypis celata sordida*) breeding on Santa Catalina Island, one of the eight Channel Islands off the coast of southern California, USA. The breeding density of the warbler population varied along a mesic to xeric habitat gradient, primarily in response to oak density and food abundance (i.e., Lepidopteran larvae). Multiple–year measures of warbler territory density on a 28–ha study plot were used to build a classification and regression tree–based model (CART) to project the distribution of warbler abundance on an island–wide scale. In the model calibration processes, normalized difference vegetation index (NDVI) and percent oak coverage were the best model predictors of warbler territory density. The fitted CART model of habitat–specific density was evaluated with an independent dataset, an island–wide distance sampling point count survey of warbler abundance. We found that density estimates from the distance sampling analysis were comparable with those from the CART model, and mirrored the predicted densities in the three habitat–specific strata produced by CART. We conclude that the habitat modeling approach based on the plot–based territory maps, followed by a model evaluation using an independent dataset on a large scale, can provide a useful tool to understand a species–habitat relationship and manage the species and its habitats.

INTRODUCTION

Many theoretical and empirical studies have sought to discover which abiotic and biotic factors influence a species' abundance and habitat selection (Block and Brennan 1993, Jones 2001). The distribution and abundance of a species may be constrained due to a wide range of abiotic factor, vegetation structure, food availability, conspecific interaction, interspecific competition, predation risk, or even phylogenetic constraints (Cody 1978, Smith and Shugart 1987, Root 1988, Stamps 1988, Suhonen et al. 1994, Bollinger 1995, Forstmeier et al. 2001). Furthermore, studies in the relationship between species abundance and habitat–related components plays an important role in developing wildlife habitat modeling approaches (Johnson 1980, van Horne and Wein 1991), which can then provide informative criteria for studying wildlife habitat selection processes in conservation biology and species management.

A diversity of statistical techniques for habitat modeling studies have been developed and frequently used in ecology, ranging from ordinary linear regression to Bayesian models and environmental envelopes (reviewed in Guisan and Zimmermann 2000, Guisan and Thuiller 2005, Elith et al. 2006). Early studies in habitat selection used correlative models of species abundance and habitat characteristics (MacArthur and Pianka 1966, Rosenzweig 1991). More recently, Classification and Regression Tree (hereafter CART) has been used in modeling wildlife habitats due to several advantages including their flexibility to work with a variety of response variable types, insensitivity to the types of explanatory variables, ease and robustness of tree construction, and easy interpretation (De'ath and Fabricius 2000, Fan et al. 2006). They are especially useful when using complex ecological data (O'Connor et al. 1996, North et al. 2000, Lawler and Edwards 2002, Becker and Beissinger 2003, Fan et al. 2003) that require flexible yet robust analytical methods that can address nonlinear relationships, high–order interactions, and missing values. Another advantage is that tree–based models can be effectively implemented and mapped by using a GIS tool to project the predicted distribution of wildlife habitats. Thus, CARTs have become a popular alternative technique to many traditional statistical methods of modeling wildlife habitats (Breiman et al. 1984, Ripley 1996).

Here, we describe a model that projects and evaluates the habitat–specific territory density of orange–crowned warblers (*Oreothlypis celata sordida*) breeding on Santa Catalina Island, off the coast of southern California (Sogge et al. 1994, Chesser et al. 2010). Grazing by non–native herbivores, fires, and development have altered the landscape of Santa Catalina Island over the past 150 years (Knapp 2002, Keeley 2006). Wildlife habitats on the island are also affected by variation in annual precipitation, which frequently results in a series of extreme dry and wet seasons (Schonher and Nicholson 1989). Furthermore, the interactive effect of this Mediterranean climate and human–related activities has led to an altered fire regime, resulting in a significant loss of wildlife habitat (Lynch and Johnson 1974, Keeley 2006). Our main goals were to 1) model spatial variation in warbler territory density using a plot–based territory mapping survey dataset, based on territory quality along a habitat gradient, 2) scale–up these environmental elements to the landscape level to project the distribution of warbler territory density across the entire island, 3) evaluate the predictions of the model using an island–wide distance sampling data of warbler abundance, and 4) use the predictions of the model to assess the degree of fire–associated habitat loss for our study species.

METHODS

Study Site and Species

We studied breeding the orange–crowned warbler (hereafter *warbler*), an 8–10 g, insectivorous passerine, on two 14–ha plots in Bulrush Canyon on Santa Catalina Island (N33°22'30", W118°25'56") from March to May in three consecutive years (2006–2008). Males establish and defend breeding territories from February through May or June. We studied warblers on two habitat types that were arrayed along a habitat gradient: one 14–ha plot was located in mesic vegetation along the canyon bottom, with relatively tall and dense island scrub–oak (*Quercus pacifica*) woodland (82.1 % of total study area), and the second 14–ha plot was situated on the canyon’s south–facing and xeric slope, which had shorter–stature and sparse oak woodland (55.3 % of total study area; see Figure 1). Common plant species included island scrub–oak, toyon (*Heteromeles arbutifolia*), lemonade berry (*Rhus integrifolia*), California sagebrush (*Artemisia californica*), black sage (*Salvia mellifera*), willow (*Salix sp.*), mule fat (*Baccharis salicifolia*), coyote bush

(*B. pilularis*), chamise (*Adenostoma fasciculatum*), Harding grass (*Phalaris aquatic*), and a range of other native and non–native grasses.

General Data Collection

Territory mapping – To facilitate individual identification and territory mapping, warblers on both study plots were captured with mist–nets, individually banded with a unique combination of three color leg bands and a U.S. Geological Survey, numbered aluminum leg band, and classified by sex and age based on plumage and morphological characters following Pyle (1997). Both study plots were delineated into 25 m x 25 m grids with flagging to facilitate mapping of warbler territories. All territories were mapped by observing territorial disputes and movements of banded males and females throughout the breeding season. In the field, we marked the location of individual warblers on a high–resolution aerial photograph during the time between 6:00 am and 12:00 pm PDT, and the points were entered and updated in ArcGIS 9.1 (ESRI Inc., 2005) every two weeks. We found warbler nests on territories in each breeding season and monitor them once every two days to measure habitat–specific reproductive success (i.e., clutch size and fledged number). We used a two–tailed *t*–test to compare breeding density (territories ha^{-1}) between the two plots and a mixed model (Restricted Maximum Likelihood, REML) to compare territory size, clutch size, and the number of fledges between two plots, controlling for year as a random effect in SPSS version 13.0 (SPSS Inc., 2004, Chicago, IL).

Foraging behavior observation – Foraging behaviors were recorded between 6:00 am and 12:00 pm PDT from March to May in 2006 and 2007 to determine the percent use of oaks and other plant species by warblers. We visually located a focal individual using 8 x 40 binoculars and waited 10 seconds before recording its foraging behavior (i.e., plant species that was used in each foraging bout; see Dobbs et al. 2007). The observation effort per individual lasted between 30 seconds and five minutes, but generally not more than two minutes. We did not take multiple observations from any individuals on the same day, and the average number of observations per individual was 2.04 ± 0.15 individuals per season, ranging from one to seven individuals.

Food abundance assessment – We used branch clipping (Johnson 2000) to quantify habitat–specific Lepidopteran larvae (hereafter caterpillar) biomass in *Q. pacifica* on the study plots. These warblers are insectivorous, mainly foraging on caterpillars in the canopy of oaks on Santa Catalina Island (Sogge et al. 1994). Once every two weeks from March to May in 2006–2007, we sampled approximately 0.5 m^3 of vegetation from 24 randomly selected oak trees (i.e., 12 trees in each plot), which were placed in plastic bags in a 0 °C freezer for approximately one week to prevent the loss of live arthropods. All arthropods were then separated from the vegetation and returned to the freezer for later processing; vegetation material was weighed to the nearest mg and discarded. Caterpillars were sorted from other arthropods and dried in an 80°C oven for 24 hours. We used caterpillar dry biomass (mg) adjusted by wet vegetation mass $(g)^{-1}$ as an index of warbler food availability. We used a mixed model to compare food abundance between the two plots, controlling for year as a random effect.

Warbler Habitat Model

Warbler territory density – We used the three–year territory map dataset to calculate mean territory size and determine a warbler neighborhood scale in GIS, which allowed us to measure variation in territory density as a numerical dependent variable.

Territory boundaries were delineated with the minimum convex polygon method (Ford and Myers 1981). Neighborhood scale was defined using a diameter of average warbler territory size (42 m) over both study plots, which was a circular polygon with the radius of 42 m (Estep et al. 2005). The dependent variable in the CART models was territory density as estimated by the number of intersected centers of territories within the neighborhood polygons from 20 randomly selected grid points per study plot and per season.

Model predictors – To build our CART model, we obtained model predictors from six raster datasets. The first four topographic elements were: 1) *aspect* (eight categories), 2) *slope* (a continuous variable in degrees), 3) *hillshade* reflecting the interactive effect of aspect and slope of the terrain (relative to the sun's azimuth and sun’s altitude) derived from a 10 m x 10 m digital elevation model (DEM) raster dataset, and 4) *landform* (canyons, north–facing / sheltered slopes, northeast– / northwest–facing slopes, east– / west–facing slopes, southeast– / southwest–facing slopes, and south–facing / exposed ridges) reflecting variation in potential insolation influenced by a combination of aspect, slope, hillshade, and TPI (Topographic Position Index; adapted from Weiss 2001). These four topographic attributes were anticipated to play a key role in determining a moisture gradient influenced by the intensity of received solar radiation on the study plots. The last two ecological predictors were: 5) *Normalized Difference Vegetation Index* (NDVI) reflecting the degree of greenness in vegetation, calculated from the near infra–red (NIR) and red (R) spectral bands as NDVI = (NIR – R) / (NIR + R) using a 5 m x 5 m IKNOS satellite image, photographed in May of 2005 (see Kumar and Monteith 1982, Goward and Huemmrich 1992 for the formula) and 6) *percent oak coverage* derived from a GIS layer of vegetation classification (Knapp 2005) constructed by the Catalina Island Conservancy (hereafter CIC). All calculations and data acquisition were performed with Hawth's Analysis Tool (Beyer 2004) in ArcGIS.

CART model calibration – Our full CART model considered six predictors (aspect, slope, hillshade, landform, NDVI, and percent oak coverage) of warbler territory density. To select a best–fitting CART model, territory density was consecutively partitioned into two exclusively homogeneous groups by a series of *if–then* split conditions of the six predictors (Breiman et al. 1984, Ripley 1996). The size of the final CART was determined by minimal cost–complexity pruning (i.e., selecting the optimal–sized tree). That is, controlling for the tree size, the number of splits was indirectly controlled by parameter complexity (c_p) that puts a cost on each additional split, where splitting stops when increases in cost outweigh reduction in misclassification rates. All analytical procedures for building a CART model were conducted using Package *rpart* (recursive partitioning and regression tree; Therneau et al. 1997) in Program R (R Development Core Team 2009). The best–fitting CART model was used in the Spatial Analyst's Raster Calculator module in ArcGIS to generate a map of warbler territory density on an island–wide scale.

Model Evaluation Using Distance Sampling Density Estimates

We evaluated the projected warbler territory density from the best–fit CART model using an independent dataset, an island–wide point count survey conducted by the CIC in mid May of 2002–2006. Eighty permanent survey points were established systematically across the island (see Figure 3); survey points were at least 400 m apart (mean distance = 717 m). A survey team of one observer and one data recorder conducted

5–min bird counts (i.e., species, number of individuals, and distance) between 6:00 am and 10:00 am PDT. Warblers were detected with both visual and aural cues, although due to the cryptic behavior of this species, the great majority of individuals were detected by vocalizations. The orange–crowned warbler breeding season typically starts ending in May on Santa Catalina Island, and song activity tends to be low as a result; most individuals, including males, females, and juveniles, communicate vocally via call or *chip* notes (Yoon et al., in prep). Therefore, the CIC distance sampling surveys were not counts of singing males.

We used Program DISTANCE (Thomas et al. 2009) to estimate warbler density (individual / ha) from the CIC dataset, and assumed the following distance sampling criteria (Buckland et al. 2001): 1) perfect detectability at zero distance from a survey point, $h(0) = 1$; 2) no movement in response to observers during the survey period; and 3) accurate measurement of direct distances from a survey point. Prior to model fitting, we inspected the histograms of survey distances and truncated obvious right–sided outliers beyond 100 m to provide a better fit of detection functions to the distance sampling data. We then used GIS and Jenks' (1967) optimization algorithm to post–stratify the 80 point count circles into three habitat types based on predicted warbler density from the best–fit CART model: *low* (less than 1.60 territories ha^{-1} predicted by the fitted CART; n = 38), *intermediate* (1.60 to 2.87 territories ha^{-1}; n = 27), or *high* (2.87 to 4.26 territories ha^{-1}; n = 15; see below). We used half–normal and hazard–rate detection functions with three adjustment terms (cosine, simple polynomial, and hermite polynomial; Buckland et al. 2001) to estimate warbler density separately for *low*, *intermediate*, and *high* habitats and for the entire island without habitat classes. Thus, we fit the four model sets, each with the six candidate models for detectability. The most parsimonious detection function within each set of six candidate models was selected with second–order Akaike's Information Criterion corrected for small sample size (AIC$_c$; Burnham and Anderson 2002), and the fit of each candidate model was assessed with a Goodness of Fit χ^2 test (Buckland et al. 2001). We estimated island–wide warbler density and also examined year–to–year variation in density for 2002– 2006 in relation to *bioyear* precipitation from July $_{\text{year(x–1)}}$ to June $_{\text{year(x)}}$ (adapted from Morrison and Bolger 2002).

RESULTS

Warbler Habitat Quality

The foraging behavior, food abundance, territory density, and reproductive output of orange–crowned warblers revealed a strong habitat quality gradient between mesic canyon bottoms and xeric uplands in Bulrush Canyon. Island scrub–oak was the primary foraging substrate used by warblers in both habitats: mesic: 86.9 % of total foraging observations (n = 282); xeric: 92.9 % (n = 99). Caterpillar biomass on scrub–oaks was significantly greater in the mesic (0.44 ± 0.07 SE mg g^{-1}) compared to the xeric habitat (0.13 ± 0.07 SE mg g^{-1}; mixed model: $F_{1,218}$ = 12.35, P = 0.001). Warbler breeding density was significantly higher on the mesic plot compared to that on the xeric plot (mesic: 4.41 ± 0.40 SE territories ha^{-1}; xeric: 1.85 ± 0.17 SE territories ha^{-1}; two–tailed t test: t_4 = 5.31, P = 0.01), and territory size was significantly smaller (mesic: 0.11 ± 0.01 SE ha; xeric: 0.23 ± 0.02 SE ha; mixed model: $F_{188.3}$ = 64.70, P < 0.001). Although we did not find significant differences in either clutch size (mesic: 3.52 ± 0.08 SE eggs / clutch; xeric: 3.40 ± 0.12 SE eggs / clutch; mixed model: $F_{1,84}$ = 0.74, P = 0.39) or number of young fledged (mesic: 1.56 ± 0.50 SE fledges; xeric: 1.02 ± 0.56 SE fledges; mixed model: $F_{1,82.1} = 1.88$, $P = 0.17$) between plots in two combined years of 2006 and 2008, higher warbler density resulted in the mesic habitat being more productive than the xeric habitat in terms of mean number of young fledged per ha (mesic: 7.83 ± 2.15 SE fledges ha^{-1}; xeric: 2.05 ± 2.15 SE fledges ha^{-1}).

Habitat Model

The best–fit CART model had a cross–validated error rate of approximately 1.19 (root node error rate x potential misleading error; Figure 2a) and predicted territory density as a function of two variables, NDVI and percent oak coverage (Figure 2b). Collectively, the areas containing more dense vegetation (i.e.,, higher NDVI value) as well as higher percent oak coverage were associated with higher warbler territory density on the plot–based study. Projection of the CART model indicated that 38.0 % if the island was *low*–density habitat (< 1.60 territories ha^{-1}), 20.4 % was *intermediate*–density habitat (1.60–2.87 territories ha^{-1}), and 41.6 % was *high*–density habitat (> 2.87 territories ha^{-1}; Figure 3). This model predicted an island–wide mean breeding density of 1.92 territories ha^{-1} (± 1.04 SD).

Model Evaluation Using Distance Sampling Data

The CIC landbird survey detected 505 total warblers in May of 2002–2006. Estimated warbler density from program DISTANCE was comparable to predicted territory densities from CART (Figure 4). Island–wide mean density was 2.89 warblers ha^{-1} weighted by five–year strata [95 % log–based confidence interval (CI): 2.30–3.64]. Detection probability was low, averaging 0.13 and ranging from 0.01 to 0.21. The hazard–rate key function with three adjustments fitted the data for detection function where the probability of Goodness of Fit (GoF) χ^2 tests ($df = 7$) ranged from 0.11 to 0.79 over the five–year data.

The post–stratified distance sampling analysis estimated that warbler density in both the *intermediate*– and *high*–density strata was higher than territory density predicted by the CART model (Figure 4). However, five–year warbler density estimates from DISTANCE followed the same pattern as the prediction from CART (i.e., *low*– < *intermediate*– < *high*–density habitats; Figure 4). In the *low*–density stratum, the hazard–rate key function with cosine and hermite polynomial adjustments fitted the data for detection function, where the probability of GoF χ^2 tests ($df = 7$) ranged from 0.17 to 0.92. In the *intermediate*–density stratum, the hazard–rate key function with three adjustments fitted the data for detection function where the probability of GoF χ^2 tests ($df = 7$) ranged from 0.01 to 0.36. In the *high*–density stratum, the hazard–rate key function with three adjustments fitted the data for detection function where the probability of GoF χ^2 tests ($df = 7$) ranged from 0.09 to 0.95. Detection probability means decreased from *low*– (0.28, ranging from 0.18 to 0.45) to *intermediate*– (0.16, ranging from 0.06 to 0.33) and *high*–density strata (0.12, ranging from 0.06 to 0.16). Density estimates also varied between years (Table 1). Two wet years, 2003 and 2005 had higher estimated warbler density that than the five year average (2.89 warblers ha^{-1}). In contrast, two dry years, 2002 and 2004 had below–average density estimates.

DISCUSSION

The distribution and structure of oak cover and the food availability associated with this vegetation appear to be the best predictor of *O. celata sordida* territory density on Santa Catalina Island. Our data suggest that larger oak patches in mesic drainages likely provide more food (i.e., Lepidopteran larvae) relative to xeric ridges, which are characterized by lower territory density and larger territories. The habitat–specific variation in warbler territory density that we document here has been found in other studies of insectivorous birds. Marshall and Cooper (2004) found that breeding red–eyed vireos (*Vireo olivaceus*) selected territories based on foliage density cues that reflected the abundance of Lepidopteran larvae. Johnson and Sherry (2001) presented a positive association between abundance of wintering American redstarts (*Setophaga ruticilla*) and arthropod biomass. Thus, breeding conspecific density is likely to be a robust predictor of resource abundance for breeding *O. celata sordida* on Santa Catalina Island.

The fitted CART model indicates that NDVI and percent oak coverage explain an ecologically important component of variation in warbler territory density on the study plots, ranging from the mesic drainage to xeric ridge habitat. Adams and Anderson (1980) found a continuous and gradual change in bird species composition along a moisture gradient from mesic to xeric habitats. Indeed, satellite–derived remote–sensing data such as NDVI have been considered as a useful predictor of environmental changes that may impact biodiversity or animal populations (reviewed in Nagendra 2001, Pettorelli et al. 2005).

Our territory mapping approach has both strengths and weaknesses as a method for evaluating and monitoring warbler habitat quality on Santa Catalina Island. This method excludes non–territorial individuals and juveniles, thereby reducing the likelihood of overestimating territory density and making spurious conclusions about density–habitat quality relationships (van Horne 1983). Moreover, intensive territory mapping minimizes the potential underestimation of density when relatively low breeding activities and detectability occur seasonally or annually. For example, the vocal activities of breeding male *O. celata sordida* decrease as the season progresses (J. Yoon, T. S. Sillett, and C. K. Ghalambor, in prep.), making territory mapping a more reliable way that is less sensitive to annual and season variation in reproductive behavior of the study species, compared to point count surveys. However, intensive territory mapping is time consuming and is most efficient with uniquely color–marked individuals. Our study plots also only encompassed two habitat types; additional data would be needed to confirm that our results apply to all habitats occupied by breeding orange–crowned warblers on Santa Catalina Island.

Our CART model and distance sampling analysis produced comparable, habitat–specific density estimates on a landscape scale although distance sampling yielded higher estimates of warbler density in high–quality habitat than did CART. Distance sampling and CART, however, consider different metrics of warbler abundance: distance sampling estimates bird density, whereas CART predicts territory density. Moreover, CIC's point count surveys were conducted in May when many territories had fledglings. This likely leads to overestimate adult warbler densities especially in *high*–density stratum where not only the fledglings could be mistaken for adults, but also per–area reproductive success would likely have been highest during this survey period. Warbler density estimates from distance sampling varied with rainfall and were relatively low in dry years when reproductive effort (Langin et al. 2009) and hence warbler vocalizations were low. We have observed that warbler territory density on the study plots tends to be stable between years. For example mean territory density in the mesic plot ranged from 3.42 to 5.28 territories ha^{-1} in 2003–2009, which was much less variable than the warbler densities estimated from the CIC point counts. Thus, the point counts are also likely to bias density estimates, depending upon annual and seasonal variation in breeding behavior of the study species.

The CART model provides a useful tool for assessing the effect of habitat loss on the Catalina warbler population. Fires have caused extensive warbler habitat degradation and destruction over the past decade (Figure 3). For example, there were a number of wild fires on this island since 1999: Goat Harbor Fire in 1999 (108 ha burned), Airport Fire in 2003 (51 ha burned), and Empire Fire in 2006 (430 ha burned). The most recent human–ignited fire in 2007, Island Fire, burned 1,900 ha, which was equivalent to approximately 4,800 warbler territories out of total 37,400 warbler territories on the island, based on the predictions of the CART model. Our data indicate that this fire destroyed approximately 12.8 % of warbler habitat on the island. An increase in the frequency of extreme droughts and human ignitions could therefore have a detrimental effect on the availability of warbler habitat on Santa Catalina Island.

The modeling framework we present here provides a foundation for understanding how the distribution and abundance of *O. c. sordida* and other California Channel Island–endemic bird populations could respond to habitat changes in the coming decades. Our models could be improved in two key ways. First, we need data on territory density and reproductive success over a broader range of habitat types and in wet versus dry years. Second, avian point count surveys should be conducted in March when many bird species initiate breeding on the California Channel Islands. We believe that the use of independent datasets to parameterize and validate habitat–specific abundance models (Gale et al. 2009) will advance our understanding of avian habitat selection.

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Table 1. Estimated density of orange–crowned warblers (individuals ha^{-1}) for Santa Catalina Island, California, from May surveys, 2002 to 2006. Parameter and variance estimates taken from the model with the smallest second–order Akaike's Information Criterion (AIC*c*; see Methods).

Year	Precipitation (cm)[1]	Model (key[2]+adjust.[3])	n[4]	*P*[5]	Density (warblers ha^{-1})	Density 95% CI
2002	11.9	HR + CO	18	0.62	**0.53**	0.28–1.01
2003	38.7	HR + HP	134	0.60	**4.18**	2.70–6.48
2004	15.2	HR + HP	90	0.37	**1.68**	1.06–2.67
2005	64.6	HR + CO	105	0.48	**4.32**	2.50–7.45
2006	22.5	HR + SP	158	0.11	**3.75**	2.75–5.10

[1] Winter precipitation from July $_{\text{year(x–1)}}$ to June $_{\text{year(x)}}$; adapted from Morrison and Bolger (2002).

[2] Key functions: HR (hazard–rate).

[3] Adjustment terms: CO (cosine), SP (simple polynomial), HP (hermite polynomial).

[4] n = the number of observations.

[5] *P* value of Goodness of Fit χ^2 test for detection function.

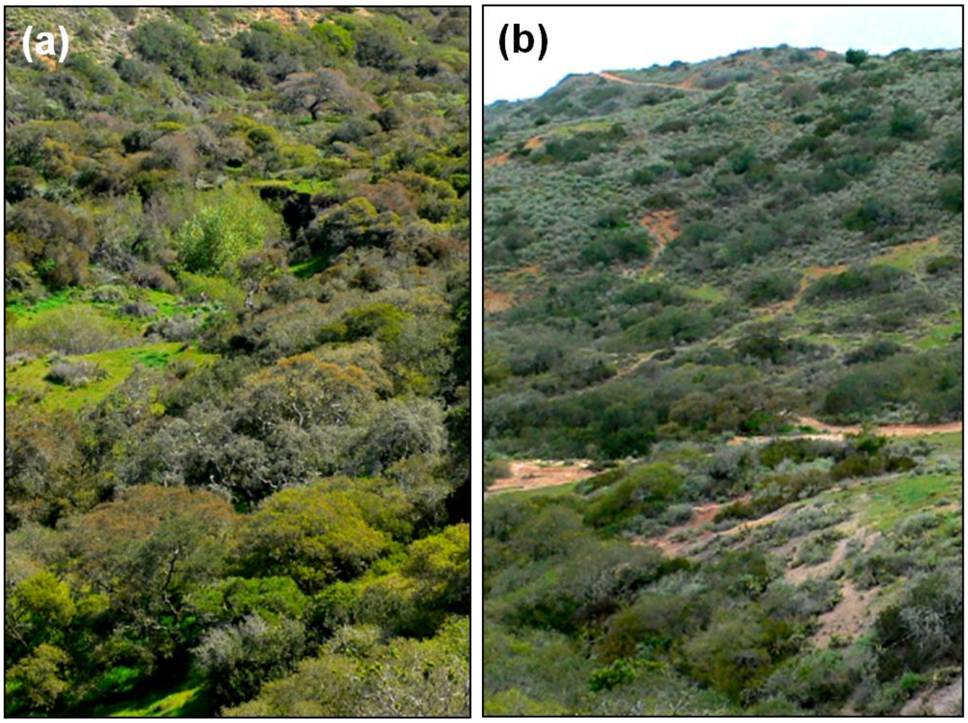

Figure 1. Oak–dominant habitats along a mesic–xeric gradient of breeding orange–crowned warblers in Bulrush Canyon on Santa Catalina Island, California: (a) a mesic drainage habitat and (b) a xeric ridge habitat

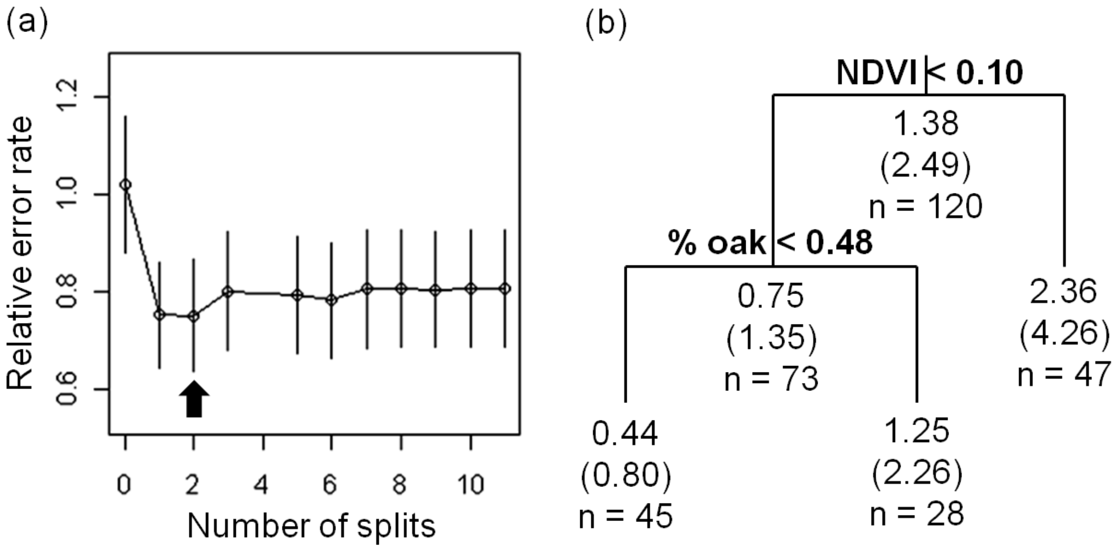

Figure 2. Graphical summary of model calibration for CART to predict orange–crowned warbler neighborhood density Bulrush Canyon, Santa Catalina Island, California, in 2006–2008. (a) Cross–validated relative error rate as a function of the number of splits; the best–fitting model has two splits and exhibits the minimum misclassification rate and the smallest tree size. (b) Decision tree for the best fit CART predicting neighborhood density in relation to Normalized Difference Vegetation Index (NDVI) and percent oak coverage (%); splits are labeled with conditional cut–off values (e.g., If NDVI is less than 0.10, then territory density is 0.75 territories neighborhood^{-1}. Otherwise, it is 2.36 territories neighborhood^{-1}); nodes denote the predicted number of territories within a neighborhood scale (with the converted territory density per hectare area in parentheses) and the number of cases assigned to parameterize the model (n).

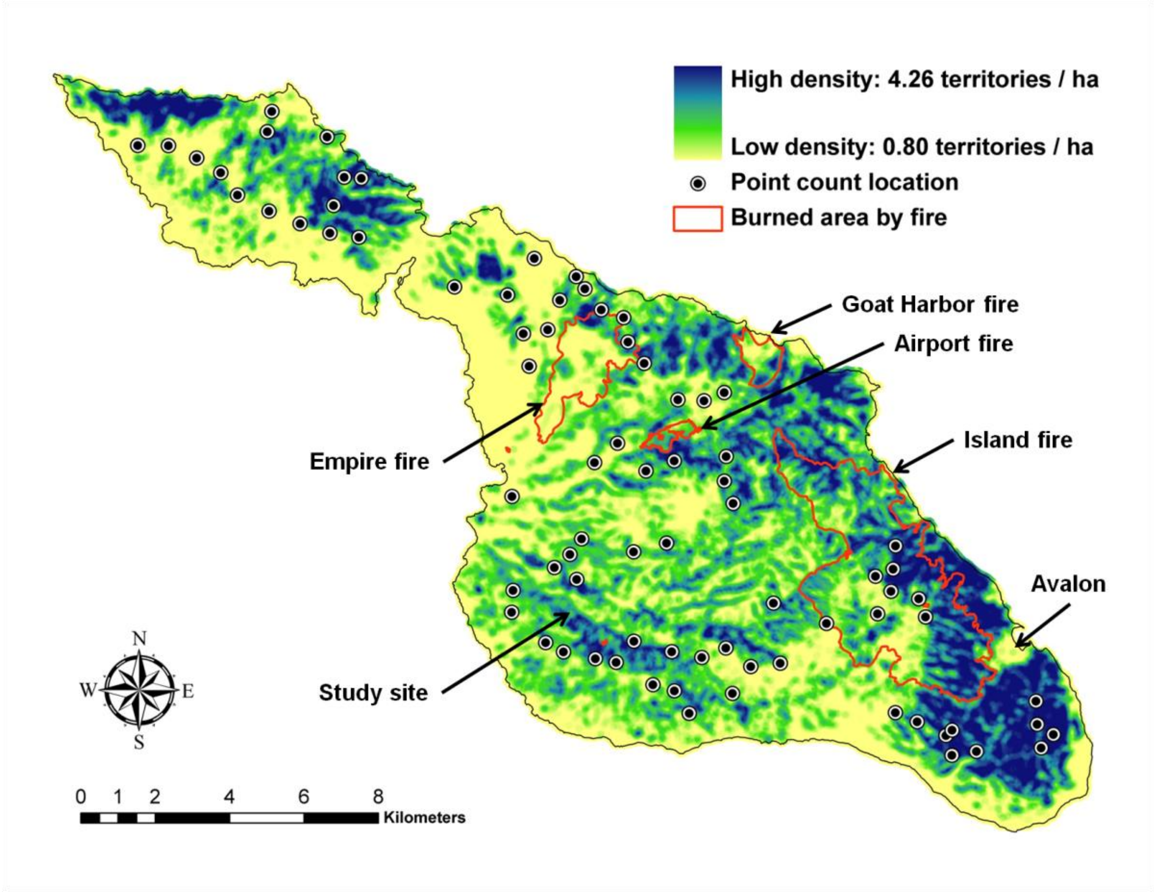

Figure 3. Territory density of breeding orange–crowned warblers on Santa Catalina Island, California, as predicted by the best–fit CART model. Black dots indicate point count survey locations. Red polygons delineate areas burned by wildfires in 1999–2007.

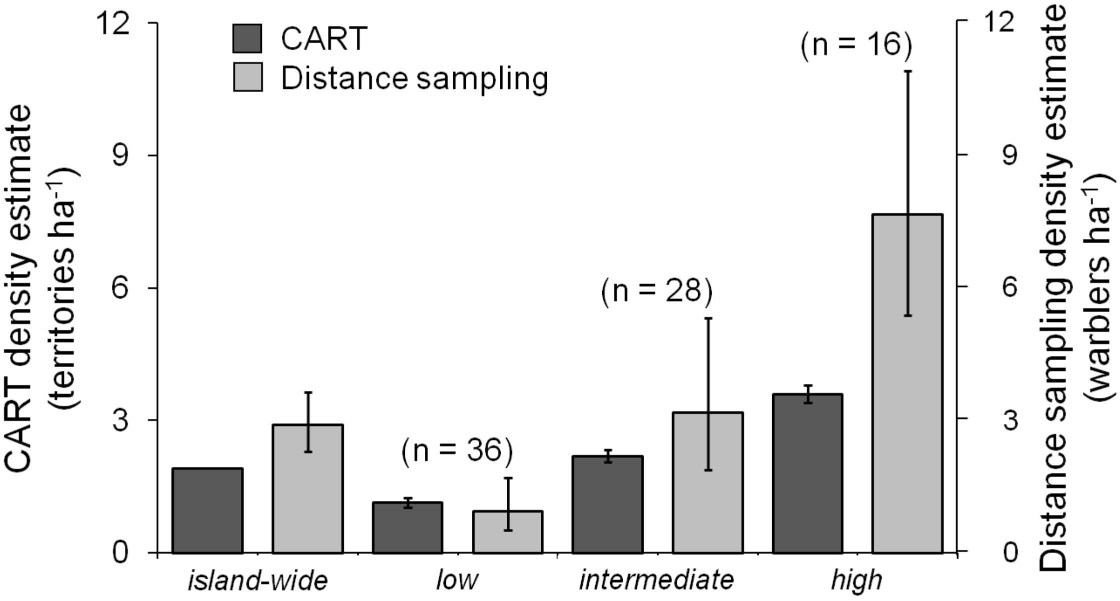

Figure 4. Evaluation of the CART habitat model using habitat–specific distance sampling density estimates: territory density (the number of territories ha^{-1}) from the CART model and warbler density (the number of individuals ha^{-1}) from the distance sampling analyses. Each bar represents mean density estimate with 95% confidence intervals with the number of survey points (See the text for the statistics).

CHAPTER 2: LIFE HISTORY AND BREEDING DENSITY SHAPE MALE AGGRESSIVE BEHAVIOR IN A PASSERINE BIRD

ABSTRACT

Variation in male–male aggression between populations of territorial animals can reflect differences in life history and competitive environments as well as differential strategies of individual recognition. Life history theory predicts that males with high residual reproductive value should avoid risk–taking behavior to minimize the cost of current reproduction. Competitive environments such as those characterized by high conspecific density should, however, favor aggressive males that can acquire limited resources. A large body of intrapopulation studies suggests that male aggression can be modulated by familiarity with territorial neighbors (dear enemy hypothesis), and that reduced aggression to neighbors versus strangers can enhance fitness. Nevertheless, in the context of intense competition, aggression level can be shaped either by "dear enemy" recognition to minimize the cost of frequent territorial encounters or by increased aggression towards neighbors to defend limited resources (nasty neighbor hypothesis). We conducted a simulated territory intrusion experiment using neighbor–stranger songs to examine how aggression level, mediated by individual recognition strategies, differs in the context of life histories and breeding densities in two populations of orange–crowned warblers (*Oreothlypis celata*). Males from a population on Santa Catalina Island, California, had high adult survival but bred in high density, compared to males from a population in Fairbanks, Alaska. We found that California males responded more aggressively towards conspecifics than Alaska males. Furthermore, the effect of song stimulus (neighbor vs. stranger) varied between populations: California males reacted more strongly to neighbors, and Alaska males reacted more strongly to strangers. Our results indicate that high breeding densities and intense territory defense against neighboring individuals lead to elevated male–male aggression, regardless of neighbor familiarity.

INTRODUCTION

We know little about how life history and conspecific competition interact to shape the patterns of male aggressive behavior. Territoriality functions to increase access to resources, breeding spaces, and mates (Brown 1964), but territorial aggression can be costly because aggressive individuals can experience physical injuries, and reduced survival, and often contribute relatively less parental care (Wingfield et al. 1990, 2001), implying that this male aggressive behavior can be related to life history strategies. Life history theory predicts that males with shorter life expectancy should invest more time and energy into current reproductive effort than into self–maintenance, compared to long–lived males (Stearns 1992, Ricklefs and Wikelski 2002, Roff 2002). Indeed, elevated aggression toward conspecifics and boldness towards predators, as a form of risk–taking behavior, has been documented to be more likely in species or populations with faster life histories (Clark 1994, Ghalambor and Martin 2001, Wolf et al. 2007). On the other hand, competitive environments, such as those with high conspecific densities and limited food, have been thought to select for elevated territoriality to acquire and defend resources (Brown 1964, Grant 1993, Stamps 1994).

Life history theory and ecological theory can make different predictions about the strength of male territorial aggression, particularly for widespread species whose populations differ in their migratory behavior. Long–distance migratory populations that exhibit relatively high adult mortality mostly caused during migration (Sillett and Holmes 2002) breed at high latitudes that are typically characterized as having access to relatively abundant food (Levey and Stiles 1992). In the context of a life history continuum, males at the fast end with relatively lower adult survival is likely to invest more into current reproduction (*sensu* Ricklefs and Wikelski 2002), which may result in higher investment in territorial behavior for resource defense while breeding and vice versa in males at the slow end. However, in the context of resource competition, resident or short–distance migrant populations that breed at low latitudes and exhibit relatively low adult mortality and annual fecundity are considered to have population sizes near carrying capacity with stronger resource competition (Ashmole 1963, Cody 1966, MacArthur 1972, Ricklefs 1980). It is possible that these populations may favor elevated male territorial aggression for resource defense in a highly competitive environment. Despite a majority of studies of the factors affecting individual variation in male aggressive behavior in single populations, little is known about how such competition interacts with life history variation to shape the strength of male aggressive behavior along a latitudinal gradient.

The level of territorial aggression in a population can be also mediated by individual recognition, a precondition to complex social interactions that can moderate aggressive behavior to enhance fitness (see Kroodsma and Miller 1996). The “dear enemy" hypothesis predicts that individuals should be less aggressive towards known individuals to avoid the costs associated with repetitive territorial encounters (Fisher 1954, Trivers 1971, Ydenberg et al. 1988). Support for the dear enemy hypothesis has been found in studies of many taxa, including insects (Heinze et al. 1996), fish (Frostman and Sherman 2004), amphibians (Jaeger 1981), reptiles (Whiting 1999), birds (Eason and Hannon 1994), and mammals (Price et al. 1990). Reduced aggression toward familiar individuals can optimize time and energy expenditure for territory defense and maximize shared mutual benefits among neighbors (Wilson 1975). Conversely, the "nasty neighbor" hypothesis predicts that selection should favor territorial owners that respond more aggressively towards neighbors (Temeles 1994). This phenomenon is thought to occur when intraspecific resource competition is strong. However, territorial males may exhibit both strategies for individual recognition depending on conditions such as high population density and resource limitation: "dear enemies" if being aggressive towards neighbors is too costly, or "nasty neighbors" when resource sharing is not negotiable (Müller et al. 2007, Briefer et al. 2008, Newey et al. 2008).

We used simulated territorial intrusion experiments to examine the factors that shape variation in male aggression and individual recognition in two populations of orange–crowned warblers (Parulidae: *Oreothlypis celata*) that differ in breeding densities and life history: *O. c. celata* in Alaska (hereafter Alaska warblers), and *O. c. sordida* on Santa Catalina Island, off the coast of southern California (hereafter California warblers). These two populations have contrasting life history strategies (Horton et al. 2010, Sillett et al., in prep.). The Alaska population has a fast life history (Ricklefs and Wikelski 2002), with low annual survival probability (0.40 ± 0.16 for males) and large clutch sizes

(5–7 eggs), compared to the slow life history of the California population, which has high annual survival probability (0.75 ± 0.02) and small clutch size (2–4 eggs). The Alaska population also breeds at a low density, and presumably in a less competitive, environment with high level of food, compared to the California population (0.48 ± 0.02 territories ha^{-1} in Alaska vs. 4.40 ± 0.24 territories ha^{-1} in California; Yoon et al., in prep.). These differences in life history and conspecific density yield contrasting predictions about male aggressive level and individual recognition. From the life history perspective, California males, which have, on average, relatively high residual reproductive value, should exhibit relatively lower aggression towards conspecifics for territory defense compared to Alaska males. From the resource competition perspective, high conspecific density should cause California males to have elevated aggression towards neighbors relative to Alaska males.

METHODS

Study Sites and Populations

The orange–crowned warbler is a widespread, socially monogamous breeder in western and northern North America (Sogge et al. 1994). We studied the Alaska population on an 88–ha plot near Fairbanks, Alaska (64°47´41´´N, 147°53´45´´W) and the California population on a 14–ha plot on Santa Catalina Island (33°20´56´´N 118°26´59´´W) from 2007–2008. Males arrived and established territories in late–February in California and in mid–May in Alaska. Territorial establishment in both populations was characterized by frequent male singing and territorial fights among neighboring males, but was less synchronized in California (occurring over approximately one month) than in Alaska (occurring over approximately two weeks). This corresponded to a relatively longer breeding season in California (100–120 days) than in Alaska (50–60 days). Renesting due to predation was more frequent in the California population than in the Alaska population (daily nest mortality: 0.20 ± 0.01 in Alaska vs. 0.40 ± 0.01 in California; Horton et al. 2010). From the combined effect of season length and nest predation rate, fertile females were present for a greater proportion of the breeding season in California relative to Alaska [breeding synchrony index for the average percentage of females that are fertile per day during the breeding season (Kempenaers 1993): 42.95 ± 2.63 % in Alaska vs. 32.23 ± 4.92 % in California; Horton et al., in prep.]. Males guarding fertile females in both populations often engaged in intense fights with neighboring males, but were generally unresponsive to conspecific playbacks (J. Yoon, personal observation).

Warblers at both study sites were color–banded, and their nesting success was monitored to facilitate the collection of individual behavioral data. Adults were captured with mist–nets and banded with a unique combination of three colored leg bands and a numbered aluminum U.S. Geological Survey band to identify each individual. Individuals’ sex and age were determined based on morphological and plumage characters (Pyle 1997). All warbler territories were mapped by observing movements and boundary disputes of banded males and females throughout the breeding season. To facilitate individual identification and territory mapping (from 04:00 am to 12:00 pm AKDT in Alaska and from 06:00 am to 12:00 pm PDT in California), our study plots were delineated into 25 m x 25 m grids with flagging, which were incorporated into ArcGIS version 9.1 (ESRI Inc. 2005). We marked the locations of individual warblers on an aerial photograph that had waypoints of grids, and we took waypoints of banded individuals using a GPS unit, which all were then transferred and updated in ArcGIS every two weeks. To monitor warbler breeding status, we found nests of 30–40 warbler pairs per site each breeding season and monitored them once every two days for the status of breeding stages.

Simulated Territorial Intrusions

We recorded songs from 30–40 focal males per study site to obtain song stimuli used in simulated territorial intrusion experiments (hereafter STIs). Songs were recorded in March in California (7:00am–11:00am PDT) and May in Alaska (4:00am–8:00am AKDT) with a parabolic microphone (P–650, Dan Gibson Electronics) and a MiniDisk recorder (MZ–NH1, Sony Inc.) at a distance of 5–10 m from singing birds. Males in both the California and Alaska populations used a single song type, a thin and fast trill in Alaska vs. a slow and lower–pitched trill in California, during the breeding season and over multiple years (J. Yoon, personal observations). In addition, we expected that playbacks using a single song type in orange–crowned warblers were less likely to hinder individual recognition (i.e., neighbors vs. strangers), compared to species with larger repertoires (Falls 1982). Songs of each focal male were assembled to create a five–min song stimulus that contained a total of 30 songs using program Syrinx (John Burt, www.syrinxpc.com, Seattle, WA, U.S.A.).

We carried out STI sessions using neighbor and stranger song playbacks to 27 territorial males in each population. Neighbors were defined as a male adjacent to a target territory, and strangers were more than two territories away from the target male. The stimulus consisted of a loudspeaker and a male *O. celata* taxidermic mount that were placed in the approximate center of a target territory. We also considered sufficient space that allowed target males to freely give any response, including aggressive flights in a range of 0–5 m from the stimulus and a perch for the male to stay in a range of 0–2 m. We used a portable speaker (frequency response: 150 Hz – 20 kHz; Creative, Inc.) connected to an MP3 player (SanDisk, Inc.). The observer was concealed 5 m from the stimulus to record behavioral responses of the target male, and waited five minutes before starting the song playback to minimize any modification of the target male's behavior. We conducted two sessions of 5–min STIs per male; one session per male was an STI with a neighbor's song, and the other was an STI with a stranger's song. STI sessions per male were at least 24 hours apart, and each male was presented with a random order of neighbor and stranger songs. The use of randomly selected songs of neighbors and strangers was designed to avoid pseudoreplication (McGregor et al. 1992). During STIs, we recorded a suite of vocal and physical response variables: the number of calls and songs, the number of flights 0–2 m from the stimulus (hereafter proximate flights), the number of flights 2–5 m from the stimulus (hereafter distant flights), responsiveness (5 minus the minute that a male approached within 0–5 m from the stimulus; McGregor 1992; hereafter latency time), and amount of time that the male stayed within 0–2 m from the stimulus. Our STIs were conducted during the focal male's incubation period, which typically occurred in April for the California population and in June for the Alaska population. The California population did not breed in 2007 due to an extreme drought (Langin et al. 2009), but STIs were conducted because males were paired with females and defended their territories until the beginning of May (J. Yoon, personal observations).

Statistical Analyses

We used a sequence of statistical methods to characterize male aggressiveness and analyze the STI data. First used a Principal Component Analysis (PCA) was used to generate an aggression score from the six correlated responses (i.e., the number of calls, the number of songs, the number of proximate flights, the number of distant flights, the latency time, and the time stayed near the stimulus) for each focal male (McGregor 1992). We next analyzed male aggressive response to the STIs with a general linear mixed model fit with restricted maximum likelihood (REML). Fixed predictor variables were site (Alaska vs. California), stimulus type (neighbor vs. stranger songs), year, playback order, and all two–way interactions. Individual male band number was included as a random effect. Fisher's least significant difference (LSD) was used to examine significant interaction effects. Our initial analyses revealed no significant effects of playback order, year, or interactions involving these variables ($P > 0.50$); therefore, we excluded year and playback order from the final analyses presented here. All statistical analyses were performed in SPSS version 13.0 (SPSS Inc., Chicago, IL). We did not need to transform any variables to meet model assumptions. Behavioral responses are presented as means ± 1·standard error (SE).

RESULTS

Alaska and California males had different patterns of behavioral response to our STI experiment (Figure 5). The first principal component (PC1) accounted for 40.6 % of the total variance in male aggressive behavior (eigenvalue = 2.43) and represented a gradient from relatively aggressive to passive response to the STI experiment (Table 2).

No other PC scores had eigenvalues ≥ 1 and were thus excluded from subsequent analysis. PC1 was positively correlated with the number of calls, proximate flights, distant flights, latency time, and the time stayed near the stimulus in both populations; number of songs was negatively correlated with PC1 in Alaska and uncorrelated in California (Table 2).

Our mixed model analysis of variance revealed that male aggression level and relative response to neighbors and strangers differed between Alaska and California males (Figure 6). Overall male aggression was higher in California than in Alaska, but the relationship between male aggression and song stimulus type differed between warbler populations ($_{\text{SITE}}\, F_{1,52} = 22.41$, $P < 0.001$; $_{\text{STIMULUS}}\, F_{1,52} = 0.02$, $P = 0.90$; $_{\text{STIMULUS X SITE}}\, F_{1,52} = 25.94$, $P < 0.001$). Specifically, the Alaska males responded less aggressively towards neighbor songs compared to stranger songs was significant (LSD: $F_{1,26} = 11.53$, $P = 0.002$; see Figure 6). In contrast, the California males responded more aggressively towards neighbor songs (LSD: $F_{1,26} = 14.63$, $P = 0.001$; Figure 6).

DISCUSSION

We conducted STIs using song playbacks to investigate natural variation in male aggressive behavior across the two populations that vary life history and conspecific density affected male aggression in orange–crowned warblers breeding at two latitudes. California males were predicted to exhibit either reduced aggression as a risk–adverse consequence of relatively high residual reproductive value associated with a slower life histories (Ricklefs and Wikelski 2002), or elevated aggression due to high breeding density and thus a highly competitive breeding environment. Our results did not support the prediction derived from life history theory. Instead, our data indicate that males from a population in California exhibited elevated territorial aggression (i.e., more frequent call notes, flights, quicker response times to the stimulus, and more time spent near the stimulus) relative to males from a population in Alaska. This is consistent with the idea that high conspecific densities as observed on Santa Catalina Island may lead to greater levels of male territorial aggression. A similar pattern has been found with European oystercatchers (*Haematopus ostralegus*): birds foraging on preferred mussel (*Mytilus edulis*) beds increased aggressiveness at higher competitor densities, but this density–dependent effect disappeared at low densities (Goss–Custard et al. 1984). Male orange–crowned warblers on Santa Catalina Island also maintained elevated testosterone levels throughout the breeding season compared to Alaska males (Horton et al. 2010). Elevated testosterone levels are often associated with high population density in other passerine species (Ball and Wingfield 1987, Wingfield and Hahn 1994). Therefore, our results suggest that interpopulation variation in male aggression in orange–crowned warblers were likely to be explained by the conspecific competition perspective, rather by the life history perspective.

Nasty Neighbors in California

In neighbor–stranger discrimination, California males responded more aggressively toward conspecific neighbors than to strangers (i.e., nasty neighbors; Temeles 1994). Mounting evidence suggests that breeding density, as a potential measure of competition, is linked with the level of territorial aggression in the context of individual recognition of conspecific neighbors. Brown (1969) also argued that territorial behavior should be driven by intense resource competition in high density populations.

Warbler territory density on our Santa Catalina Island plot was approximately ten times higher than territory density in Alaska (Yoon et al., in prep.). Moreover, little to no buffer existed between warbler territories on Santa Catalina Island, whereas territories in Alaska were often separated by unoccupied space. Conspecific neighbors share a common interest in resource use so that intense competition among neighbors should occur potentially through recognizing one another as a threat (Temeles 1994). This nasty neighbor hypothesis has been supported by a number of observational studies of conspecific competition for resources or mates. Female northern harriers (*Circus cyaneus*) on winter feeding territories retaliated against neighbors with a greater intensity of territorial aggression than against floaters (Temeles 1990). Colonial termite soldiers (*Nasutitermes corniger*) were capable of using chemical cues to discriminate familiar from unfamiliar colonies and responded with relatively higher territorial aggression against unfamiliar colonies (Dunn and Messier 1999). Banded mongooses (*Mungos mungo*) were more likely to vocalize at neighbors compared to strangers (Müller and Manser 2007). Female New Zealand bellbirds (*Anthornis melanura*) exhibited the nasty neighbor phenomenon during the courtship and nestling periods in order to prevent potential polygyny and to compete for food against neighboring females (Brunton et al. 2008).

Nasty neighbor recognition among California males could also be due to their longer breeding season, high nest predation (see Horton et al. 2010), and the resulting asynchrony in breeding stage among territories. Asynchronous breeding could increase the opportunities for mate competition between neighbors because some proportion of males would always be mate–guarding fertile females, whereas other males with incubating females would be emancipated from mate–guarding and seek additional mating opportunities (Birkhead and Biggings 1987, Birkhead and Møller 1992). Male orange–crowned warblers on Santa Catalina Island appear to compete aggressively for access to fertile females and thus extra–pair matings occur throughout their three to four month–long breeding season (J. Yoon, personal observations). In Alaska, the orange–crowned warbler breeding seasons lasts only six to eight weeks, and nest predation rates are relatively lower (Horton et al. 2010; also lower nest predation at high latitude; see McKinnon et al. 2010), which appears to produce a comparatively synchronized breeding season and fewer opportunities for sustained and aggressive interactions between males for guarding sexually receptive mates and seeking additional mating opportunities in different breeding stages.

Dear Enemies in Alaska

A higher tolerance against known neighbors is thought to reduce the frequency of costly interactions among neighbors (i.e., dear enemies; Fisher 1954). Alaska males responded less aggressively toward neighbors than toward strangers. Conspecific competition is likely reduced at high latitudes due to a seasonal burst of food abundance and the relatively small number of breeding pairs caused by higher adult mortality (Ashmole 1963, Ricklefs 1980, Levey and Stiles 1992). Resources and nest sites are thus less likely to be a limiting factor for the Alaska population. In addition, relatively low breeding densities, larger territory sizes, and more unoccupied space between territories probably reduced the need for aggressive interactions between neighboring males in Alaska. Dear enemy recognition therefore appears to be a reliable strategy in this less competitive context.

We also found that Alaska males respond less aggressively towards neighbors than toward strangers because the strength of competitive interaction is relatively low. However, many experimental and observational studies have documented a conditional strategy in dear enemy recognition in which neighbors fail to cooperate when the frequency of interactions increases or when resources become limited. For example, male hooded warblers (*Wilsonia citrina*) increased territorial aggression toward neighbors after repeated intrusions at the shared boundaries (Godard 1993). Male sand fiddler crabs (*Uca pugilator*) initially exhibited the dear enemy phenomenon, but resident–resident territorial contests increased when the accessibility of the number of burrows was experimentally reduced (Pratt and McLain 2006). Additional experimental work is needed to test if orange–crowned warblers in Alaska would adjust their response to neighbors in a similar fashion.

Interpopulation Variation in Male Aggression towards Strangers

Male aggression toward strangers, such as unknown individuals or non–territorial floaters, is still higher in California than in Alaska. We suspect that floaters are more common (see Langin et al. 2009), and thus territory incursions from floaters are more frequent on Santa Catalina Island than Alaska. A latitudinal gradient in territory turnover rate and the difference in number of floaters between populations can be caused by differential adult survival. For example, populations in the tropics are thought to include a large number of floaters due to longer periods of territory tenure (Smith 1978, Zack and Stutchbury 1992). The return rate of California males was 66.71 ± 1.78 % (n = 6 years) whereas that of Alaska males was 44.12 ± 5.88 % (n = 2 years). Although measuring floater population size is difficult, many non–territorial males were captured while target–netting for territorial males in the California population, whereas this rarely occurred in Alaska (J. Yoon, personal observation). These non–territorial males also tended to establish territories where they were captured in previous years if the previous owner did not return. Therefore, higher overall male aggression toward strangers on Santa Catalina Island may reflect intense competition for territory sites in this long–lived, resident population.

Our experimental design revealed not only how male aggression level differed between populations, but also how individual recognition strategies mediated male territorial behavior. Male territorial aggression in orange–crowned warblers appears to be explained by the intensity of conspecific competition for space and also presumably for additional mating opportunities throughout the breeding season. Divergent male aggression between Alaska and California may be also shaped by different frequencies of territorial incursions in the two populations. Further research is needed to determine if life history plays an important role in shaping aggressive behavior in other species of territorial animals.

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Table 2. Pearson correlation coefficients between six aggressive behaviors and PC1 (see the methods) for male orange–crowned warblers breeding in Fairbanks, Alaska and on Santa Catalina Island, California.

	Alaska (n = 54)		California (n = 54)	
Response type	Coefficient	*P*	Coefficient	*P*
Calls	**0.66**	< 0.001	**0.66**	< 0.001
Songs	**–0.44**	0.001	–0.16	0.259
Proximate flights	**0.59**	< 0.001	**0.71**	< 0.001
Distance flights	**0.48**	< 0.001	**0.71**	< 0.001
Latency time*	**0.83**	< 0.001	**0.73**	< 0.001
Time stayed	**0.35**	0.009	**0.63**	< 0.001

* Responsiveness (5 minus the minute that a male approached within 0–5 m from the stimulus)

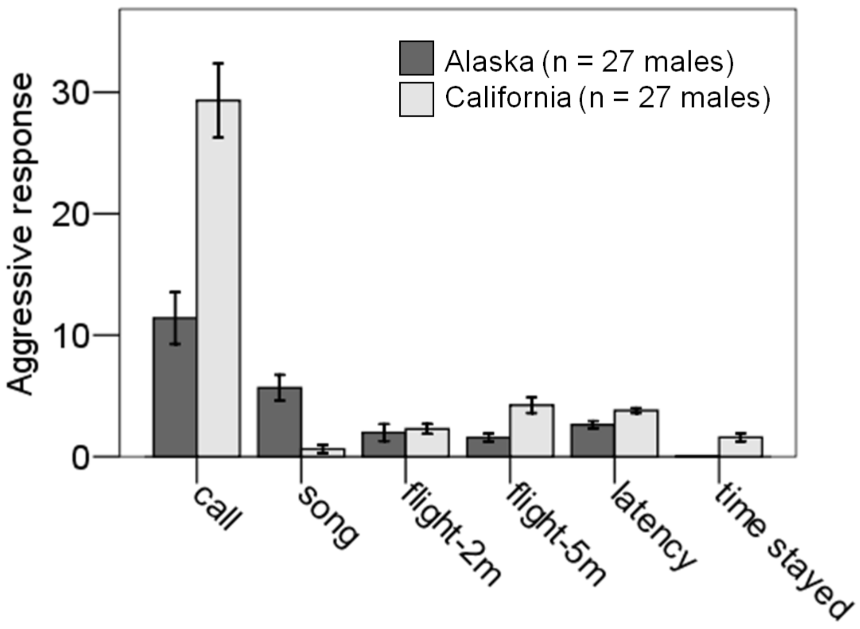

Figure 5. Six behavioral descriptors of male aggression in breeding orange–crowned warblers in Fairbanks, Alaska and on Santa Catalina Island, California in response to territorial intrusions simulated by song playbacks and a taxidermy mount: the numbers of calls, songs, proximate flights in a range of 0–2 m from the stimulus, distant flights in a range of 2–5 m from the stimulus, rescaled latency time (i.e., responsiveness; 5 minus the minute that a male approached within 0–5 m from the stimulus), and the minute time stayed in a range of 0–2 from the stimulus. Bars represent means ± 1 SE.

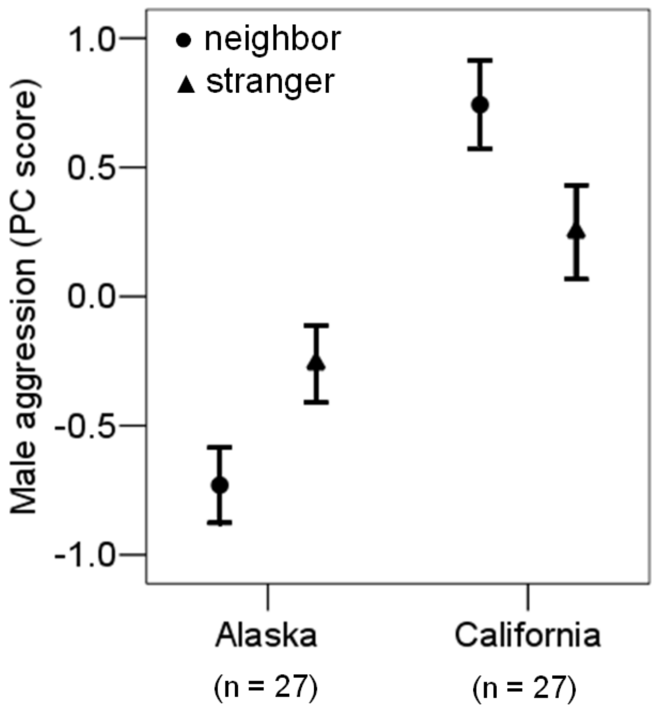

Figure 6. Patterns of aggression level and response to neighbors versus strangers of male orange–crowned warblers breeding in Fairbanks, Alaska and on Santa Catalina Island, California in response to neighbor and stranger song playbacks. Error bars represent means ± 1 SE of the first PC score, which increases with male aggression (see the results).

CHAPTER 3: GEOGRAPHIC VARIATION IN PARENTAL BEHAVIOR OF ORANGE–CROWNED WARBLERS: ECOLOGICAL CORRELATES OF MALE AND FEMALE POST–HATCHING CARE

ABSTRACT

Comparative studies of populations occupying different environments can provide insight into the conditions that lead to differences in parental care strategies. In birds, differences in food limitation, extra–pair paternity, and climate has been suggested to drive variation in the amount and type of parental care provided by each sex. We tested these hypotheses during the post–hatching period in two populations of the orange–crowned warbler (*Oreothlypis celata*) breeding near the northern limit of its geographic range in Fairbanks, Alaska (*O. c. celata*; 64°N) and near the southern limit of its breeding range on Santa Catalina Island, California (*O. c. sordid*; 33°N). We videotaped nests for 3 hour and 24 hour sessions to obtain parental care data. In Alaska, we found that males provided the majority of food to offspring, and that females spent a large amount of time brooding young. In California, males and females contributed equally to nestling provisioning and females brooded young significantly less than females in Alaska. Lastly, despite a longer day length and a longer active period, we found Alaska parents delivered a similar amount of food to the nest as their California counterparts. None of the hypotheses we tested provided a simple explanation to the patterns we observed. Food limitation and breeding density likely result in a more competitive environment in the California population compared to the Alaska population, which explained high male–female food delivery rates in California, but did not explain the patterns of male–female food delivery rates. Likewise, extra–pair paternity was not significantly different between populations. Temperatures during the breeding season are slightly warmer in Alaska, which fails to predict the higher brooding and lower food delivery rates of females. We propose that females in Alaska brood at a high rate to facilitate rapid nestling growth and males compensate for reduced female provisioning by increasing their relative food delivery rate during the short breeding season with high food levels. In California, we propose that high levels of nestling provisioning by both parents results in a significantly higher nestling provisioning rate which may increase the chances of offspring recruiting into the highly competitive island population.

INTRODUCTION

A central tenet of life–history theory is that investment in current reproduction comes at the expense of future reproduction and survival (Williams 1966, Stearns 1992, Roff 2002). In organisms that provide parental care for their offspring, the optimal level of parental investment should therefore reflect the trade–offs between the fitness benefits and costs associated with care over the lifetime of the adults (Trivers 1972, Clutton–Brock 1991). However, such trade–offs are complicated in organisms that exhibit biparental care (i.e. where both sexes cooperate to jointly care for dependent young) because of the inherent conflict over how much each sex should invest in offspring care versus other fitness related activities (Houston et al. 2005). For example, males might maximize lifetime reproductive success by contributing more to offspring care than to self–maintenance, or alternatively seek out additional mating opportunities at the expense of parental care depending on who they are mated to (Emlen and Oring 1977, Burley 1988, Westneat and Sargent 1996, Sheldon 2000, Ricklefs and Wikelski 2002, Chapman et al. 2003, Magrath and Komdeur 2003). To date, most studies of sexual roles during parental care have focused on how such conflicts play out by evaluating the changes in parental effort of one sex in response to changes in parental effort of the opposite sex (reviewed in Harrison et al. 2009). Yet, substantial variation also exists between populations and species in the amount and type of parental care provided by each sex, and the evolutionary, ecological and social factors responsible for this variation remains unclear (e.g. Silver et al. 1985, Møller and Birkhead 1993, Reynolds and Székely 1997, Schwagmeyer et al. 1999, Møller and Cuervo 2000, Cockburn 2006, Olson et al. 2009). Birds in particular have played an important role in developing and testing theory on the roles of the sexes during the period of parental care (Lack 1968, Cockburn 2006). In species with altricial young, both parents often provision offspring with food, and this form of parental care is thought to represent a significant energetic and survival cost to the parents (Wittenberger 1979, Clutton–Brock 1991, Ketterson and Nolan 1994, Roff 2002, Liker and Székely 2005). Important ecological factors that have been suggested to influence the costs and benefits of providing care and leading to differences among populations and species in the effort of the sexes include food limitation, sexual selection, and climate (Orians 1969, Emlen and Oring 1977, Clutton–Brock 1991, Badyaev and Ghalambor 2001).

Food limitation has long been thought to be a major ecological factor directly and indirectly shaping levels of parental care (Lack 1954, 1968, Martin 1987). Food limitation is thought to have direct effects on the amount of parental care provided by each sex when females are unable to sufficiently provision offspring alone, thus favoring increased male participation in provisioning offspring (Emlen and Oring 1977, Whittingham 1989, Leisler et al. 2002, Strong et al. 2004). Evidence supporting the direct effects of food limitation on the sexes comes from male removal experiments that find female–only provisioning tends to result in lower nestling quality, elongated nestling period, lower fledgling survival, or longer inter–brood intervals (Gowaty 1983, Lyon et al. 1987, Bart and Tornes 1989, Dunn and Roberston 1992, Bjørnstad and Lifjeld 1996, Lynn and Wingfield 2003). However, the magnitude of these effects varies between studies, and the ability of females to raise offspring by themselves may depend on the degree to which food limitation exists in a population (e.g. Dunn and Roberston 1992). Alternatively, food limitation may indirectly influence parental care if males are forced to shift time and energy towards increased territory defense at the expense of provisioning offspring (challenge hypothesis: Wingfield et al. 1990). Such conditions have been invoked in competitive environments such as high breeding densities, which result in elevated aggression and levels of testosterone (T) that in turn reduce male paternal behaviors (Wingfield et al. 1990, Veiga et al. 2002). For example, correlative and experimental studies show that males with higher T increase singing rates, but decrease provisioning rates (Dittami et al. 1991, Ketterson et al. 1992, Beletsky et al. 1995, Hoi–Leitner et al. 2000, Van Roo 2004). Thus, food limitation may directly favor increased male parental care because females are unable to deliver sufficient food on their own, or may indirectly favor reduced male care when competition for resources and density–dependent interactions results in agonistic behaviors that inhibit male parental care.

Variation in the strength of sexual selection is a commonly invoked mechanism constraining the amount of male parental care (Trivers 1972, Emlen and Oring 1977). Theoretical and empirical work suggests that males should alter the amount of parental care that they provide in relation to their confidence of paternity (Dixon et al. 1994, Møller and Cuervo 2000, Hunt and Simmons 2002) and as a function of time spent seeking alternative mating opportunities such as extra–pair matings (Ketterson and Nolan 1994, Magrath and Elgar 1997; see also Magrath and Komdeur 2003). Environmental factors that influence the timing and accessibility of fertile females, such as breeding synchrony and density have been suggested to drive variation in extra–pair matings between populations (Møller and Birkhead 1992, 1993, Westneat and Sherman 1997, Neudorf 2004). High breeding synchrony has been suggested to increase extra–pair matings because it allows females to simultaneously compare the displays of multiple males and choose which males to mate with during the short fertile period (breeding synchrony hypothesis: Stutchbury and Morton 1995, Stutchbury 1998, Schwagmeyer and Ketterson 1999, Neudorf 2004). Alternatively, reduced breeding synchrony may favor increased extra–pair matings if it provides males with greater opportunities to seek out fertile females without having to sacrifice guarding their social mates against extra–pair males (breeding asynchrony hypothesis: Birkhead and Biggins 1987, Birkhead and Møller 1992). Similarly, high breeding density could lead to more frequent interactions between neighboring pairs and lead to increased extra–pair matings relative to conditions where breeding pairs are more widely dispersed (Møller and Birkhead 1992, 1993, Westneat and Sherman 1997). Regardless of the underlying mechanism, differences among populations or species in the frequency of extra–pair fertilizations should be correlated with reduced male parental care. Yet, relatively few comparative studies of populations have investigated the relationship among breeding synchrony, density, extra–pair matings, and the role of the sexes during parental care (Westneat and Sherman 1997).

Lastly, climatic factors such as temperature or precipitation during the breeding season may influence the amount and form of parental care in partners. Temperature has been historically thought to be an important determinant of incubation behavior in males and females (Martin and Ghalambor 1999, Conway and Martin 2000), but it may also be important during the nestling period (Webb 1993, Lyon and Montgomerie 1985, Lyon et al. 1987, Dawson et al. 2005, Badyaev and Ghalambor 2001). For example, low temperatures may reduce insect activity and in turn increase the amount of time required for parents to find insectivorous prey and reduce their overall prey delivery to offspring (Avery and Krebs 1984, Low et al. 2008). Alternatively, colder temperatures may favor higher nestling provisioning rates to offset higher thermoregulatory demands of chicks (Lyon et al. 1987, Hoset et al. 2004). Such temperature effects may also be associated with increased precipitation, which can exacerbate the time required to find food (Avery and Krebs 1984, Westerterp and Bryant 1984, Dawson and Bortolotti 2000) and the thermoregulatory costs of the offspring (Walsberg 1993, Wolf and Walsberg 1996, Rauter and Reyer 2000). Variation in these climatic factors along latitudinal or altitudinal gradients could lead to population and species differences in the role of the sexes, particularly if suboptimal temperatures (i.e. either extremes in cold or heat) force parents to allocate more time to buffering nestlings from environmental temperatures (Johnson and Best 1982, Wiebe and Elchuk 2003; see also Lobato 2008). Indeed, in most passerines such buffering behavior falls on females who are responsible for brooding their nestlings, particularly in the early stages of development when the young are unable to thermoregulate (Dawson and Evans 1960, Olson 1992, Konarzewski 1995). Higher levels of female brooding could in turn require males to compensate by assuming a greater proportion of offspring provisioning (Lyon and Montgomerie 1985, Briskie 1995, Martin and Ghalambor 1999, Badyaev and Ghalambor 2001, Johnson et al. 2007). However, relatively few comparative studies have specifically investigated how variation in climatic conditions drives differences in patterns of parental care between populations (e.g. Briskie 1995, Badyaev and Ghalambor 2001, Johnson et al. 2007).

Here, we examine variation in paternal and maternal behaviors for offspring care in two populations of a small passerine, the orange–crowned warbler [*Oreothlypis celata*; formerly the genus *Vermivora* (Chesser et al. 2010)]. We compare two populations that differ in their life histories and ecological conditions. Specifically, we contrast a population that breeds at the northern edge of the breeding range in central Alaska, with a population at the southern edge of the breeding range in southern California. The main goal of the present study was to quantify the patterns of parental behavior during the nestling stage and examine how interpopulation variation in parental care was correlated with: 1) food limitation, 2) breeding density, 3) sexual selection, and 4) climatic variables.

METHODS

Study Species and Areas

The orange–crowned warbler is a small insectivorous passerine with a broad geographic range that spans western and northern North America (Sogge et al. 1994). We studied the parental behavior of two populations that represented the northern and southern ends of the breeding distribution. The northern study site was located near Fairbanks, Alaska (64°50’N, 147°43’W). The Alaska population was studied from 2006–2008 and is a long–distance migrant that winters along the Gulf Coast of the United States and belongs to the *O. c. celata* subspecies, whose breeding range extends east throughout boreal Canada and into the northeastern United States (Sogge et al. 1994). The southern study site was located on Santa Catalina Island, off the coast of southern California (33°22’N, 118°22’W). The California population was studied from 2003–2009 and is a resident or a short–distant migrant to the mainland and belongs to the *O. c. sordida* subspecies, whose breeding distribution is largely confined to the California Channel Islands (Sogge et al. 1994). Parental behavior data were collected in Alaska from 2006 to 2008 and in California from 2005 to 2009, except 2007 when birds failed to breed during a severe drought (Langin et al. 2009).

The two populations and the habitats that they occupied differed in several important respects. The 88–ha study site for the Alaska population was a spruce (*Picea*)–birch (*Betula*)–willow (*Salix*) dominated habitat, characterized by a short breeding season (50–60 days) where the birds experienced nearly continuous daylight during breeding. In contrast, the 14–ha study site for the California population was an oak (*Quercus*) and scrub dominated habitat, with a relatively long breeding season (100–120 days). The two populations also exhibited significant life history differences (see Horton et al. 2010, Sillett et al., in prep.). The Alaska population exhibited lower annual adult survival rates (40 ± 16 %) and larger clutch sizes (5–7 eggs), relative to the California population that had a higher annual adult survival (65 ± 2 %) and smaller clutch sizes (2–4 eggs). Both populations were socially monogamous, only females incubate eggs for 11–12 days in both populations, and males rarely fed their incubating females (Sogge et al. 1994, Sillett et al., in prep.). After hatching, females brooded nestlings, and both parents contributed to nestling provisioning by delivering insect prey items that consisted largely of Lepidopteran larvae (Sogge et al. 1994). However, the length of the nestling period was shorter in the Alaska population (8–10 days), compared to in the California population (10–13 days; Sillett et al., in prep.).

Geographic Variation in Parental Behavior in Partners

We used standardized methods for field data collection at both study sites. Briefly, individual warblers were captured by mist–netting and banded with a unique combination of color bands and a numbered, aluminum U.S. Geological Survey to identify each individual. At the time of capture, their sex and age were recorded, based on plumage and morphological traits (Pyle 1997). We found nests and monitored them approximately once every two days to determine their stage and fate. Nests for approximately 30 territorial pairs were monitored per site during each breeding season.

To quantify paternal and maternal behaviors during the nestling stage, we filmed parental activities at the nest using a small bullet camera (Swann Inc., CA) that was remotely connected to a digital camcorder (DCR–TRV900, Sony Inc., Japan) for the first three hours after sunrise (approximately 03:30am to 06:30am in Alaska; approximately

06:30am to 09:30am in California). Filming occurred when nestlings were three days old after the hatch day (hereafter *early* nestling stage) in both populations and when nestlings were six days old in Alaska and seven days old in California (hereafter *late* nestling stage). These *late* nestling stages were offset by a day to control for the developmental stage; the day of filming corresponded with the time when primary pin–feathers break their sheaths. Comparisons of *early* versus *late* nestling stages allow for comparisons of how parental roles change with the increasing energetic demands of the nestlings as they acquire the ability to thermoregulate. For a subset of nests, we also filmed for 24 hours during the *late* nestling stage to 1) test how representative the three–hour nest observations were of parental behavior, and 2) to test how the longer day–length in Alaska (approximately eight hours longer) influenced the total amount of care provided by parents. The 24–hour recordings used the same bullet camera design, but the camera was connected to a digital video recorder that allowed longer periods of nest videos (Archos 505, Archos Inc., CO).

We transcribed nest videos and quantified the patterns of the following parental behaviors by sex: 1) hourly feeding rate (the number of feeding trips to the nest / hour) from both three– and 24–hour data, 2) hourly food delivery rate (feeding trips x food load / hour; see below for description of how food load was calculated) from both three– and 24–hour data, 3) daily food delivery rate (feeding trips x food load / day) from 24–hour data, 4) the proportion of male feeding rate {male hourly feeding (or food delivery) rate / [male hourly feeding (or food delivery) rate + female hourly feeding (or food delivery) rate]} from both three– and 24–hour data, and 5) percent female brooding time (minutes spent on the nest / total video minutes from both three– and 24–hour data; brooding time was recorded only when we observed direct contact between the female and nestlings).

We first tested for differences in hourly feeding rate and food delivery rate, during the *early* and *late* stage of the nestling period using data obtained from the three–hour videos. Differences in hourly feeding rate and hourly food delivery rate were examined using mixed model analyses that tested the fixed effects of site (Alaska vs. California), parental sex (male vs. female), and the two–way interaction between them (sex x site) in each nestling stage; the model also included the random effect of the nest of the parental pair.

We then examined variation in daily feeding and food delivery rates from the 24–hour data recorded during the *late* nestling stage using the same statistical approach as with the three–hour data. To visualize diurnal patterns of nestling provisioning, we plotted the male–female food delivery rate during the active hours within the 24–hour data. To test how representative the three–hour samples of food delivery rate were of the daily patterns, we used a mixed model analysis that tested the fixed effects of sex and video length (three– vs. 24–hour) and their two–way interaction in each population.

We used the three–hour data to test for differences in the percent time females spent brooding their offspring using a mixed model analysis that included the fixed effects of site, nestling stage (*early* vs. *late* stage) and stage x site, while controlling for each nest as a random effect. We then plotted the diurnal pattern of hourly brooding time over the active hours using the 24–hour data recorded during the *late* stage of development. We tested for differences in the percent time females spent brooding as a function of the site, time of day, and a time x site interaction. To test how representative the three–hour data was of the 24–hour data, we used a mixed model that tested the fixed effects of site and video length (three–vs. 24–hour) and their two–way interaction in each population. Here, all statistical procedures were performed in SPSS version 13.0 (SPSS Inc., 2004, Chicago, IL).

Correlates of Geographic Variation in Parental Behavior in Partners

Food limitation – Food limitation is a challenging variable to measure in natural populations of birds. To test for differences in food limitation between the two populations, we used the food load brought by the parents to the nest during the *late* nestling stage (three–hour nest video data) as an indirect measure of food availability. Orange–crowned warblers typically bring single or multiple prey items in their beaks while feeding nestlings. Food load was taken from still nest video pictures and was calculated as the total area of visible prey items relative to the parent's beak size. For example, if the visible area of food was equal to the beak size, the load was scored as a one, 0.5 if the load was half the size of the beak, two if the load was twice the size of the beak. The same criterion was applied for all individuals, and food load scores ranged from 0.5 to 6.5 in our video data. The assumption of using this method was that parents foraging for food items were sampling the availability of food on their territories, such that increased food loads reflected greater availability (see also Thiollay 1988, Sæther 1994, Martin et al. 2000). To test for differences in food load, we used a mixed model analysis that controlled for nest as a random effect, and tested the fixed effects of site, sex, and a site x sex interaction.

Breeding density – To test if increased breeding density reduced the amount of male parental care because of presumed trade–offs associated with territorial behavior we quantified breeding density by mapping all territories in Alaska (2007–2008) and California (2003–2009). All territories were mapped by observing territorial disputes and movements of banded males and females throughout the season (from 04:00 am to 12:00 pm AKDT in Alaska and from 06:00 am to 12:00 pm PDT in California). To facilitate individual identification and territory mapping, 1) our study plots were delineated into 25 m x 25 m grids with flagging, which were incorporated into ArcGIS version 9.1 (ESRI Inc., 2005, Redlands, CA, U.S.A.); 2) we took waypoints of banded individuals using a GPS unit; 3) we also marked the locations of individual warblers on an aerial photograph that had waypoints of grids, which all were then transferred and updated in ArcGIS every two weeks. Final territory boundaries were determined by a minimum convex polygon (Ford and Myers 1981) in ArcGIS. Breeding density was calculated as the number of territories divided by the total area of each study plot. When territories partially overlapped with the fixed extent of the study site, the proportion of territory size was included (e.g. less than one). We used a two–sample *t* test to compare the means of breeding densities between the two populations.

Extra–pair paternity (EPP) – Because males should reduce the amount of parental care they provide if they have reduced confidence of paternity, we examined the degrees of breeding synchrony and extra–pair paternity rates between two populations. First, the breeding synchrony index (BSI) is the average proportion of sexually receptive females per day during the breeding season (Kempenaers 1993). Here, the female’s fertile period was defined as –10 days from the laying day of the penultimate egg for both populations to the beginning of nest–building. This period corresponded to the peak of mate guarding by males along with nest building by females (J. Yoon, personal observation). We used a two–sample *t* test to compare population means of BSIs between Alaska (2006–2008) and California (2004–2008, except 2007). Second, we used a molecular approach to determine the proportion of extra–pair offspring relative to within–pair offspring. Blood (15µL) was collected from the brachial vein of nestlings in the late nestling stage (day 6 in Alaska and day 7 in California) and stored in lysis buffer. DNA was extracted using a QIAGEN Biosprint 96 extraction robot and associated kit for whole animal blood. We used 7 variable microsatellite loci to assign paternity. Five of these markers (Dpµ01, Dpµ16, LSWµ7, LSWµ18, and Pat43) were previously used in an orange–crowned warbler population genetics study (Bull 2005), and two were developed for Kirtland's warblers (*Dki*B12 and *Dk*iD128; King et al. 2005). Fluorescently labeled forward primers [Applied Biosystems Inc. (ABI)] were used to tag PCR products, and PCR amplicons from markers were analyzed with an ABI 3100 automated capillary sequencer. Fragments were sized using GENESCAN ROX, and genotypes assigned using GENEMAPPER v. 4.01 (ABI). The number of alleles per marker ranged from 6 to 37 in the Alaska population and from 5 to 15 in the California population, providing a total of 132 and 75 independently assorting alleles in the Alaska and California population, respectively.

All markers were screened for allele frequencies, gene diversity, allelic richness, heterozygosity, and tested for linkage and Hardy–Weinberg equilibrium using FSTAT v 2.9.3.2 (Goudet 2002). We used CERVUS 3.0 (Kalinowski et al. 2007) to assign paternity of offspring. Specifically, to minimize the chances that offspring were assigned to adults by chance, we used the maximum likelihood approach of CERVUS, which took into account allelic frequencies, the number of candidate sires, and the proportion of potential sires sampled. In most cases, mothers were genotyped, and with this known first parent our combined exclusion probability was 0.99 for the Alaska nestling and 0.92 for the California nestling. We assigned paternity using strict (95%) and relaxed (80%) confidence levels in conjunction with a ‘total evidence’ approach (see Ryder et al. 2009). Genetic work was conducted at the Smithsonian Center for Conservation and Evolutionary Genetics at the National Zoological Park in collaboration with Dr. Robert Fleischer. We used a two–sample *t* test to compare the mean number of extra–pair young within broods (% EPY) between the two populations.

Climatic data – Because colder temperatures or frequent rainfalls should reduce feeding rates and increase female brooding of nestlings, we tested for climatic differences between and within populations. We obtained hourly ambient temperature data from the Historical Weather Data Archives, NOAA National Severe Storms Laboratory (website: http://data.nssl.noaa.gov) and monthly precipitation data from the Alaska Climate Research Center (website: http://climate.gi.alaska.edu) for Alaska and from Catalina Island Conservancy for California (website: http://catalinaconservancy.org). The weather stations were located at Fairbanks International Airport that was approximately 3.4 km away from the Alaska study site, and in Avalon that was approximately 11.4 km away from the California study site. We limited the climatic data to those periods of time that corresponded with the nestling period in each study site (Alaska for June in 1999–2008; California for April in 2000–2009). We used a two–sample *t* test to compare the means of two climate factors between the two study sites.

RESULTS

Geographic Variation in Nestling Provisioning Behavior in Partners

Hourly feeding rate (trips / hour) – The patterns of parental (both sexes combined) feeding rates differed between the two populations (1.76 ± 0.40 in Alaska vs. 4.50 ± 0.43 in California; $_{\mathrm{SITE}}\ F_{1,15} = 22.04$, $P < 0.001$) and were marginally different between the sexes (3.60 ± 0.37 in males vs. 2.66 ± 0.37 in females; $_{\mathrm{SEX}}\ F_{1,15} = 4.23$, $P = 0.05$) during the *early* nestling stage (Figure 7a). The higher feeding rate in California was driven by both sexes feeding more frequently than their Alaska counterparts (Figure 7a). The marginally significant difference between the sexes was largely driven by Alaska females feeding young at a lower rate than their males (Figure 7a) although a two–way interaction was not significant ($_{\mathrm{SEX\ X\ SITE}}\ F_{1,15} = 0.68$, $P = 0.42$).

The same general patterns were observed during the *late* nestling stage (Figure 7b). California parents provisioned nestlings with a higher feeding rate than did Alaska parents (3.87 ± 0.33 in Alaska vs. 7.84 ± 0.29 in California; $_{\mathrm{SITE}}\ F_{1,128} = 81.40$, $P < 0.001$), without a significant difference between the sexes (6.06 ± 0.31 in males vs. 5.65 ± 0.31 in females; $_{\mathrm{SEX}}\ F_{1,128} = 0.86$, $P = 0.36$), but in this case there was a significant two–way interaction ($_{\mathrm{SEX\ X\ SITE}}\ F_{1,128} = 6.99$, $P = 0.01$) driven by a difference in female and male feeding rate in Alaska, which was similar to that observed for the *early* nestling stage. Indeed, Alaska females made fewer feeding trips per hour to the nest than did males during the *late* nestling stage (4.66 ± 0.47 in male vs. 3.08 ± 0.47 in female) whereas the sexes did not differ in their feeding rate in California (7.46 ± 0.41 in male vs. 8.22 ± 0.41 in female). Proportionally, Alaska males were responsible for 68.4 ± 5.5 % of total feeding rate during the *early* nestling stage and 61.3 ± 3.1 % during the *late* nestling stage.

In contrast, California male’s were responsible for 49.3 ± 5.7 % of the total feeding rate during the *early* nestling stage and 47.7 ± 2.7 % during the *late* nestling stage.

Hourly food delivery rate (trips x food load / hour) – When food load was incorporated into the feeding rate (see the methods), the contribution of Alaska males to nestling provisioning was further enhanced (Figures 7c, d). During the *early* nestling stage (Figure 7c), the food delivery rate did not differ between the two populations (3.46 ± 0.37 in Alaska vs. 3.23 ± 0.43 in California: $_{\text{SITE}}\ F_{1,20} = 0.16$, $P = 0.69$), but it significantly differed between the sexes (4.51 ± 0.39 in male vs. 2.18 ± 0.41 in female; $_{\text{SEX}}\ F_{1,20} = 16.95$, $P = 0.001$) because Alaska females delivered less food than their males resulting in a significant two–way interaction ($_{\text{SEX X SITE}}\ F_{1,20} = 14.59$, $P = 0.001$). That is, in Alaska, males delivered more food per hour to the nest than did their females (5.70 ± 0.48 in male vs. 1.22 ± 0.55 in female) whereas this food delivery rate did not differ between sexes in California (3.31 ± 0.61 in male vs. 3.15 ± 0.61 in female).

During the *late* nestling stage (Figure 7d), the same pattern of food delivery rate was observed with the exception that California parents delivered more food overall compared to Alaska parents (7.82 ± 0.80 in Alaska vs. 10.39 ± 0.73 in California; $_{\text{SITE}}\ F_{1,58.1} = 5.60$, $P = 0.02$) because Alaska females delivered significantly less food than either Alaska males or either sex in California resulting in significant differences between the sexes (10.25 ± 0.68 in male vs. 7.95 ± 0.66 in female; $_{\text{SEX}}\ F_{1,57.1} = 8.66$, $P = 0.01$) and a two–way interaction ($_{\text{SEX X SITE}}\ F_{1,57.1} = 17.47$, $P < 0.001$). That is, in Alaska, males delivered more food to the nest per hour than did females (10.60 ± 1.00 in male vs. 5.04 ± 0.98 in female) whereas this food delivery rate did not differ between the sexes in California (9.91 ± 0.91 in male vs. 10.98 ± 0.89). Collectively, the proportion of the total food delivery rate made by Alaska males was 82.2 ± 7.3 % during the *early* nestling stage and 69.5 ± 3.4 % during the *late* nestling stage. In contrast, males from California were responsible for 47.0 ± 7.1 % of the total feedings during the *early* nestling stage and 47.6 ± 2.8 % during the *late* nestling stage.

Daily nestling provisioning behavior – Because day length was considerably longer in Alaska, we wanted to test how representative the three–hour data were of the total active time available for parental feeding. On average, Alaska parents provisioned nestlings from 03:37 (± 0:08) to 22:42 (± 0:08) resulting in a total of 19.08 ± 0.18 hours (n = 14 nests) of activity. In contrast, California parents provisioned nestlings from 06:18 (± 0:06) to 19:28 (± 0:06) resulting in a total active time of 13.16 ± 0.15 hours (n = 10 nests). Despite the additional six hours of active provisioning by parents in Alaska, the total feeding trips per day was significantly lower in Alaska (59.00 ± 5.98; n = 10 nests) than in California (92.75 ± 6.69; n = 8 nests; $_{\text{SITE}}\ F_{1,32} = 14.14$, $P = 0.001$), and it was not different between parental sexes (74.71 ± 6.35 in male vs. 77.04 ± 6.35 in female; $_{\text{SEX}}\ F_{1,32} = 0.07$, $P = 0.80$). But a significant two–way interaction ($_{\text{SEX X SITE}}\ F_{1,32} = 4.93$, $P = 0.03$) indicated slightly higher number of daily feeding trips by Alaska males relative to their females (67.80 ± 8.46 in male vs. 50.20 ± 8.46 in female) and vice versa in California (81.63 ± 9.46 in male vs. 103.88 ± 9.46 in female).

Accounting for the size of food load per feeding trip, the total daily food delivery rate (trips x food load / day) was similar between the two populations (Figure 8a; 168.78 ± 24.22 in Alaska vs. 169.87 ± 26.16 in California; $_{\text{SITE}}\ F_{1,22} < 0.01$, $P = 0.98$). The similar daily food delivery rate was largely due to the reduced provisioning rate of Alaska females, resulting in a significant difference between the sexes (207.42 ± 25.21 in male vs. 131.23 ± 25.21 in female; $_{\text{SEX}}\,F_{1,22} = 4.57$, $P = 0.04$), and a significant two–way interaction ($_{\text{SEX X SITE}}\,F_{1,22} = 6.67$, $P = 0.02$; Figure 8a). Indeed, Alaska males delivered significantly more food to the nest over 24 hours than did Alaska females (252.91 ± 34.26 in male vs. 84.64 ± 34.26 in female). In contrast, this daily food amount did not differ between the sexes in California (161.92 ± 37.00 in male vs. 177.82 ± 37.00 in female). Visualization of the male (Figure 8b) and female (Figure 8c) daily provisioning rate shows the same pattern; differences between populations are driven by the reduced food delivery rate by Alaska females (Figure 8c), not Alaska males (Figure 8b).

Observations of parental provisioning behavior observed during the three–hour nest videos were comparable to those observed during the active hours in the 24–hour nest videos during the late nestling state. First, the patterns of food delivery rate by sexes were not influenced by the lengths of video time in both populations. Specifically, no effect of video time length was found during the *late* nestling stage in Alaska (male: 10.51 ± 0.92 in three–hour vs. 10.81 ± 1.32 in 24–hour; female: 4.76 ± 0.92 in three–hour vs. 5.02 ± 1.32 in 24–hour; $_{\text{SEX}}\,F_{1,51.6} = 28.03$, $P < 0.001$; $_{\text{LENGTH}}\,F_{1,73.1} = 0.06$, $P = 0.81$; $_{\text{LENGTH X SEX}}\,F_{1,51.6} < 0.001$, $P = 0.98$). In California, no effect of video time length was also found (male: 9.92 ± 0.94 in three–hour vs. 10.41 ± 1.81 in 24–hour; female: 10.69 ± 0.94 in three–hour vs. 10.84 ± 1.81 in 24–hour; mixed model: $_{\text{SEX}}\,F_{1,38.4} = 0.30$, $P = 0.59$; $_{\text{LENGTH}}\,F_{1,67.1} = 0.04$, $P = 0.84$; $_{\text{LENGTH X SEX}}\,F_{1,38.4} = 0.02$, $P = 0.88$).

Geographic Variation in Nestling Brooding Behavior by Female

We quantified female brooding of nestlings during the *early* and *late* nestling stages, using three–hour data (Figure 9a). We found that the percent of time females spent brooding was significantly higher in Alaska than in California (0.63 ± 0.03 in

Alaska vs. 0.28 ± 0.03 in California; $_{\text{SITE}}\ F_{1,77} = 60.45$, $P < 0.001$), and it significantly decreased from the *early* to *late* nestling stage in both populations (0.66 ± 0.04 during the *early* stage vs. 0.26 ± 0.02 during the *late* stage; $_{\text{STAGE}}\ F_{1,77} = 80.02$, $P < 0.001$), but there was no significant two–way interaction ($_{\text{STAGE X SITE}}\ F_{1,77} = 0.10$ $P = 0.76$). That is, within populations, Alaska and California females' brooding time decreased from the *early* nestling stage to the *late* nestling stage (84.1 ± 5.5 % to 42.4 ± 3.1 %), and (47.6 ± 5.8 % to 8.7 ± 2.7 %) respectively. Using the 24–hour nest videos during the *late* nestling stage (Figure 9b), hourly female brooding rate was maintained at a consistent level during the active hours in both populations, (mixed model: $_{\text{SITE}}\ F_{1,23.3} = 64.47$, $P < 0.001$; $_{\text{TIME}}\ F_{12,207.5} = 1.70$, $P = 0.07$; $_{\text{TIME X SITE}}\ F_{8,207.5} = 1.68$, $P = 0.11$; Figure 9b). The percent female brooding rate from the three–hour nest videos recorded during the early time of the day tended to be lower than that during the active hours from the 24–hour nest videos recorded during the active hours (Alaska: 0.42 ± 0.03 in three–hour vs. 0.56 ± 0.05 in 24–hour; California: 0.09 ± 0.03 in three–hour vs. 0.11 ± 0.05 in 24–hour). The patterns of female brooding rate between the two time scales was marginally influenced by the lengths of video time in both populations ($_{\text{LENGTH}}\ F_{1,83} = 3.87$, $P = 0.05$), but there was no difference between sites ($_{\text{LENGTH X SITE}}\ F_{1,83} = 1.85$, $P = 0.18$).

Geographic Variation in Food Load, Breeding Density, Paternity, and Climate

Food load – We measured mean food load as an indirect measure of food limitation using the three–hour nest video data during the *late* nestling stage and found significant differences in the mean load size between populations (Table 3). Specifically, the per–trip food load was significantly larger in the Alaska population than in the California population ($_{\text{SITE}}\ F_{1,59.2} = 14.71$, $P < 0.001$; Figure 10), and males brought larger food loads than females ($_{\mathrm{SEX}}\ F_{1,57.7} = 13.42$, $P = 0.01$). However, differences between sites and sexes were complicated by the interaction between site and sex ($_{\mathrm{SEX\ X\ SITE}}\ F_{1,57.7} = 21.66$, $P < 0.001$). Within populations, Alaska males delivered larger food loads per trip than their females (2.31 ± 0.13 in male vs. 1.55 ± 0.13 in female) whereas California males and females delivered similar food loads (1.29 ± 0.12 in male vs. 1.38 ±0.12 in female).

Breeding Density – Breeding density was significantly lower in Alaska compared to California (Table 3). Breeding densities in Alaska ranged from 0.46 and 0.49 territories ha^{-1} in 2007 and 2008 whereas in California the densities ranged from 3.42 to 5.28 territories ha^{-1} in 2003–2009 (Table 3).

Extra–pair paternity rates – The degree of breeding synchrony and the rate of extra–pair paternity did not significantly differ between the two populations (Table 3). In Alaska, 50.0 ± 8.2 % of 38 nests contained at least one EPY in 2006–2008 whereas in California 58.0 ± 7.1 % of 50 nests contained at least one extra–pair young in 2005–2008, except 2007. Extra–pair paternity ranged from zero to one in both Alaska and California. The percentage of EPY within broods did not significantly differ between the two populations despite a slightly higher rate of EPP in California (Table 3).

Climatic data – Ambient temperatures during the nestling period (i.e. June in 1999–2008 for Alaska and April in 2000–2009 for California) were on average higher in Alaska than in California (Table 3). Mean, maximum, and minimum daily temperatures in Alaska ranged from 3.2 °C to 24.1 °C, from 6.7 °C to 31.7 °C, and from –1.1 °C to 18.3 °C respectively. In California, the mean, maximum, and minimum temperatures ranged from 7.1 °C to 28.2 °C, from 9.4 °C to 32.8 °C, and from 5.6 °C to 25.0 °C. In the comparison of ten–year ambient temperatures between two study areas, the average of mean temperature was approximately 3.42 °C higher in Alaska than in California, the average of minimum temperatures was approximately 0.80 °C higher in Alaska, and the average of maximum temperatures was also approximately 4.94 °C higher in Alaska. Second, precipitation during the nestling period (i.e. June in 1999–2008 for Alaska and April in 2000–2009 for California) was significantly higher in Alaska than in California (Table 3).

DISCUSSION

Understanding the factors that drive variation in parental care patterns between species and populations remains an open question. Here, we examined patterns of male and female parental care during the post–hatching period in two populations of *O. celata* breeding in central Alaska and southern California. We found several interesting patterns: 1) females in Alaska provisioned offspring significantly less than males, 2) despite an additional six hours of activity, parents in Alaska delivered almost the same amount of food to their nestlings as did parents in California, and 3) Alaska females spent significantly more time brooding their offspring than did California females. While our ability to make strong generalizations is limited by only having two populations for comparison, below we attempt to explain these patterns in light of the diversity of hypotheses for different ecological and social correlates that might explain the observed differences in parental care.

Direct and Indirect Effects of Food Limitation

We hypothesized that with increasing food limitation males would be required to participate more in provisioning of offspring (Bart and Tornes 1989, Dunn and Roberston 1992). Such direct effects of food limitation have been suggested to explain variation in the amount of male parental care between different populations (Dunn and Roberston 1992). Food limitation could also indirectly influence the amount of male parental care, if increased population density forces males to allocate more time to territorial defense (Wingfield et al. 1990, Beletsky et al. 1995). While food limitation is a difficult variable to measure in nature, our results suggest that if food limitation is acting in these populations, it is likely to be more important in the California population. California parents brought significantly smaller food loads each trip to the nest and population density was significantly higher compared to Alaska. If smaller food loads reflect increased food limitation, we would have expected males in California to exhibit higher feeding rates relative to males in Alaska. We did find that compared to Alaska, California males made more trips to the nest per hour during both the *early* and *late* nestling stages, consistent with the prediction from food limitation. However, a comparison of the sexes shows that Alaska males feed significantly more often than their females, which is opposite the prediction if food availability is greater in Alaska. The larger food loads delivered by Alaska males compared to females further exaggerates the difference in contribution of the sexes, whereas in California the contribution of the sexes is very similar. These results also argue against an indirect role of food limitation due to increased allocation of time to territorial defense, because we would have expected California males to exhibit reduced provisioning of offspring. While California males are more aggressive than Alaska males (Chapter 2) and have higher T levels (Horton et al. 2010), such aggression does not seem to interfere with parental care. If food availability is playing a role in these populations, it may be acting through female behavior. The primary pattern that requires explanation is why Alaska females feed so infrequently and why they bring such small food loads. Greater food availability in Alaska may allow females to allocate more time to other activities such as brooding offspring (see below). Indeed, Wolf et al. (1990) found that experimental removal of males resulted in females having to spend less time brooding, and more time provisioning their offspring. Thus, greater food availability may allow females to brood more often and shift the burden of nestling provisioning to males. Experimental removal of males or food supplementation experiments in these populations could be used in the future to test this hypothesis.

Extra–pair Paternity and Male Parental Care

Differences in ecological or social conditions between populations can alter the frequency of extra–pair paternity, and in turn alter patterns of male parental care between populations. Males with uncertainty of their paternity in current offspring are hypothesized to provide less offspring care (Trivers 1972, Maynard Smith 1977, Xia 1992). Thus, differences in breeding synchrony or breeding density that result in higher extra–pair paternity could result in population differences in the amount of care provided by males (Møller and Birkhead 1992, 1993, Westneat and Sherman 1997). Yet, we found no evidence of differences in the breeding synchrony and extra–pair paternity rate between the Alaska and California populations. Furthermore, male differences in parental care were far less pronounced than differences among females, suggesting that extra–pair paternity plays little role in explaining variation between populations.

Climatic Variation and Parental Care

Cold, unpredictable, and extreme environments have been invoked as explanations for altitudinal and latitudinal variation in patterns of avian parental care (Briskie 1995, Badyaev and Ghalambor 2001, Summers and Nicoll 2004). Yet, we found little evidence for a clear climatic explanation to the patterns of parental care we observed. Colder temperatures during the nestling period did not explain the high levels of female brooding in Alaska. However, ambient temperatures were slightly warmer in Alaska compared to California, which are consistent with the interior continental climate of Fairbanks and the moderate marine climate of Santa Catalina Island. Rainfall was significantly higher in Alaska compared to California during the nestling period, so it is possible that rainfall differences could contribute to higher female brooding. However, all video recordings of nests in California and Alaska were conducted during dry conditions (video cameras were not water–proof and no recordings occurred on rainy days), so it is unlikely that rainfall could explain any behavioral differences between sites.

The Ecological Context of Life History Strategies and Parental Care and Proposed Alternative Hypotheses

Life history theory suggests that the evolution of different parental care strategies should arise as a function of differences in the costs and benefits of providing care (Trivers 1972, Clutton–Brock 1991). Such costs and benefits are strongly tied to the ecological conditions that parents face (Partridge and Harvey 1988). Thus, understanding between population and species variation in parental care requires new hypotheses that consider how multiple life history traits such as growth and development, fecundity, and age–specific survival are related. Here, the warbler populations we contrasted exhibit divergent life history strategies. The Alaska population exhibits a “faster” life history, reflected in its low annual adult survival, increased fecundity, and faster post–hatching growth (see above). The California population in contrast exhibits a “slower” life history with relatively high annual adult survival, reduced fecundity, and slower post–hatching growth. In light of these life history differences and the ecological conditions occupied by these populations we propose two non–mutually exclusive hypotheses that might explain the differences in parental care we observe in Alaska versus California.

The sub–arctic climate near Fairbanks, Alaska is characterized by a short growing season and long days, which in turn create a short window of highly favorable climatic and food conditions for passerine birds to breed. Migratory birds, like the orange–crowned warbler, must travel long distances from their wintering grounds to take advantage of these northern sites, and such migratory behavior has been shown to impose significant mortality on adults (Sillett and Holmes 2002). High mortality during migration may also provide an explanation for the evolution of the fast life history (Sillett et al., in prep.). A short–breeding season and a fast life history are both predicted to favor rapid development and growth, thus any parental behaviors that can facilitate rapid development and growth should be favored. To date, most attention for rapid growth has focused on parental provisioning behavior (Price 1985, Martin 1987, Schew and Ricklefs 1998, Konarzewski and Starck 2000, Searcy et al. 2004). However, female brooding of nestlings may be an overlooked component of parental care that also facilitates rapid development. Brooding behavior transfers heat to the nestlings through contact with the female’s brood patch and has long been known to play an important role in nestling thermoregulation prior to the chicks achieving the ability to become endothermic (e.g.

Webb 1993). Indeed, warmer temperatures and the transition from ecothermy to endothermy in the nestlings are commonly associated with a reduction in the amount of time females brood their nestlings (e.g. Gotie and Kroll 1973, Marsh 1980, Johnson and Best 1982), and a reduction in the amount of time females brood their nestlings is also observed in both populations studied here . What is less commonly appreciated is that in both early (ectothermic) and late (endothermic) nestlings energy provided to nestlings in the form of food must be allocated to the competing demands of growth, thermoregulation, and begging behavior (Ricklefs 1974, Dunn 1980, Olson 1992, Pearson 1998). Thus, any behavior by the parents that reduces thermoregulatory costs (e.g. constructing a more insulated nest, Rowher and Law 2010; a warmer nest site, Dawson et al. 2005, Pérez et al. 2008; increased female brooding, Rensel et al. 2010) could help speed up development. We propose the following hypothesis: the shorter nestling period and faster growth rate in Alaska (8–10 days) compared to California (10–13 days) warblers (Sillett et al., in prep, Sofaer et al., in prep.) is achieved through the combined effects of increased female brooding and a relatively high daily food delivery rate by males. This strategy is achieved because food availability is relatively high and day length is long, allowing males compensate for the reduced female provisioning. Future tests of this hypothesis could include male removals in Alaska and measuring the response of both the female brooding time and the nestling growth and development period. Alternatively, females could be experimentally removed or have their time brooding decreased, and the response of the males and nestlings could be measured. Finally, reviewing published literature to see if other sub–arctic birds with fast–life histories exhibit a similar pattern of parental care and nestling growth would test the generality of this hypothesis.

The California population is notable for occurring on a semi–arid island with a relatively mild climate. Most warblers on Santa Catalina Island leave the island in summer and migrate a short distance to the nearby mainland, but do not undergo the potentially risky long–distance migration of their Alaska counterparts. Such short annual movements are likely to explain their higher annual adult survival and may explain the significantly higher breeding density on Santa Catalina Island compared to the Alaska study site. The high breeding density in turn likely explains the high T levels of California males (Horton et al. 2010) and their higher levels of territorial aggression (Chapter 2) compared to Alaska males. These results in combination with small food loads, small territory sizes and high population density collectively suggest that the California population is closer to its carrying capacity and more likely to experience stronger intra–specific competition for territories and food. Increased intraspecific competition is frequently invoked as an important process in insular island populations that leads to slow life histories and larger body size (MacArthur and Wilson 1967, Van Valen 1973, Clegg and Owens 2002, Lomolino 2005). Theory and empirical studies argue that in highly competitive environments, parents maximize fitness by producing fewer, higher quality offspring, as a strategy to increase offspring recruitment into the population (Lack 1954, MacArthur and Wilson 1967, Sinervo et al. 2000, Svensson and Sinervo 2000). In birds, higher survival of offspring is known to be achieved by extending parental provisioning effort into the post–fledging period (Moreau 1947, Lack 1954, Russell 2000). With this conceptual framework, we hypothesize that the relatively high *and* similar levels of food delivery by both sexes in California represent a strategy for increasing the probability of offspring recruitments in the competitive island environment they occupy. Furthermore, the comparative study of sex hormone in males does not agree with the patterns of male parental behavior found in the present study. T levels of California males are also significantly higher than those in Alaska males during the nestling period (Horton et al. 2010). However, the same STI song playbacks applied to males during the nestling stage do not appear to affect nestling provisioning behavior of males in both populations (J. Yoon et al., unpublished data). Recent studies have shown that T–implanted males did not completely reduce parental care although they exhibited an increase in singing or territorial behavior (see studies by Hunt et al 1999; Lynn et al. 2002, 2005). This type of dissociation between T levels and paternal care is thought to be more common than previously suggested (Lynn and Wingfield 2008). It is possible that although the Californian males exhibit high T levels, they provide substantial parental care along with reduced territorial aggression when the demand of male care is critical especially in a population with food limitation (i.e., essential paternal care hypothesis; Lynn 2008). In addition, experimental removal of parents after fledging would be predicted to have greater consequences in California relative to Alaska for offspring survival and recruitment.

We found differences in the patterns of parental care between orange–crowned warblers breeding in Alaska versus California, most notably that in Alaska males provided the majority of food to offspring and females spent a large portion of their time brooding. Simple hypotheses related to food limitation, extra–pair paternity, and climate did not provide any clear explanations to these patterns. Instead, we propose that parental care patterns reflect local adaptation of life histories to different environments. In Alaska, females allocate more time to brooding young as a means of facilitating rapid growth, and high food availability and long days allow males to compensate for females by providing most of the food delivered to the young. In California, parents equally contribute to a high food delivery rate as a strategy to increase the probability of offspring survival and offset the challenges of recruiting offspring into a competitive environment. Ultimately more comparative studies of populations and species occupying different environments are needed before we can generalize what ecological and social factors drive variation in parental care behavior.

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Table 3. Ecological factors in relation to geographic variation in parental behavior in partners of breeding orange–crowned warblers (*Oreothlypis celata*) in Fairbanks, Alaska (*O. c. celata*) and on Santa Catalina Island, California (*O. c. sordida*): 1) per–trip food load as an indirect measure of food availability in Alaska (2006–2008) and California (2005–2009), 2) breeding density (territories ha^{-1}) in Alaska (2007–2008) and California (2003–2009), 3) percent extra–pair young within broods in Alaska (2006–2008) and California (2004–2008 except 2007), and 4) ten–year averages of ambient temperature (°C; mean, minimum, and maximum temperatures) with precipitation (mm) during the nestling stage in Alaska (June of 1999–2008) and California (April of 2000–2009).

	Alaska			California				
Factor	mean	± SE	(n)	mean	± SE	(n)	*t* [a]	*P*
Food load [b]	**1.93**	± 0.12	(27)	**1.34**	± 0.11	(32)		**< 0.001**
Breeding density	**0.48**	± 0.02	(2)	**4.40**	± 0.24	(7)	–8.48	**< 0.001**
Synchrony index [c]	42.95	± 2.63	(3)	32.23	± 4.92	(4)	1.72	0.145
Extra–pair paternity	0.24	± 0.05	(38)	0.38	± 0.06	(50)	–1.84	0.070
Temperature [d]	**16.36**	± 0.18	(294)	**12.94**	± 0.26	(255)	10.81	**< 0.001**
Minimum	**10.76**	± 0.17	(294)	**9.96**	± 0.22	(255)	2.95	**0.003**
Maximum	**21.50**	± 0.22	(294)	**16.56**	± 0.32	(255)	12.77	**< 0.001**
Precipitation [d]	**27.45**	± 5.11	(10)	**0.95**	± 0.48	(10)	5.17	**0.010**

[a] Two–sample *t* test statistics

[b] Mean food loads were scored based on the criterion that the volume of load per parental feeding trip was one when a parent brought the beak–size food items. See the results for the statistics.

[c] Breeding synchrony index (% BSI; see Kempenaers 1993)

[d] Long–term temperature data were obtained from a weather station in Fairbanks International Airport in Fairbanks, Alaska and from a weather station in Avalon on Santa Catalina Island, California.

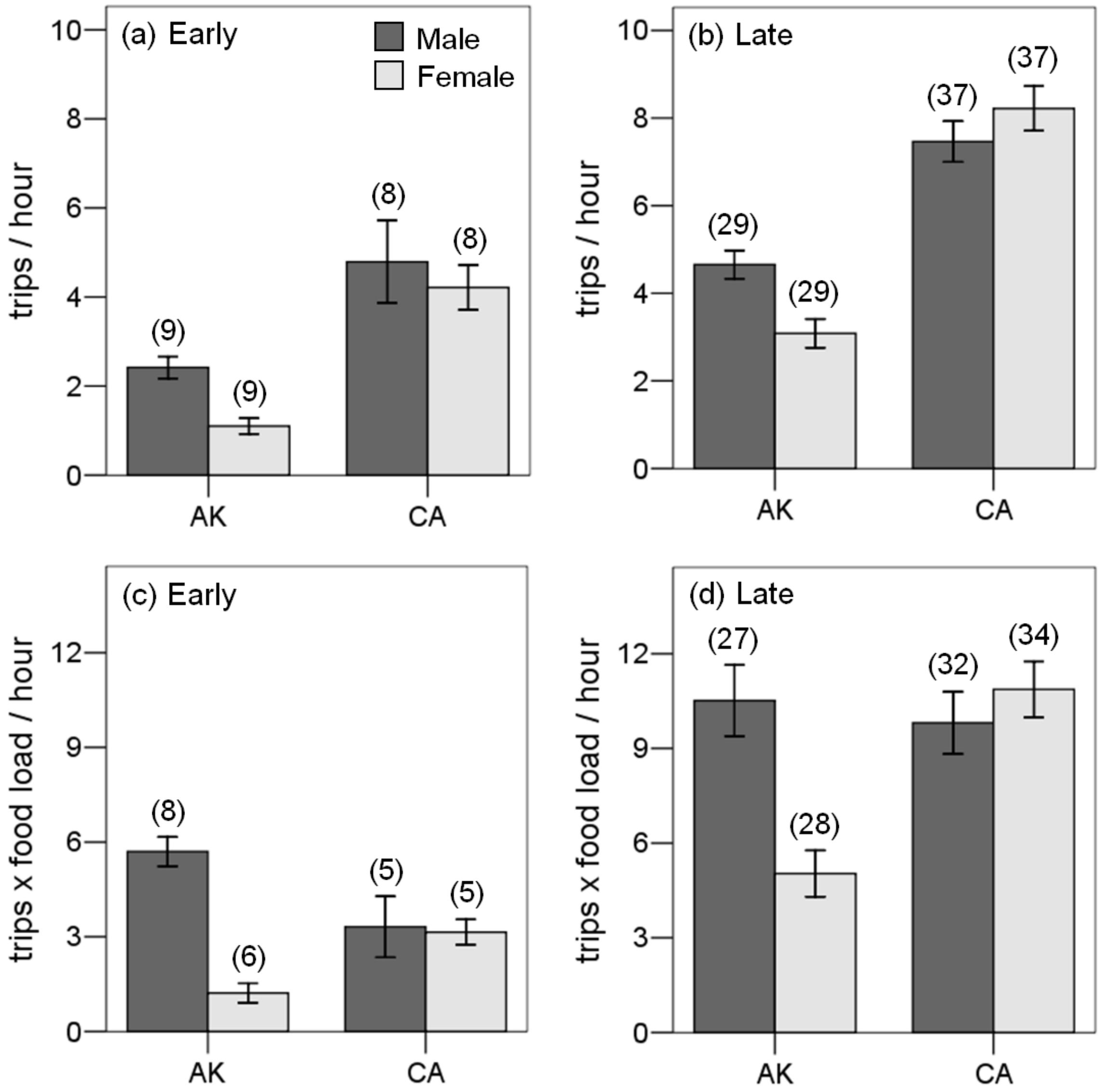

Figure 7. Hourly nestling provisioning effort in partners of orange–crowned warblers (*Oreothlypis celata*) in Fairbanks, Alaska (*O. c. celata*) and on Santa Catalina Island, California (*O. c. sordida*): (a, b) feeding rates (trips / hour) in the *early* and *late* nestling stages, and (c, d) food delivery rates (trips x food load / hour) in the *early* and *late* nestling stages. Here, *early* stage was on nestling day 3 after hatching in both populations, and *late* stage was nestling day 6 in Alaska and day 7 in California. Three–hour nest videos were collected from 2006 to 2008 in Alaska and from 2005 to 2009 in California (except 2007). Error bars represent means ± SE, and the numbers above bar denote the number of nests.

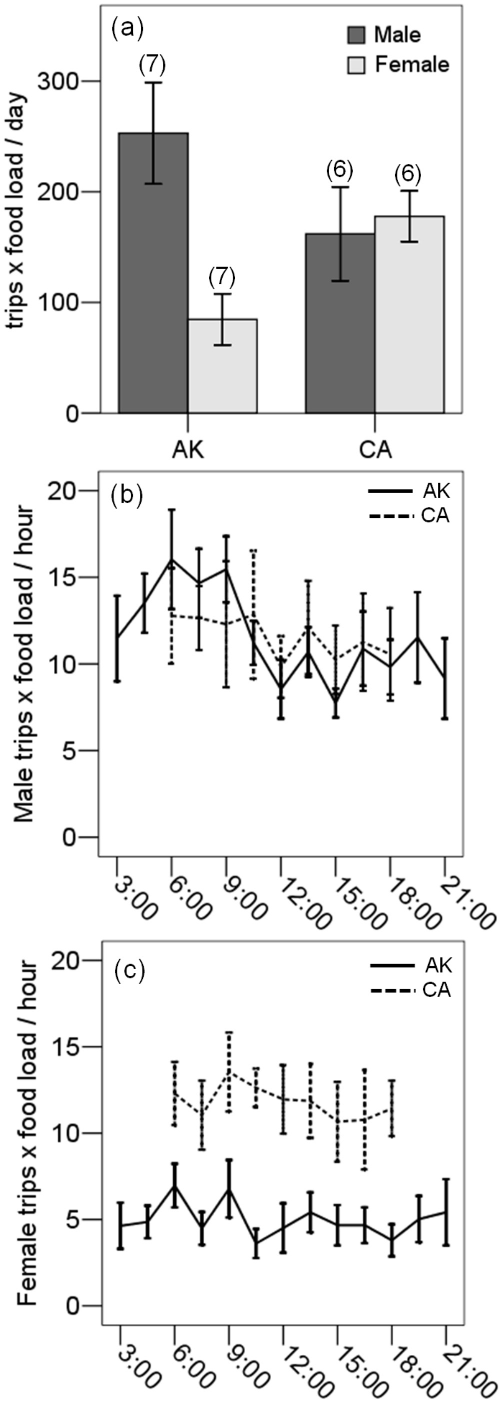

Figure 8. Daily nestling provisioning effort in partners of orange–crowned warblers in Fairbanks, Alaska (2007–2008) and on Santa Catalina Island, California (2009): (a) daily food delivery in partners (trips x food load / day) in Alaska (n = 7 nests) and California (n = 6 nests); temporal variations in hourly food delivery rates of males (b) and females (c) in Alaska (n = 13 nests) and California (n = 10 nests) during the active hours. Error bars represent means ± SE.

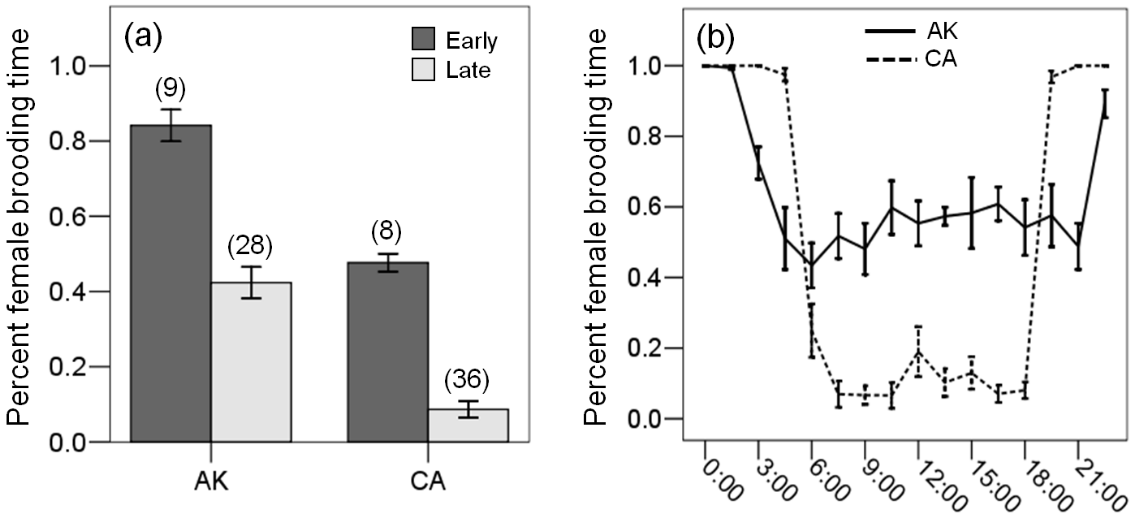

Figure 9. Differential nestling brooding effort by female orange–crowned warblers breeding in Fairbanks, Alaska and on Santa Catalina Island, California: (a) percent female brooding time (brooding minutes / 60 minutes) in the early (nestling day 3) and late (day 6 in AK, day 7 in CA) nestling stages from the three–hour nest videos in Alaska (2007–2008) and California (2005–2009 except 2007); (b) temporal variations in percent female brooding time in the *late* nestling stage from the 24–hour nest videos in Alaska (2007–2008, n = 13 nests) and California (2009; n = 10 nests). Error bars represent means ± SE. Numbers above bars denote the number of nests.

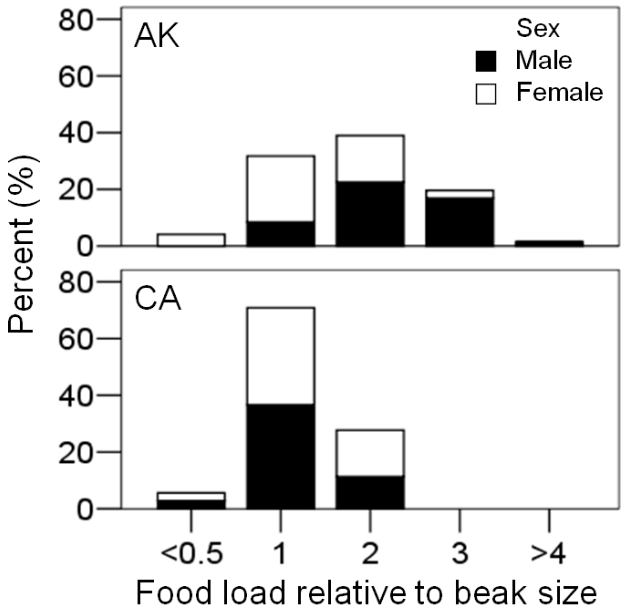

Figure 10. Distribution of per–trip food load, an indirect measure of food availability, of orange–crowned warblers in Fairbanks, Alaska (2006–2008) and on Santa Catalina Island, California (2005–2009 except 2007) in the *late* nestling stage (nestling day 6 in Alaska and day 7 in California) from the three–hour nest videos. Here, food load was scored as one if the volume of food load was equal to the beak size (see the methods).