

DISSERTATION

DEMOGRAPHY AND PARENTAL INVESTMENT IN ORANGE-CROWNED WARBLERS:  
TESTING LIFE HISTORY THEORY

Submitted by

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Graduate Degree Program in Ecology

In partial fulfillment of the requirements

For the Degree of Doctor of Philosophy

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Fort Collins, Colorado

Fall 2012

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## ABSTRACT

### DEMOGRAPHY AND PARENTAL INVESTMENT IN ORANGE-CROWNED WARBLERS: TESTING LIFE HISTORY THEORY

Understanding the diversification of life history strategies is a major goal of evolutionary ecology. Research on avian life history strategies has historically focused on explaining variation in clutch size, and most studies have tested whether this variation can be explained by variation in a single ecological factor, such as food availability or mortality risk. However, relatively few studies have evaluated whether the causes of variation within populations are distinct from or similar to the causes of variation between populations. In my dissertation, I compare the life history strategies of orange-crowned warbler (*Oreothlypis celata*) populations and study the causes of variation in clutch sizes, incubation behavior, nestling provisioning rates, nestling growth rates, and breeding phenology. I tested alternative hypotheses for the ecological causes of divergent life histories, and assessed the consequences of these different reproductive strategies for parents and offspring. My results indicate that no single ecological factor can explain life history variation either within or between populations. Instead, life history and behavioral traits differ in their sensitivities to different ecological factors, and while differences between nearby populations can reflect plastic responses to ecological variation, populations that are more geographically and evolutionarily distant can differ in both their responses to ecological variation and in the consequences of variation in parental behavior for offspring growth and development.

## ACKNOWLEDGEMENTS

I would like to thank Cameron Ghalambor and Scott Sillett, whose mentorship fostered my intellectual development. My committee members, Barry Noon and Colleen Webb, provided insightful advice, and Phillip Chapman helped me develop statistical skills. Equally important to me was the support of my family and friends, especially my fellow graduate students in the Ghalambor lab. Luke Caldwell supported me throughout this process; the time we spent exploring the Channel Islands and Alaska together was the highlight of these years. I also thank Cassidy Caldwell, who let me get this done while she slept and brightened my days when she woke.

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## INTRODUCTION

### *Background*

Organisms exhibit an incredible diversity of reproductive strategies, and understanding the processes that have favored this diversification is a major goal of evolutionary ecology. Life history theory suggests that reproductive investment can be affected by factors that shape age-specific mortality rates, such as predation and parasitism (Michod 1979, Law 1979, Agnew 2000), and by factors that affect resource availability, such as food abundance (Lack 1947, Reznick 2000), seasonality (Ashmole 1963), and the strength of intraspecific competition (Brockelman 1975). Because life history strategies vary along a single major axis, from fast life history strategies with high fecundity and low adult survival to slow life histories with low fecundity and high adult survival, many studies have focused on understanding how variation in a single ecological factor could have favored the evolution of different strategies along this continuum (e.g. Reznick et al. 1990). However, less progress has been made towards understanding how the factors affecting mortality and resource availability jointly shape patterns of life history diversity, and in many cases it is unclear whether the conditions that lead to variation within populations are distinct from or mirror those that underlie variation between populations.

Studies of birds have been central to the development of life history theory (reviewed in Ricklefs 2000; Martin 2004), and many studies have focused on explaining the latitudinal increase in avian clutch sizes. For example, Lack (1947; 1968) proposed that food availability could explain variation in clutch sizes both within and between species, while Skutch (1949) suggested that the latitudinal gradient in clutch size arose from a latitudinal gradient in nest predation risk. These hypotheses have largely been considered alternatives (Ricklefs 2000,

Martin et al. 2000), despite the recognition that food availability and predation risk can interact to shape traits such as foraging behavior and habitat choice (reviewed in Lima 1998). However, several recent studies have highlighted the potential for food availability and predation risk to interact to shape avian clutch sizes and parental behavior (Eggers et al. 2008; Zanette et al. 2006). Studies that consider the joint effects of food availability (Lack 1947) and nest predation risk (Skutch 1949), as well as the effects of additional ecological variables including population density (Ashmole 1963; Brockelman 1975) and adult mortality rates (Williams 1966), therefore have the potential to build a more nuanced understanding of the causes of avian life history variation.

Although the major hypotheses to explain avian life history variation were proposed in the context of understanding variation between species and across latitudes, many tests of these hypotheses have been conducted within single populations. For example, brood manipulation studies have frequently been used to test Lack's hypothesis, and because birds can generally provision larger broods than they naturally raise, these studies have been interpreted as refuting Lack (reviewed in VanderWerf 1992). However, this interpretation assumes that the same ecological factors that affect plasticity within populations also underlie the diversification between populations (Martin 2004), and few studies have explicitly tested whether patterns of plasticity mirror predicted evolutionary effects (Ghalambor and Martin 2002). In addition, comparisons between species have been used to understand evolution along the life history continuum (Ricklefs 1980; Saether 1994; Martin et al. 2000), but ecological conditions such as food quantity and quality are difficult to quantify and compare between species. Intraspecific comparisons can complement studies within single populations and interspecific work by



providing a situation with both variation in life history strategies and a greater ability to compare ecological and behavioral traits across populations.

In my dissertation, I compared patterns of reproductive investment within and between populations to understand patterns of life history diversity. I quantified how birds adjust their clutch sizes and parental behavior in response to variation in ecological conditions, and I measured how this variation in reproductive strategies translated into variation in offspring growth rates. In addition, I compared patterns of plasticity in parental behavior and in nestling growth rates between populations to assess whether similar processes underlie variation within and between populations. This approach increases our understanding of both the causes of life history variation between populations and the fitness implications of variation in reproductive strategies within populations.

### *Study System*

My dissertation compares three orange-crowned warbler (*Oreothlypis celata*) populations to document life history variation and understand its causes. Orange-crowned warblers are small insectivorous passerine birds whose breeding populations span a large latitudinal range in western North America (Gilbert et al. 2010). This species has biparental care and is socially monogamous, but clutch size and other measures of reproductive investment differ between breeding populations. My coauthors and I exploit these life history differences, as well as differences in the ecological communities in which these populations breed, to evaluate the causes of variation in warbler reproductive behavior and demography. The intraspecific nature of this comparison allows us to directly compare traits such as clutch sizes, nest initiation dates, nestling provisioning rates, and nestling growth rates between, as well as within, populations.

Four orange-crowned warbler subspecies have been recognized (Gilbert et al. 2010), and we studied variation in reproductive behavior within populations and between two populations of the same subspecies (*O. c. sordida*) and two populations of different subspecies (*O. c. sordida* and *O. c. celata*). Of the four subspecies, *O. c. sordida* has the smallest breeding range, which is limited to California's Channel Islands and adjacent areas of mainland Southern California. Individuals in this subspecies are resident on the Channel Islands or are short-distance migrants that winter along the coast of mainland California and Baja California, Mexico. Populations breeding on different islands experience different ecological conditions, and I compared a population on Santa Catalina Island, California (hereafter, Catalina Island) with a population on Santa Cruz Island, California to evaluate how variation in rainfall and nest predation risk affected breeding phenology, clutch size, and behavior. Next, I analyzed seven years of data from birds breeding on Catalina Island to study the mechanisms by which density-independent and density-dependent factors acted to shape the fecundity and adult survival of birds in that population.

In the second half of my dissertation, I compared parental investment and behavior between birds breeding on Catalina Island (*O. c. sordida*) and in Fairbanks, Alaska (*O. c. celata*). Individuals breeding in Alaska are long-distance migrants that winter along the Gulf Coast in the southern United States; birds in this population also have faster life history strategies than birds breeding in California. I studied the differences between these populations as a case study for understanding the causes of latitudinal differences in clutch size, nestling provisioning rates, and nestling growth rates among birds.

## *Research Overview*

In the first chapter of my dissertation, my coauthors and I used birds' responses to spatial and temporal variation in ecological factors to study the sensitivity of different reproductive traits to variation in food abundance and nest predation risk. We compared breeding phenology, clutch sizes, nest heights, and feeding rates between wet and dry years, and between Catalina Island, which has no visually-oriented nest predators (Peluc et al. 2008) and Santa Cruz Island, which has an endemic visually-oriented nest predator, the island scrub-jay (*Aphelocoma insularis*). We showed that rainfall during the winter was correlated with the abundance of insect larvae in the spring, and that birds initiated breeding earlier, had longer breeding seasons, and laid larger clutch sizes in years with wet winters. On Santa Cruz Island, where nest predation risk was higher, birds built lower nests and made fewer trips to the nest during both incubation and the nestling period. However, despite a lower feeding rate, nest predation did not affect clutch sizes, contrary to the hypothesis first proposed by Alexander Skutch (1949). Our results have important implications because they show that behavioral and life history traits can differ in their sensitivity to variation in ecological conditions; specifically, clutch size and breeding phenology were more sensitive to variation in food abundance, while nest height and visitation rate were more sensitive to variation in nest predation risk.

The phenotypic variation we observed within and between islands was very likely to reflect plastic responses to ecological variation, as we found little genetic divergence between islands, and variation in rainfall could fully explain variation in breeding phenology and clutch size both between and within islands. In addition, the plastic responses we observed were in the same direction as the predicted evolutionary effects of food abundance and nest predation risk.

This result suggests that adaptive plasticity can underlie differences in reproductive behavior both within and between avian populations.

In the second chapter of my dissertation, my coauthors and I evaluated how rainfall and population density affected the fecundity and adult survival of orange-crowned warblers breeding on Catalina Island. We predicted that the demographic effects of intraspecific competition would be strong in this insular population, which breeds at high densities and where males react strongly to perceived territorial intruders (Yoon et al. 2012). Because the mechanisms of population regulation and limitation can affect life history evolution (Bassar et al. 2010) but are poorly understood for most species, we evaluated how population density and variation in food abundance shaped the demographic rates of warblers breeding on Catalina Island.

We found that nest predation was density-dependent, which was surprising because nest predators are typically thought to limit, rather than regulate, avian populations (Newton 1993). We did not find any effects of population density on the number of young fledged by successful pairs, suggesting that intraspecific competition for food resources did not affect fecundity. However, annual variation in rainfall and food abundance did affect the probability of reproductive success or failure, likely by influencing decisions regarding when to initiate breeding and when to reneest. Adult survival was not strongly affected by population density or rainfall, either on the island or on the mainland wintering grounds. Our results suggest that snakes and/or small mammals can have functional or numeric responses that allow them to regulate avian populations via nest predation and raise the possibility that warbler nest site selection on Catalina Island has been shaped by density-dependent nest predation.

In the third chapter of my dissertation, my coauthors and I analyzed nestling mass gain from hatching through fledging to compare the growth trajectories of warblers in California and Alaska. We fit a logistic function to our growth data, and found that nestlings in Alaska reached the inflection point of their growth curve at a younger age and also had a higher growth rate than birds in California. Asymptotic mass did not differ between populations. The mixed models we used also allowed us to evaluate the amount of variation between individual nestlings and groups of siblings. We found that nests and nestling varied in their asymptotic masses and in the inflection points of their growth curves, but that there was little variation in the growth rate constant within populations. Because altricial birds are the fastest growing vertebrates (Case 1978), and are generally thought to have little adaptive intraspecific variation in their growth rates (Starck and Ricklefs 1998), researchers have suggested that they may grow at their physiological maximum (Ricklefs 1969; Werschkul and Jackson 1979). Our results indicate that intraspecific passerine populations can differ in their growth rates, and that birds in California do not grow at their physiological maximum, perhaps to avoid the fitness costs of rapid growth (Arendt 1997; Dmitriew 2011).

In the fourth chapter of my dissertation, my coauthors and I tested whether variation in food availability could explain variation in clutch and brood sizes between populations. Although David Lack (1947) first proposed this hypothesis decades ago, and despite extensive testing (reviewed in Martin 1987; Godfray 1991), few studies have evaluated whether variation in day length allows birds breeding at high latitude to feed their young for more hours per day and thereby bring more total food to the nest (Hussell 1972). In addition, Lack (1947; 1968) assumed that per-nestling investment would not differ between populations, and that the relationship between per-nestling investment and measures of offspring fitness, such as growth,

would also be consistent within a species. These latter assumptions have received very little attention in birds, but studies of life history variation in other taxa have shown that competitive environments can favor higher per-offspring investment (Roff 1992; Sinervo 1992).

We compared 24-hour nestling provisioning and growth rates between warblers breeding on Catalina Island, California and in Fairbanks, Alaska to test Lack's predictions and assumptions. We found that birds in Alaska fed their young for an average of 19 hours per day, approximately six hours more than birds in California. On average, birds in Alaska brought more total food to the nest, but the smaller brood sizes in California led to higher per-nestling provisioning rates in that population. Per-nestling provisioning rates did not vary with brood size within Alaska, but in California per-nestling food delivery was up to three times higher in small broods than in large broods. In addition, insect larvae had more calories but lower levels of protein and minerals in California, suggesting comparative studies of food quality will be important to understanding geographic variation in food delivery rates.

Surprisingly, we found that within California, nestlings from nests with higher per-nestling food delivery rates did not grow more quickly over 24-hours. By contrast, higher per-nestling food delivery was associated with greater mass gain, tarsus growth, and feather growth within Alaska. Birds in Alaska also showed greater feather growth over the 24-hour period than those in California, whereas mass gain and tarsus growth did not differ between populations. Our results raise the possibility that nestlings in these populations may allocate resources differently, with those in Alaska prioritizing rapid growth, perhaps reflecting their short breeding season. In addition, it shows that for growth rates, plasticity within populations does not mirror differences between populations, supporting previous work suggesting countergradient variation is frequently seen for measures of growth (Conover et al. 2009).

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CHAPTER 1:  
THE EFFECTS OF FOOD ABUNDANCE AND NEST PREDATION RISK ON AVIAN  
REPRODUCTIVE STRATEGIES<sup>1</sup>

SUMMARY

Resource abundance and predation risk often vary temporally and spatially, and these dynamic conditions can favor the evolution of phenotypic plasticity as a means of tracking environmental variation. However, because ecological conditions often covary in nature, it is difficult to identify the ecological factors that underlie observed variation in phenotypic traits. Here, we compare patterns of parental investment and behavior over a 7-year period in two island populations of orange-crowned warbler (*Oreothlypis celata*). We find that these populations show little genetic divergence and experience dramatic annual variation in rainfall, and that the islands also predictably differ in their risk of nest predation. The amount of rainfall in each year was correlated with food availability, and birds on both islands initiated breeding earlier and laid larger clutches in wetter years. By contrast, parental nest visitation rates were not affected by rainfall and instead reflected variation in nest predation risk within and between islands. Overall, we found considerable plasticity in response to spatial and temporal variation in

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environmental conditions, and the direction of this plasticity appeared adaptive. Our results also suggest that while the effects of food availability and nest predation have been viewed as mutually exclusive drivers of entire suites of life history and behavioral traits, each trait can differ in its sensitivity to resource abundance or mortality risk, and traits that are often correlated can be decoupled under appropriate environmental conditions.

## INTRODUCTION

Variation in ecological conditions such as age-specific mortality rates and resource abundance is thought to drive the evolution of life history and parental care strategies by altering the fitness costs and benefits associated with investment in different traits (Clutton-Brock 1991; Roff 1992; Stearns 1992). However, spatial and temporal variation in ecological factors often means that no single behavioral phenotype will be consistently optimal (Levins 1968). Theory predicts that spatial (e.g. Sultan and Spencer 2002) and temporal (e.g. Moran 1992) variation in ecological conditions should favor the evolution of adaptive phenotypic plasticity as a way of tracking environmental change. Yet, while studies of natural populations often find evidence for phenotypic plasticity in reproductive traits, it is difficult to establish which aspects of the environment specific traits are responding to because multiple biotic and abiotic factors often act simultaneously (e.g. Johansson et al. 2001; Stillwell et al. 2007). One way to identify the influences of different ecological factors is to use spatial and temporal comparisons in populations where the effects of each ecological factor on specific traits make opposing predictions.

Nest predation risk and food availability have long been considered the major ecological factors driving the evolution and expression of avian life histories (Lack 1947; Skutch 1949;

Martin et al. 2000; Ricklefs 2000). Such perspectives have traditionally treated nest predation risk and food availability as alternative, and often mutually exclusive, hypotheses to explain variation in parental investment, particularly clutch size (Lack 1947; Skutch 1949; Martin et al. 2000; Ricklefs 2000). Lack (1947) first championed the role of food availability in shaping nestling feeding rates, which he argued should constrain the evolution and expression of clutch sizes. In support of Lack's hypothesis, studies have shown that spatial and temporal variation in food availability often leads to plasticity in the timing of breeding, clutch size, and parental effort (e.g. Högstedt 1980; Perrins 1991; Grant et al. 2000; Thomas et al. 2001; Visser et al. 2006). In response to Lack, Skutch (1949) suggested that avian parental activity at nest sites could attract the attention of visually-oriented nest predators, so that nest visitation rates, and therefore clutch sizes, may be constrained by nest predation risk. As with food availability, nest predation risk varies over space and time, and parents can adjust nest site selection, clutch size, and nest visitation rates in response to perceived changes in risk (Ghalambor and Martin 2001, 2002; Eggers et al. 2005, 2006; Fontaine and Martin 2006; Schmidt et al. 2006; Lima 2009; Zanette et al. 2011).

Although studies have established that both food availability and nest predation risk affect avian parental investment and behavior, understanding the relative importance of each factor in shaping specific traits remains challenging because both factors simultaneously operate in all avian populations and often covary in ways that make similar predictions. For example, because it is generally thought that nest predation decreases with latitude while food availability increases with latitude, latitudinal comparisons of avian life histories are often unable to separate the effects of these two ecological factors (e.g. Martin 1996; Ricklefs and Wikelski 2002; McKinnon et al. 2010; Robinson et al. 2010). Where their joint effects have been studied, neither

food nor predation risk alone explains all variation in parental behavior and clutch sizes (e.g. Martin et al. 2000; Ferretti et al. 2005), but instead research suggests these factors can interact to shape parental phenotypes (Zanette et al. 2006; Eggers et al. 2008). Overcoming these challenges in natural populations can be achieved by quantifying how multiple traits track variation in predation risk and food abundance, and comparing systems where the predicted effects of each factor make opposing predictions.

Here, we exploit spatial and temporal variation in food abundance and nest predation risk to understand the mechanisms underlying variation in the reproductive behavior and life history strategies of orange-crowned warblers (*Oreothlypis celata*) breeding on Santa Catalina (hereafter Catalina) and Santa Cruz Islands. These are two of California's Channel Islands, and both islands have a mediterranean climate that is subject to dramatic changes in annual rainfall owing in large part to El Niño-driven dynamics (Cody and Mooney 1978; Polis et al. 1997). The islands are located approximately 150km from each other and have very similar biotic communities (Schoenherr et al. 1999), but two major differences provide a system that allows us to separate the effects of nest predation risk and food availability on avian parental strategies. First, the island scrub-jay (*Aphelocoma insularis*) is a visually-oriented nest predator found only on Santa Cruz Island, where it breeds in the same oak-dominated habitats as the warblers. No jay species occurs on Catalina Island and warblers there have no major visually-oriented nest predators (Peluc et al. 2008). Second, despite large annual fluctuations in rainfall, Santa Cruz Island averages more rainfall per year than Catalina Island (Langin et al. 2009), and below we demonstrate a positive relationship between rainfall and food abundance.

To understand the effects of food abundance and nest predation risk on variation in parental strategies, we quantified behavioral and life history traits 1) over a 7-year period, 2)

between Catalina and Santa Cruz Islands, and 3) across a gradient of nest predation risk within Santa Cruz Island. We also quantified the level of genetic divergence between warblers on these two islands. We then tested whether variation in food abundance or nest predation risk could better explain spatial and temporal patterns in a suite of reproductive traits. These comparisons are most informative when food availability and nest predation risk make opposing predictions, particularly when comparing between islands. For example, we predicted that the effects of nest predation would favor lower nestling visitation rates (Fontaine and Martin 2006) and smaller clutch sizes (Skutch 1949) on Santa Cruz Island compared to Catalina Island (Table 1.1). By contrast, higher rainfall and greater food availability on Santa Cruz Island predicts higher nest visitation rates and larger clutch sizes (Lack 1947; Perrins 1991). In addition, nest predation should favor lower nest placement on Santa Cruz Island (Peluc et al. 2008), and temporal variation in rainfall should lead warblers on both islands to breed earlier, have longer breeding seasons, lay larger clutches, and have higher incubation attentiveness and nestling visitation rates in wetter years, when food is more abundant (Martin 1987; Table 1.1). Such comparisons within and between islands allow us to assess which life history and behavioral traits are more sensitive to variation in food availability or to differences in nest predation risk.

## METHODS

### *Study Areas and Nest Monitoring*

Breeding orange-crowned warblers were intensively studied between 2003-09 in Bulrush Canyon (33°20'N, 118°26'W) on Catalina Island, California and between 2006-08 in Coches Prietos Canyon (33°58'N, 119°42'W) and between 2005-06 in Islay Canyon (33°59'N, 119°43'W) on Santa Cruz Island, which is approximately 150 km away. Warblers in our study

population belong to the *sordida* subspecies, which is endemic to coastal southern California and northern Baja California. During the breeding season this subspecies is largely confined to oak woodland and scrub habitats on the Channel Islands, although many individuals winter on the mainland. Aside from the presence of the island scrub-jay on Santa Cruz Island, nest predator communities are similar on both islands (Schoenherr et al. 1999). Gopher snakes (*Pituophis melanoleucus*) have been observed depredating nests on both islands, and other potential or observed nest predators include island foxes (*Urocyon littoralis*), deer mice (*Peromyscus maniculatus*), and on Catalina Island, feral cats (*Felis domesticus*). During each year of the study, populations were monitored from March through May and adults on the study plots were captured in mist-nets and uniquely marked with colored leg bands for individual identification. We mapped territorial boundaries and searched for all nesting attempts of 15-30 breeding pairs at each site. In this species, only females incubate eggs, while both parents feed the nestlings. We observed nests for activity at least every three days and checked nest contents to determine clutch sizes and clutch completion and hatch dates. We measured nest height after each nest fledged or failed.

To quantify parental behavior during the incubation and nestling periods, we videotaped nests for three hours during the morning. Sample sizes of nests monitored were smaller on Santa Cruz (incubation:  $n = 25$ ; nestling:  $n = 12$ ) than on Catalina Island (incubation:  $n = 44$ ; nestling:  $n = 84$ ) due to the fewer years of study and the extremely high nest predation rates on Santa Cruz Island (see below). Incubation videos were recorded on Catalina Island in 2004-05 and 2008-09, and on Santa Cruz Island in 2005, 2007, and 2008. We videotaped most nests during mid-incubation, and found no effect of incubation day on parental visitation rate among nests of known age ( $F_{1, 51} = 0.01$ ,  $P = 0.92$ ). We calculated incubation on-bout length as the mean

number of minutes of complete on-bouts (i.e. excluding those where a portion of the on-bout was not captured on video), and incubation attentiveness as the percentage of each video that the female was incubating. Incubation and nestling visitation rates were calculated as the number of trips per hour to the nest; we excluded any non-feeding visits during the nestling period. We were unable to quantify food load sizes because vegetation often obscured the bird's bill in our videos, however, nestling visitation rates have been shown to be positively correlated with food delivery rate (Martin et al. 2000). Nestling videos were recorded on day 7 or 8 post-hatch, from 2004-06 and 2008-09 on Catalina Island and in 2005 and 2007 on Santa Cruz Island.

#### *Genetic differences between individuals on different islands*

To quantify genetic divergence between warblers breeding on each island, we genotyped 198 adults from Catalina Island and 40 adults from Santa Cruz Island at seven variable microsatellite loci. Five (Dp $\mu$ 01, Dp $\mu$ 16, LSW $\mu$ 7, LSW $\mu$ 18, and Pat43) were previously used in an orange-crowned warbler population genetics study (Bull 2005), and two were developed for Kirtland's warblers (DkiB12 and DkiD128; King et al. 2005). Blood (30-100 $\mu$ L) was collected from the brachial vein of adults and stored in lysis buffer. DNA was extracted using a QIAGEN Biosprint 96 extraction robot and associated kit for whole animal blood.

Polymerase chain reactions (PCRs) were run in 10  $\mu$ l volumes for Dp $\mu$ 01, Dp $\mu$ 16, LSW $\mu$ 7, LSW $\mu$ 18, and Pat43, and 11  $\mu$ l volumes for DkiB12 and DkiD128. Each contained 1  $\mu$ l of genomic DNA (except LSW $\mu$ 18, which contained 1.5  $\mu$ l of DNA), 1  $\mu$ l of dNTPs (1mM deoxynucleotide triphosphates), 0.1  $\mu$ l of 1x Taq buffer, 0.5  $\mu$ l each of forward and reverse primers, and 1  $\mu$ l of FlexiTaq polymerase (Promega Corp., Wisconsin). Dp $\mu$ 01, Dp $\mu$ 16, DkiB12, and DkiD128 were run with 1  $\mu$ l of 25 mM MgCl<sub>2</sub>, while LSW $\mu$ 7, LSW $\mu$ 18, and Pat43 were run



with 0.9  $\mu$ l, 1.1  $\mu$ l, and 0.75  $\mu$ l of MgCl<sub>2</sub>, respectively. LSW $\mu$ 7 was run with 0.15  $\mu$ l of 2.5x bovine serum albumin (BSA), while DkiB12 and DkiD128 were run with 1  $\mu$ l of BSA.

PCR conditions consisted of initial denaturing at 94°C for 3 min, followed by 30 cycles of denaturation at 94°C for 30 sec, annealing for 30 sec, extension at 72°C for 45 sec, followed by a final extension at 72°C for 5 min. The annealing temperature was 61°C for Dp $\mu$ 01, 55°C for Dp $\mu$ 16, 57.5°C for LSW $\mu$ 7, 53°C for LSW $\mu$ 18, 58°C for Pat43, and 52°C for DkiB12 and DkiD128. Fluorescently labeled forward primers [Applied Biosystems Inc. (ABI)] were used to tag PCR products, and PCR amplicons from markers were pooled and analyzed using an ABI 3100 automated capillary sequencer. Fragments were sized using an internal size standard, GENESCAN ROX, and genotypes assigned using GENEMAPPER v. 4.01 (ABI).

Exact probabilities for Hardy-Weinberg proportions, expected and observed heterozygosity, linkage disequilibrium probabilities, and  $F_{ST}$  values were calculated in GENEPOP 4.0.10 (Raymond and Rousset 1995). Alleles at one locus, DkiD128, slightly deviated from Hardy-Weinberg proportions ( $\chi^2 = 9.72$ ,  $df = 4$ ,  $P = 0.0454$ ), while alleles at LSW $\mu$ 18 were found to be in linkage disequilibrium with both DkiB12 ( $\chi^2 = 12.66$ ,  $df = 4$ ,  $P = 0.0131$ ) and DkiD128 ( $\chi^2 = 11.92$ ,  $df = 4$ ,  $P = 0.0180$ ); these latter loci were not linked to each other ( $\chi^2 = 6.09$ ,  $df = 4$ ,  $P = 0.1923$ ). All other loci conformed to null expectations, and the number of alleles per locus ranged from 5 - 17 (Table S1.1). We calculated  $F_{ST}$  values using all seven loci and while excluding DkiB12 or LSW $\mu$ 18.

We used the program STRUCTURE 2.3.2 (Pritchard et al. 2000) to compare the fit of models with  $k = 1$  versus  $k = 2$  subpopulations. We used the admixture model of allele frequencies, and ran both a correlated and uncorrelated allele frequency model using a burn-in

period of 10,000 followed by 100,000 MCMC repetitions. Each model was run ten times, and we compared the likelihoods for one versus two subpopulations. All loci were included in this analysis.

### *Phenotypic variation between islands*

To quantify differences in nest predation risk between islands, we estimated daily nest survival probabilities using maximum likelihood methods in Program MARK (Dinsmore et al. 2002). Because we were interested in nest predation, rather than all sources of nest failure, we restricted the nests included in the analysis to those that were successful or depredated ( $n = 517$  nests). Predation was the primary source of nest failure on both islands. For failed nests in which at least one egg was laid, 85% of failures were due to predation, 9% were abandoned, 2% failed due to weather, 2% failed to hatch, 2% failed due to unknown causes, and only two nests (<1%) failed due to starvation. We considered five *a priori* models of the factors affecting nest survival: a constant model ( $S_{\text{Null}}$ ), an island effect ( $S_{\text{Island}}$ ), a nest height effect ( $S_{\text{Height}}$ ), an additive model with island and height ( $S_{\text{Island} + \text{Height}}$ ), and a model with both additive effects and an island by height interaction ( $S_{\text{Island} * \text{Height}}$ ). We fit all models with a logit-link function, and ranked them using Akaike's Information Criterion adjusted for small sample sizes ( $AIC_c$ ; Burnham and Anderson 2002). To visualize the variation in daily nest survival between islands and among years, we also fit separate models for each island and year (Fig. 1.1a). Orange-crowned warblers on Catalina built lower nests in response to simulated presentations of scrub-jays (Peluc et al. 2008), so we tested for a difference in nest heights between islands using a t-test assuming unequal variances (Catalina Island:  $n = 519$  nests, Santa Cruz Island:  $n = 97$  nests). In addition, we compared the percentage of nests in major vegetative strata (grasses/leaf

litter/ferns/herbaceous plants, vines, woody shrubs, and oaks) on both islands (Catalina Island: n = 478 nests, Santa Cruz Island n = 87 nests).

We compared nest visitation rates between islands to test Skutch's prediction of lower nest visitation rates in the presence of a visually-oriented nest predator. However, it is important to note that the effects of high predation risk and high food abundance on incubation visitation rates are potentially confounded, whereas the effects of nest predation risk and food abundance on nestling visitation rates lead to opposing predictions (see Table 1.1). Incubation visitation rates were modeled as a linear function of island, ambient temperature, and day of year. With the exception of three females, only a single nest from each female was included in the analysis of incubation visitation rates, so we did not include a random effect of bird identity in the model. To quantify variation in nestling feeding rates between islands, we modeled nestling visitation rates as a linear function of island and day of year. We did not include an effect of brood size because nest predation risk is expected to affect total visitation rates, rather than per-nestling visitation rates. We began by including a random effect of male identity because 10 of 69 banded males had video recordings from multiple nests included in our analysis; male identity was chosen because fewer males than females were not individually color-banded (15 males versus 35 females). However, male identity did not explain any variation in the data, and this random effect was removed.

To evaluate how clutch size varied across space, we tested for a difference in clutch size between islands. When we detected a significant seasonal decline in clutch size, based on Poisson regression (Agresti 2002), we limited our analysis to nests that were completed within 30 days of the first clutch completion date of the season and included only the first nest of each female. This was done to avoid confounding the effects of breeding season length and island, as

birds were always followed to the end of the breeding season on Catalina Island, but not on Santa Cruz Island. We excluded all nests that failed during laying or that were not located until the nestling period. We used a contingency test based on Pearson's Chi-squared statistic to test for a difference in clutch sizes between Santa Cruz (n = 59 nests) and Catalina Islands (n = 272 nests); to maintain sufficiently high probabilities for each cell, we excluded a single nest on Catalina Island with five eggs (this nest was included in Fig. 2b and in the analysis of clutch size versus rainfall; see below). All other clutches on both islands contained 2-4 eggs.

#### *Effects of relative scrub-jay abundance on nest visitation rates within Santa Cruz Island*

We quantified spatial variation in scrub-jay abundance within Coches Prietos Canyon on Santa Cruz Island from 2007-08, and tested for an effect of the relative abundance of this nest predator on nest visitation rates. Variation in island scrub-jay presence was quantified using five-minute surveys in each warbler territory. We placed survey points approximately 10m from warbler nests, and conducted a survey prior to each nest check. These surveys also limited the probability that a scrub-jay was present during nest checks. When the nest site was unknown, we did a survey during each territory visit near the suspected nest site or the center of warbler activity. All visual and auditory scrub-jay detections were recorded. The mean ( $\pm 1$  SE) number of scrub-jay surveys conducted in each territory in 2007 and 2008 was  $18.5 \pm 0.9$  and  $26.1 \pm 1.4$  surveys, respectively. Relative scrub-jay abundance, an index of scrub-jay habitat use in each territory, was calculated as the proportion of surveys in each territory in which at least one scrub-jay was detected. We modeled incubation visitation rate as a function of relative scrub-jay abundance, year, and an interaction between relative scrub-jay abundance and year (n = 15 territories). Nestling visitation rates were measured seven days post-hatch at five nests in 2007;

the small sample size reflects the rarity with which nests survived to the late nestling period. We used simple linear regression to test if relative scrub-jay abundance was correlated with nestling visitation rates.

### *Effects of rainfall on food abundance and phenotypic variation between years*

To test whether rainfall was associated with food abundance, we sampled insects and modeled larval counts as a function of precipitation. We calculated precipitation as the total rainfall from November through April using data from the Catalina Island Conservancy and Western Regional Climate Center stations located within several kilometers of our field sites (Fig. 1.1b; <http://www.wrcc.dri.edu/>). We sampled insects at two-week intervals from 2003-09 on Catalina Island and from 2006-08 on Santa Cruz Island by collecting branch clippings from oak trees at 12 randomly-generated grid locations in each study plot (Johnson and Sherry 2001); grid points were 25m apart. Foraging observations and nest videos showed warblers primarily foraged on insect larvae (dominated by Lepidoptera spp.). We based our analysis on larval counts from insect samples because the mean dry mass of each individual larva did not vary with rainfall (i.e. larvae were not larger in wetter years).

We used a zero-inflated model to analyze larval counts because over 20% of insect samples contained no larvae. Zero-inflated models are mixture models in which one set of predictor variables affects the probability of a zero count, and another (or the same) set of regressors is used to model the count; zeros can also arise from the count side of the model (see Martin et al. 2005 for further explanation). We modeled larval counts assuming a negative binomial distribution with a log-link function (Agresti 2002), while the probability of a zero count was inflated with probability  $p$ , modeled with a binomial distribution and a logit-link

function. The count-side model included a normally-distributed random effect which grouped samples from each island in each year (i.e. each level of precipitation), and potential fixed effects on both the count side and the zero-inflated side of the model were precipitation, island, and the wet mass of leaves from the branch clipping. Models with additive combinations of these fixed effects were fit using the adaptive Gaussian quadrature method for maximum likelihood estimation, and  $AIC_c$  values were used to select the most parsimonious model. The shape of the relationship between date and larvae number varied considerably between years, but we did not have the sample size to model this variability. We saw no evidence that rainfall simply shifted the timing of peak insect abundance. We therefore chose to model the number of insects collected at a fixed time, and restricted our analysis to samples collected during March because that was the month in which birds usually began breeding. The analysis was done using the NLMIXED procedure in SAS (SAS Institute 2008).

Our subsequent analyses were aimed at understanding patterns of phenotypic variation associated with variation in food abundance, and we used precipitation as a proxy for food abundance because the zero-inflated distribution of larval counts precluded their use in parametric statistical tests. We tested for effects of rainfall on the initiation of breeding and the length of the breeding season. We modeled the first clutch completion date on each island in each year as an additive linear function of rainfall and island. The latest clutch completion date on Catalina Island was modeled as a simple linear function of rainfall; field crews could not consistently remain on Santa Cruz Island until the end of each breeding season. Breeding season length on Catalina Island was calculated as the number of days between the earliest and latest clutch completion date in each year, reflecting the length of time that birds were initiating breeding, and was modeled as a simple linear function of rainfall ( $n = 7$  years). The length of the

breeding season on Catalina Island was highly correlated with both earliest ( $r = -0.88$ ) and latest ( $r = 0.90$ ) clutch completion date.

We also tested for effects of rainfall on incubation behavior, and focused on incubation attentiveness because it is predicted to increase with food availability (Chalfoun and Martin 2007). Incubation attentiveness was positively correlated with on-bout duration ( $r = 0.66$ ), and was negatively correlated with incubation visitation rate ( $r = -0.44$ ). Attentiveness was modeled as a linear function of precipitation, island, day of year, and ambient temperature. By including an island effect, we were able to capture any differences in behavior due to differences in the nest predator community. The inclusion of both a rainfall and an island effect therefore allowed us to understand how food abundance and nest predation risk jointly shaped avian behavior. We included a random effect that grouped nests from each island in each year; this random effect accounted for the lack of independence of the nests in each group relative to the level of precipitation. We used maximum likelihood to fit models with all additive combinations of the four fixed effects and compared AIC values to select the top model. Similarly, to test for an effect of rainfall on nestling feeding rates, we built models with additive combinations of precipitation, day of year, and island. Each model included a random effect that grouped nests from each island in each year, as in our analysis of incubation behavior. These analyses were done in the lme4 package in R (R Development Core Team 2009; Bates et al. 2011).

To test for a relationship between clutch size and precipitation, we assumed a quasi-Poisson distribution (Ver Hoef and Boveng 2007) of clutch sizes, in which the variance differed from the mean by a factor  $k$  to allow for underdispersion of the clutch size data relative to the Poisson distribution. Our model's estimate of the underdispersion parameter was  $k = 0.098$ , indicating that the estimated variance was approximately one tenth of the estimated mean, and

justifying our use of the quasi-Poisson. Results were statistically indistinguishable with an identity versus a log link function (reflecting the small range of clutch size values), so the identity link was used for ease of interpreting estimates. We included fixed effects for precipitation and island, and a random effect grouping nests from each island in each year. Our previous analysis demonstrated that birds on Santa Cruz Island laid larger clutches (see below), and this analysis was designed to evaluate if differences between islands were explained by variation in precipitation or whether a significant island effect remained after accounting for Santa Cruz Island's wetter climate. This analysis was based on the clutch size data described above, and was done using the GLIMMIX procedure in SAS (SAS Institute 2008).

## RESULTS

### *Genetic differences between individuals on different islands*

Our data indicated that genetic divergence between warbler populations on Catalina and Santa Cruz Islands was minimal. Including all loci, the overall  $F_{ST} = 0.0037$ . Our results were robust to excluding loci that violated test assumptions; without DkiB12 the  $F_{ST} = 0.0039$ , while without LSW $\mu$ 18 the  $F_{ST} = 0.0049$ . Results from program STRUCTURE also provide no support for population substructure. Under both the correlated and uncorrelated allele frequency models, the likelihood was higher in all runs assuming a single population than in runs assuming two subpopulations. In addition, for models assuming  $k = 2$ , individuals from both islands were equally likely to be assigned to each of the two subpopulations. Collectively, these results suggest that birds on these two islands show little genetic divergence. Because these islands have never been connected and birds from these islands winter on the mainland and willingly cross open water, this lack of divergence likely reflects gene flow rather than a recent divergence.



### *Phenotypic variation between islands*

Nest survival rates were higher on Catalina Island (where scrub-jays are absent) compared to Santa Cruz Island (Fig. 1.1a), and increased with nest height on both islands. Based on our top model ( $S_{\text{Island} + \text{Height}}$ ), estimated daily nest survival rates for a nest on the ground were  $0.952 \pm 0.004$  (95% CI: 0.944, 0.959) on Catalina Island and  $0.909 \pm 0.011$  (95% CI: 0.885, 0.928) on Santa Cruz Island. We found no support for an interaction between island and nest height, as the second-ranked model ( $S_{\text{Island} * \text{Height}}$ ) had one more parameter than the top model and had a  $\Delta\text{AIC}_c$  value of 1.97. Visual comparisons also reveal that the higher nest survival on Catalina Island was maintained across all years, with the exception of 2009 (Fig. 1.1a).

Nest heights were significantly higher on Catalina Island compared to Santa Cruz Island ( $t_{181.6} = -6.25$ ,  $P < 0.0001$ ; Fig. 2a). On Catalina Island, 28.2% of nests were built in grasses, leaf litter, ferns, or herbaceous plants, while 56.3% of nests on Santa Cruz Island were built in this class of vegetation. By contrast, 28.5% of nests on Catalina Island were built in oaks (of any height), while only 10.3% of nests on Santa Cruz Island were built in oaks; the vast majority of remaining nests on both islands were built in woody shrubs, while a few birds on Catalina Island nested in vines. These results suggest that the difference in nest heights between islands is unlikely to solely reflect differences in nest-site availability, as all breeding pairs on both islands had woody shrubs and oak trees in their territories.

Significant differences in incubation behavior were observed between the islands. Incubation visitation rates ( $\pm 1$  SE) were higher on Catalina ( $2.81 \pm 0.17$  trips/hr,  $n = 44$ ) compared to Santa Cruz ( $1.36 \pm 0.06$  trips/hr,  $n = 25$ ). Island had a significant effect on incubation visitation rate (island effect:  $F_{1, 62} = 36.83$ ,  $P < 0.0001$ ; whole model:  $F_{3, 62} = 14.93$ ,  $P < 0.0001$ ,  $R^2 = 0.42$ ), which was affected by day of year ( $F_{1, 62} = 4.86$ ,  $P = 0.031$ ) but not ambient

temperature ( $F_{1,62} = 0.58, P = 0.45$ ). Incubation visitation rate was negatively correlated with on-bout duration ( $r = -0.78$ ) and nest attentiveness ( $r = -0.44$ ), so we limited our statistical analysis to the visitation rate. However, birds on Catalina Island had shorter on-bouts ( $16.43 \pm 1.15$  min,  $n = 44$ ) and a lower percent attentiveness ( $67.23 \pm 1.28, n = 44$ ) than those on Santa Cruz Island ( $36.61 \pm 2.44$  min and  $76.91 \pm 1.26$ , respectively;  $n = 25$ ).

Birds on Santa Cruz Island had lower nestling visitation rates but laid larger clutches than individuals on Catalina Island (Fig. 1.2b,c). Nestling visitation rates were significantly lower on Santa Cruz Island (island effect:  $F_{1,93} = 21.20, P < 0.0001$ ; whole model:  $F_{2,93} = 11.25, P < 0.0001$ ), and were not affected by day of year ( $F_{1,93} = 0.80, P = 0.37$ ). Clutch sizes were significantly larger on Santa Cruz than on Catalina Island (Pearson  $\chi^2_{2, n=331} = 9.45, P = 0.0089$ ).

#### *Effects of relative scrub-jay abundance on nest visitation rates within Santa Cruz Island*

Warblers on Santa Cruz Island exhibited a significant reduction in activity at the nest in response to spatial variation in relative nest predator abundance (Fig. 1.3). Incubation visitation rate was negatively correlated with relative scrub-jay abundance (Fig. 1.3; relative scrub-jay abundance effect:  $F_{1,11} = 14.69, P = 0.0028$ ; whole model:  $F_{3,11} = 7.53, P = 0.0052, R^2 = 0.67$ ), and also differed between years, with more frequent visitations (i.e. shorter on-bouts) in 2007, a drought year, than in 2008 (Fig. 1.3; year effect:  $F_{1,11} = 17.98, P = 0.0014$ ). The interaction between relative scrub-jay abundance and year was not significant ( $F_{1,11} = 0.06, P = 0.81$ ). Mean ( $\pm 1$  SE) on-bout length was  $31.5 \pm 2.0$  minutes in 2007, and  $45.5 \pm 5.1$  minutes in 2008. Nestling visitation rates were also significantly negatively correlated with relative scrub-jay abundance ( $F_{1,3} = 15.74, P = 0.029, R^2 = 0.84$ ).

### *Effects of rainfall on food abundance and phenotypic variation between years*

There was substantial variation in rainfall on both islands during the course of this study (Fig. 1.1b). In turn, we found a positive relationship between rainfall and the abundance of insect larvae. The top model contained fixed effects for precipitation and island on the count side, and for leaf mass on the zero-inflated side. However, we found equivalent support for a reduced model without an island effect on the count side, as the  $\Delta AIC_c$  value for this model was only 0.3; the direction of the weak island effect indicated higher counts on Santa Cruz Island. Both models supported a positive correlation between rainfall and larval count (top model:  $t_9 = 2.41$ ,  $P = 0.039$ ), and a lower probability of a zero count as the mass of the branch clipping increased ( $t_9 = -3.03$ ,  $P = 0.014$ ).

Rainfall had strong effects on breeding phenology and clutch size (Fig. 1.4), but did not affect parental behavior. Birds initiated breeding earlier in wetter years (Fig. 1.4a; rainfall effect:  $F_{1,8} = 10.73$ ,  $P = 0.0113$ ; whole model:  $F_{2,8} = 6.89$ ,  $P = 0.0182$ ,  $R^2 = 0.63$ ), with no effect of island ( $F_{1,8} = 0.31$ ,  $P = 0.59$ ). On Catalina Island, the latest clutch completion date was positively correlated with rainfall ( $F_{1,5} = 18.23$ ,  $P = 0.0079$ ,  $R^2 = 0.78$ ), as was breeding season length ( $F_{1,5} = 45.89$ ,  $P = 0.0011$ ,  $R^2 = 0.90$ ). Thus, in wetter years birds bred earlier and longer.

We found no support for an effect of precipitation on incubation attentiveness or nestling feeding rates. Our top model of incubation attentiveness included fixed effects for island and temperature, and a likelihood ratio test indicated the addition of a precipitation effect did not provide a substantially better fit ( $P > 0.9$ ). Model selection results from an analysis of incubation visitation rates, rather than attentiveness, also failed to support a precipitation effect. In addition, nestling feeding rates were not affected by rainfall, as our top model included fixed effects of

island and day of year, and a likelihood ratio test did not support the addition of a precipitation effect ( $P > 0.8$ ).

Across both islands, clutch sizes were significantly larger in wetter years (Fig. 1.4b;  $F_{1, 321} = 9.39$ ,  $P = 0.0024$ ). We found no support for an additional island effect ( $F_{1, 321} = 0.65$ ,  $P = 0.42$ ), suggesting that larger clutch sizes on Santa Cruz Island reflect higher rainfall on that island.

## DISCUSSION

Theory predicts that ecological variation should favor adaptive phenotypic plasticity as a means of tracking dynamic environments (Levins 1968; Moran 1992; Sultan and Spencer 2002; Ghalambor et al. 2010). In birds, food abundance and nest predation risk are thought to shape life history traits, but because both factors operate simultaneously, few studies have effectively partitioned their effects on multiple traits (Martin 1996). We found that orange-crowned warblers breeding on Catalina and Santa Cruz Islands experienced substantial spatial and temporal variation in nest predation risk (Fig. 1.1a) and rainfall (Fig. 1.1b), and food abundance was higher in wetter years. Because these populations showed little genetic differentiation, individuals with a similar genetic background experienced considerable variation in ecological conditions. In the face of this variation, these warblers plastically adjusted their parental investment and behavior between years, between islands, and across a spatial gradient of nest predation risk on Santa Cruz Island. Specifically, nest visitation rate (Fig. 1.2c, 1.3) and nest height (Fig. 1.2a) responded to variation in nest predation risk, whereas clutch size and breeding phenology were correlated with rainfall (Fig. 1.4), and therefore with food abundance. Therefore, while warblers appear to track ecological variation, each trait differed in its sensitivity to food

abundance and nest predation risk. Below we describe patterns of plasticity in these traits in more detail, and discuss how these patterns can inform our understanding of evolutionary changes in parental strategies.

### *The effects of food abundance and nest predation risk*

The selective pressures imposed by variation in food abundance and nest predation risk have often been considered alternative hypotheses to explain avian life history variation (reviewed in Ricklefs 2000). Both Lack (1947) and Skutch (1949) predicted that clutch and brood sizes should generally be proportional to food delivery, although they differed in whether variation in these traits could be explained by food availability or nest predation risk, respectively. We found that nestling visitation rates did not constrain clutch sizes, as birds on Santa Cruz Island had both larger clutches and lower nestling visitation rates (Fig. 1.2b,c). This decoupling allowed some predictions from both hypotheses to be supported: as Skutch predicted, variation in nestling visitation rates between islands (Fig. 1.2c) and within Santa Cruz Island (Fig. 1.3) likely reflected the constraint of visually-oriented nest predators, but as Lack predicted, birds on both islands laid larger clutches in wetter years (Fig. 1.4b), when food was more abundant. Yet counter to their predictions (Table 1.1), variation in rainfall did not increase nestling visitation rates, and nest predation risk had no apparent effect on clutch sizes. Birds on Santa Cruz Island may have achieved their larger brood sizes while maintaining lower nestling visitation rates by bringing more food per visit, but food load sizes were not visible in most videos from Santa Cruz Island. Nevertheless, the different sensitivities of these traits to different types of ecological variation indicates that while measures of parental investment such as clutch

size and nestling visitation rates are often correlated, we should not assume that they are primarily shaped by the same ecological factor.

In wetter years, birds began breeding earlier and laid larger clutches (Fig. 1.4), likely reflecting their responses to variation food abundance - an interpretation supported not only by our insect sampling but also by previous studies. Although nest predation rates can be lower in wetter years (Morrison and Bolger 2002; Chase et al. 2005), our evidence suggests rainfall did not affect nest predation risk or adult survival on Catalina Island (see Chapter 2). In addition, studies in dry climates have shown that productivity and food availability for birds increases with rainfall (Noy-Meir 1973; Smith 1982; Boag and Grant 1984), and suggested that birds lay larger clutch sizes in wetter years in response to variation in food abundance (Rotenberry and Wiens 1991; Newton 1998; Lloyd 1999; Patten and Rotenberry 1999; Grant et al. 2000). A similar pattern is seen with variation in breeding phenology (Hau et al. 2004; Illera and Diaz 2006; Boulton et al. 2011). Our results suggest a shared reaction norm between birds on Catalina and Santa Cruz Island for these traits because after accounting for the effect of rainfall, breeding phenology and clutch sizes did not differ between islands (Fig. 1.4). Higher rainfall on Santa Cruz Island can therefore explain the larger clutch sizes we observed there, and combined with the observation that these populations show little genetic divergence, this suggests that inter-island variation in clutch size reflects phenotypic plasticity, rather than fixed genetic differences.

While most traits we analyzed appeared to primarily respond to either food abundance or nest predation risk, these ecological factors can also jointly affect each trait (e.g. Zanette et al. 2006; Eggers et al. 2008). We saw this pattern with incubation visitation rates on Santa Cruz Island, which were affected by relative nest predator abundance and were also higher in 2007, a drought year (Langin et al. 2009), than in 2008 (Fig. 1.3). The difference in visitation rate was

the result of shorter on-bouts in the drier year, supporting previous studies suggesting that on-bout length is constrained by resource availability (e.g. Chaurand and Weimerskirch 1994). In contrast, the incubation behavior of females on Catalina Island, where visitation rates are unconstrained by visually-oriented predators, did not vary with precipitation. This pattern raises the possibility that when nest visitation rates are constrained by predators, on-bout lengths may more closely reflect parental energetics than when birds can go back and forth from their nests without increasing nest predation risk.

#### *Scale and fitness consequences of behavioral responses*

In addition to increasing our understanding of how different behavioral traits may be most sensitive to different ecological conditions, studies of plasticity also highlight the spatial and temporal scales at which birds respond to ecological variation. Studies have long attributed spatial and temporal variation in phenology, behavior, and clutch sizes to variation in food abundance (reviewed in Martin 1987). However, fewer studies have assessed the scale at which birds respond to nest predation risk (Fontaine and Martin 2006; Lima 2009; Emmering and Schmidt 2011). We show that birds on Santa Cruz Island whose territories had a higher relative abundance of scrub-jays had lower visitation rates than other pairs breeding in the same drainage (Fig. 1.3), suggesting birds can assess nest predation risk at a small spatial scale, perhaps at the territory level.

The behavioral responses to nest predation risk that we observed within Santa Cruz Island and between islands mirror plasticity observed within Catalina Island, where experimental presentations of scrub-jays led to lower nest placement and lower nestling visitation rates, despite the absence of jays on that island (Peluc et al. 2008). These insular endemic (*O. c.*

*sordida*) populations show an exceptional degree of plasticity in nest height and in the vegetative strata used for nesting, as nest placement is often evolutionarily conserved (Collias and Collias 1984). Given the lack of genetic differentiation that we observed, that corvid nest predators may be more likely to depredate higher nests (Soderstrom et al. 1998), and that species with higher nest predation risk have lower visitation rates (Conway and Martin 2000; Martin et al. 2000), these differences in visitation rates and nest placement likely reflect adaptive behavioral plasticity in response to the presence of the island scrub-jay.

Interestingly, our analysis of nest success did not reveal a nest height by island interaction, which would be expected if scrub-jays are the warbler's main nest predator on Santa Cruz Island and primarily depredate higher nests. Instead, we suspect that although the presence of the scrub-jay induces warblers to nest on or near the ground, lower nest sites are more vulnerable to snakes and small mammals (Peluc et al. 2008), and these predators may actually depredate the majority of nests on Santa Cruz Island. In addition, lowering nest height may have been rendered less effective because overgrazing by feral livestock had substantially reduced understory vegetation on Santa Cruz Island. The last of these non-native herbivores was removed in 2006 (Morrison 2007). As native vegetation recovers, more concealed nest sites should become available, which will likely benefit orange-crowned warblers and other passerines (Langin et al. 2009).

#### *Plasticity in avian reproductive strategies*

Studies of plasticity can increase our understanding of the relative importance of the ecological factors that drive life history evolution because plastic responses to environmental cues may shift the distribution of phenotypes in a population in the same direction that is



predicted to evolve under directional selection on alleles with fixed effects (e.g. Aubret et al. 2004; Huizinga et al. 2009; Scoville and Pfrender 2010). Given that plasticity can facilitate adaptive evolution (reviewed in West-Eberhard 2003; Ghalambor et al. 2007; Pfennig et al. 2010), documenting patterns of plasticity can enhance our understanding of how organisms adapt to ecological variation and how multiple ecological factors interact to shape life history traits. Indeed, our results show that plastic responses to predators and food availability are the same as the expected evolved responses. While neither Lack's nor Skutch's hypotheses distinguish between plastic versus evolved responses, many tests of these hypotheses have been predicated on individuals' ability to perceive and respond to environmental variation, and Lack (1954) noted that the strongest evidence for his hypothesis came from intraspecific studies.

Studies of plasticity across environments with rare or unique combinations of ecological factors can be particularly informative because they allow researchers to assess whether frequently observed correlations between traits are maintained. In our study, high nest predation risk was associated with high food abundance, whereas these factors may often be negatively correlated in latitudinal comparisons (Martin 1996; Ricklefs and Wikelski 2002; McKinnon et al. 2010; Robinson et al. 2010). Our results show that the phenotypic correlation between traits such as nestling visitation rate and clutch size, which is often assumed to be positive (e.g. Skutch 1949), can be reversed. The negative correlation we observed between these traits, with lower nestling visitation rates and higher clutch sizes on Santa Cruz Island, instead appeared to reflect the different sensitivities of each trait to food abundance and nest predation risk. Collectively, our results emphasize that phenotypic correlations between traits can reflect correlated ecological conditions, and that individual traits can be shaped to a different extent by ecological factors such as food abundance and predation risk.

## RECOGNITION

This work was supported by The Nature Conservancy, the Smithsonian Institution, an American Ornithologists' Union Graduate Research Award (HRS), a Frank M. Chapman Memorial Grant from the American Museum of Natural History (HRS), and a UCR / NRS Mildred E. Mathias Graduate Student Research Grant (SIP). HRS was supported by Colorado State University, NSF-IGERT Grant DGE-#0221595 (administered by the PRIMES program at Colorado State University), NSF Grant #846175 to CKG, and by a Smithsonian Institution Predoctoral Fellowship. This work was performed (in part) at the University of California Natural Reserve System's Santa Cruz Island Reserve on property owned and managed by The Nature Conservancy. Logistical support was provided by the Catalina Island Conservancy, The Nature Conservancy of California, and the University of California's Santa Cruz Island Reserve. Genetics lab work was conducted at the Smithsonian Center for Conservation and Evolutionary Genetics at the National Zoological Park in collaboration with Robert C. Fleischer, Brent Horton, and Spencer Galen. We thank many students and field technicians, especially K. M. Langin, J. Yoon, H. Montag, and J. Coumoutso-Hoppert, for help with data collection and with transcribing nest videos. P. L. Chapman provided statistical advice, and W. C. Funk, B. R. Noon, T. B. Ryder, and C. T. Webb provided helpful advice and comments on the manuscript.

TABLES AND FIGURES

Table 1.1: Summary of the predicted effects of spatial and temporal variation in food abundance and nest predation risk. The effects of food abundance and nest predation risk make opposing predictions for nestling visitation rate and clutch size, as high nest predation risk should favor lower nestling visitation rates and smaller clutch sizes while high food abundance is expected to increase both feeding trips and clutch sizes. Indirect effects on incubation behaviors arise because incubation visitation rate, on-bout lengths, and attentiveness are often negatively correlated. For example, high nest predation risk is expected to favor lower incubation visitation rates, but high food abundance may increase on-bout lengths, and thereby also lead to lower incubation visitation rates.

	Nest Height	Breeding phenology	Incubation visitation rate	Incubation attentiveness	Nestling visitation rate	Clutch Size
Food abundance	0	Earlier breeding	Indirect only	+	+	+
Nest predation risk	-	Variable	-	Indirect only	-	-

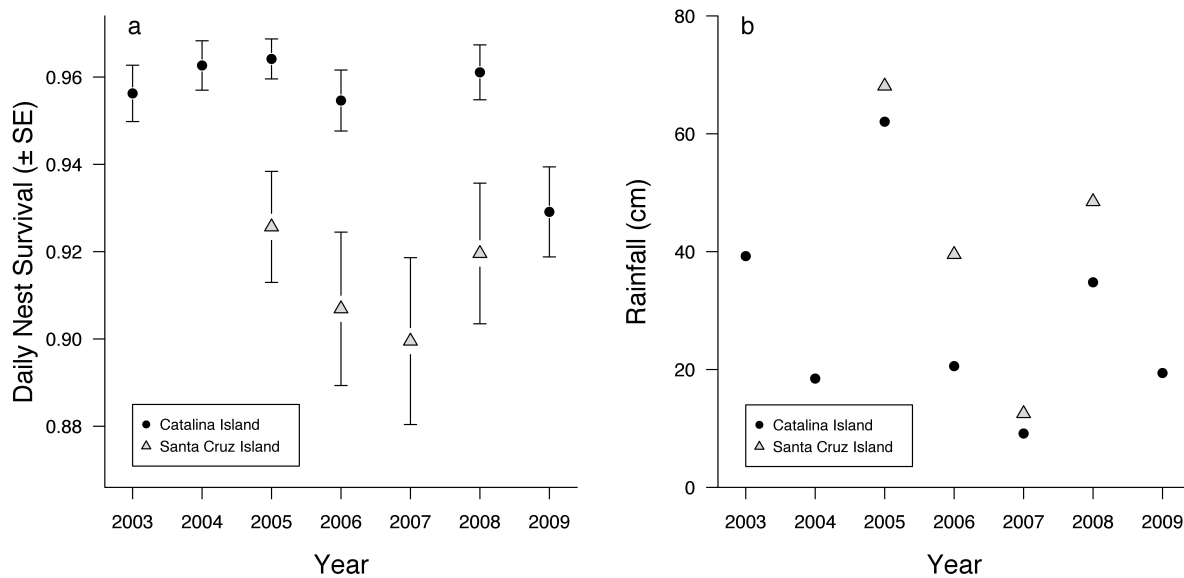


Figure 1.1: Spatial and temporal variation in daily nest survival and precipitation. (a) Daily nest survival was higher on Catalina Island than on Santa Cruz Island. (b) Total rainfall during winter and spring varied considerably between years, with Santa Cruz Island always receiving more rainfall in a given year than Catalina Island.

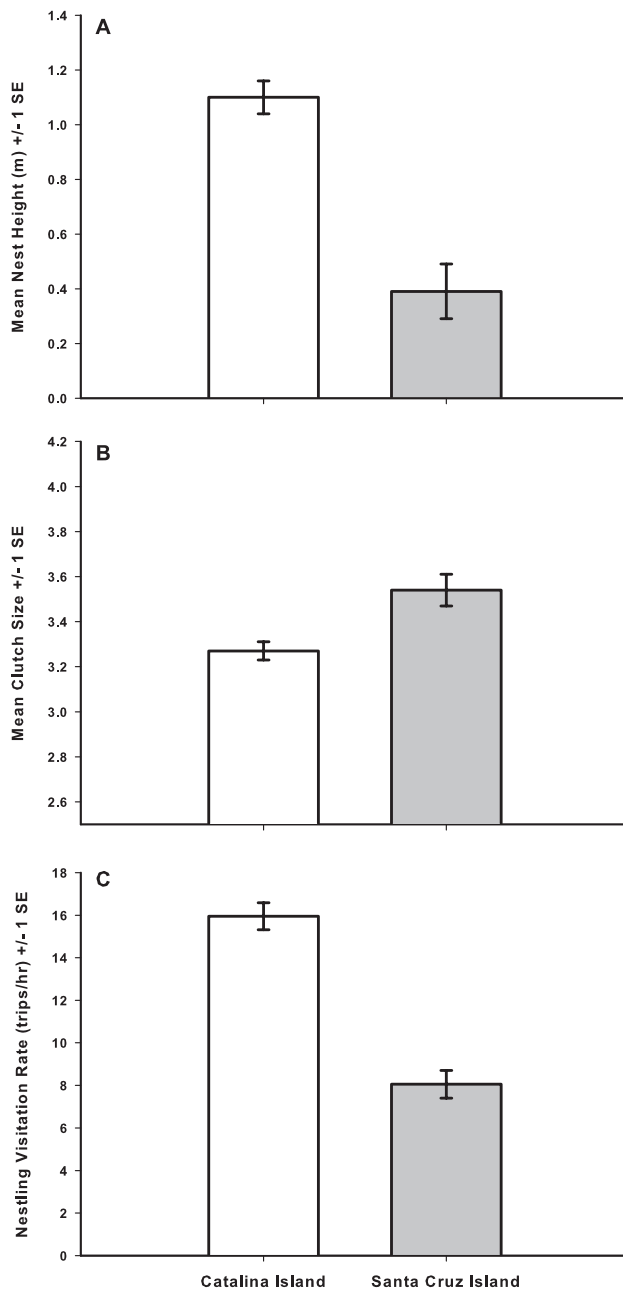


Figure 1.2: Divergence in reproductive traits between the two islands ( $\pm 1$  SE). (a) Mean nest height (m; n = 519 Catalina, n=97 Santa Cruz), (b) Mean clutch size (n = 273 nests, mode = 3 Catalina; n = 59 nests, mode=4, Santa Cruz), (c) Mean nestling visitation rates (trips/hr; n = 84 Catalina, n=12 Santa Cruz).

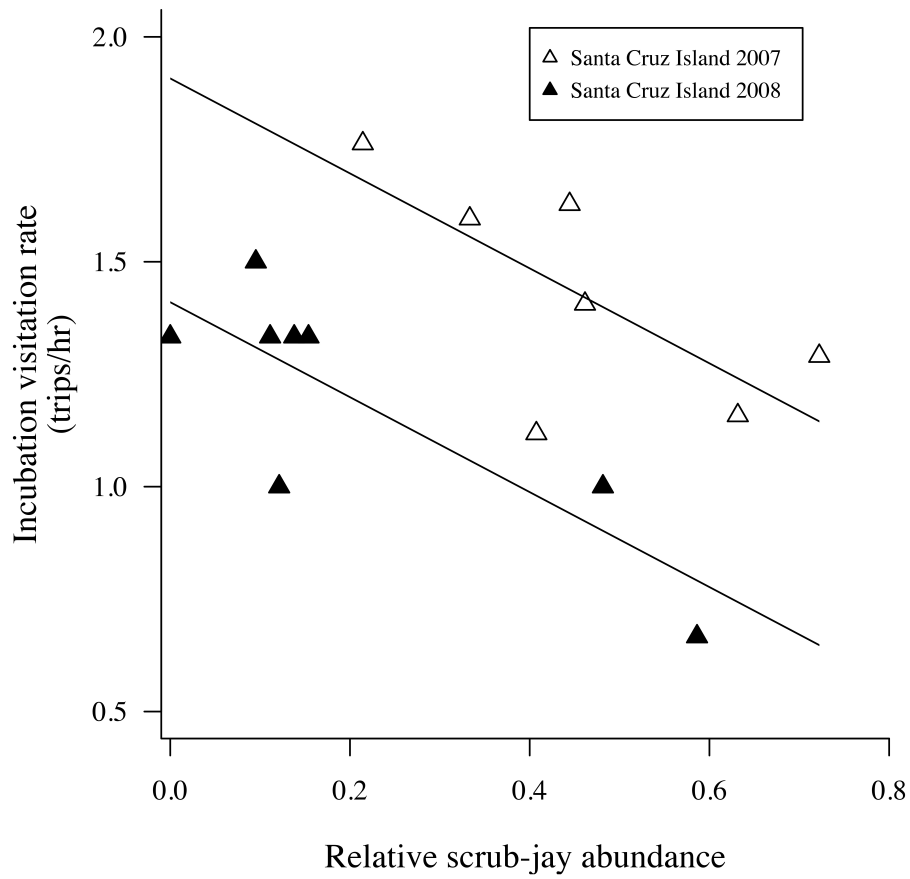


Figure 1.3: Nest visitation rates declined with increasing relative scrub-jay abundance. Nest visitation rates were significantly higher in 2007, a drought year, and there was no significant interaction between year and relative scrub-jay abundance.

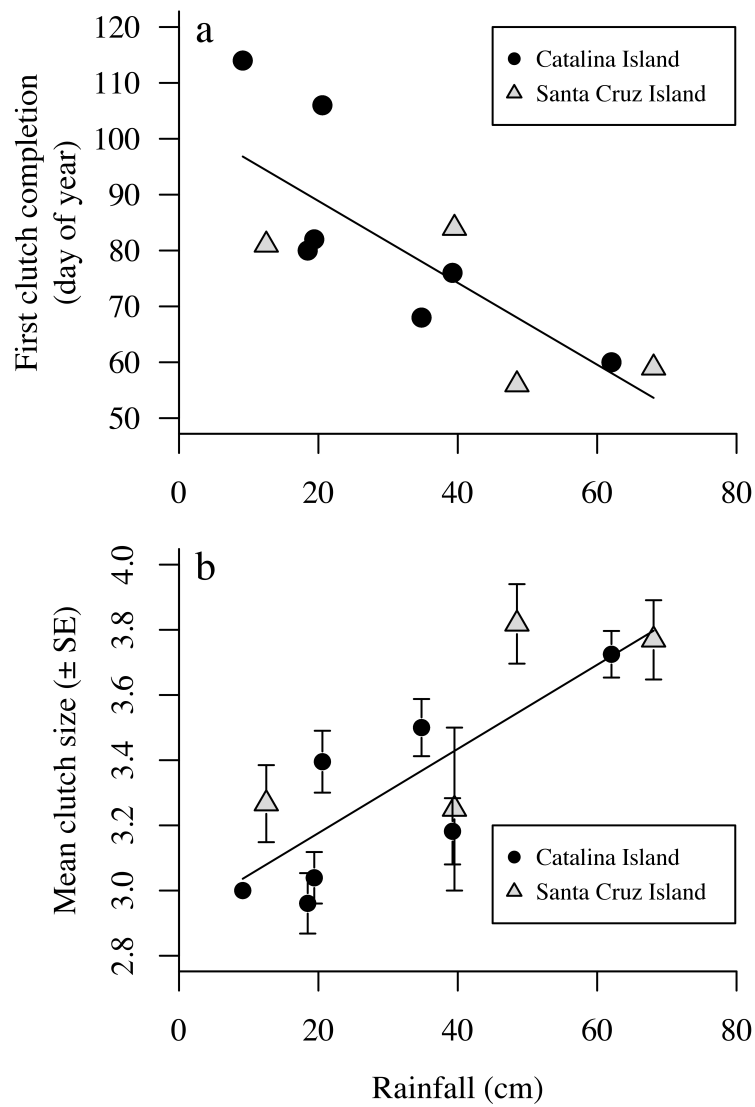


Figure 1.4: Birds on both islands responded similarly to annual variation in precipitation by (a) initiating breeding earlier and (b) laying larger clutches in wetter years.

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## APPENDIX I

Table S1.1: Details of the seven microsatellite loci used to quantify population differentiation.

All values are given for the Catalina Island population followed by the Santa Cruz Island population. Results from tests for deviation from Hardy-Weinberg proportions are given for both populations combined as well as for within each population.

Locus	# of alleles	# of individuals genotyped	H-W probability test	H <sub>obs</sub>	H <sub>exp</sub>
Dpμ01	15 / 11	193 / 38	0.373 (0.163 / 0.735)	0.720 / 0.737	0.698 / 0.741
Dpμ16	5 / 4	196 / 38	0.631 (0.379 / 0.728)	0.531 / 0.605	0.585 / 0.633
LSWμ7	7 / 6	197 / 40	0.854 (0.706 / 0.724)	0.660 / 0.675	0.683 / 0.665
LSWμ18	17 / 14	195 / 40	0.217 (0.294 / 0.189)	0.872 / 0.925	0.882 / 0.894
Pat43	9 / 7	196 / 40	0.639 (0.331 / 0.851)	0.857 / 0.750	0.840 / 0.757
DkiB12	10 / 8	192 / 38	0.404 (0.828 / 0.162)	0.849 / 0.895	0.830 / 0.780
DkiD128	16 / 13	183 / 38	0.045 (0.031 / 0.252)	0.896 / 0.947	0.907 / 0.920



CHAPTER 2:  
EFFECTS OF RAINFALL AND DENSITY-DEPENDENT NEST PREDATION ON THE  
DEMOGRAPHY OF AN ISLAND BIRD POPULATION<sup>2</sup>

SUMMARY

The ecological mechanisms responsible for population limitation and regulation remain unknown for most species. Studies of these mechanisms have revealed a role of intraspecific competition, but few have simultaneously evaluated the effects of predation, changes in resource abundance, and fluctuations in weather. Here we assess the strength of density-dependent and density-independent effects on the demography of orange-crowned warblers (*Oreothlypis celata*) breeding on Santa Catalina Island, California over a 7 year period. In this system, rainfall was a major driver of food abundance during the breeding season and warbler fecundity was higher in wetter years, highlighting the density-independent effects of weather. Adult survival was not strongly influenced by rainfall, breeding densities, or wintering densities in mainland Southern California. Fecundity was regulated by density-dependent nest predation, but we did not find evidence that competition for food varied with warbler density. These results show how density-dependent nest predation can underlie the relationship between population density and fecundity, even in a high-density island population where intraspecific competition was expected to be

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important. In addition, our methods highlight how zero-inflated models can be applied to understand the mechanisms by which ecological factors influence demography.

## INTRODUCTION

Understanding population dynamics requires identifying the factors that limit and regulate natural populations (Nicholson 1933; Sinclair 1989; Murdoch 1994). Yet, while the historical debate over the importance of limiting versus regulating factors has ended with a consensus that both have important effects on population demography (Kingsland 1995), few studies have examined how competition, predation, and weather collectively affect demography. Although competition for food or other resources may be the most frequent mechanism underlying population regulation (Lack 1954; Arcese and Smith 1988; Harrison and Cappuccino 1995; Dobson and Oli 2001; Sinclair 2003), predators may also regulate populations through functional or numeric responses to prey density (Holling 1959; Calef 1973; Hixon and Carr 1997). In addition, weather can limit resource abundance and thus can have a major influence on demography (Grant et al. 2000; Morrison and Bolger 2002), but although both density-independent variation in weather and density-dependent biotic processes like competition and predation can shape variation in fecundity and survival (Forchhammer et al. 1998; Coulson et al. 2000; Sillett et al. 2004), the mechanisms by which these processes act are rarely known.

Avian populations have long been model systems for developing and testing mechanistic hypotheses to explain how density-dependent and density-independent processes affect fecundity and survival. Early theory predicted that the limits to population growth would be strongest during the season when food resources were most limiting, and so would generally affect overwinter survival for populations in temperate regions (Lack 1954; Fretwell 1972). Yet

subsequent empirical research has shown that the factors that limit and regulate avian populations may act via either fecundity (Both 1998; Sillett and Holmes 2005; Brouwer et al. 2009), survival (Smith et al. 1980; Jansson et al. 1981; Sherry and Holmes 1996), or both demographic rates (Arcese et al. 1992; Gunnarsson et al. 2005). However, few studies have quantified how variation in weather, resource abundance, and population density jointly shape vital rates across the annual cycle, particularly in migratory birds, where our understanding of population regulation remains limited to only a few well-studied species (Sillett and Holmes 2005; Faaborg et al. 2010).

Here, we quantify the effects of breeding and non-breeding densities on the fecundity and survival of orange-crowned warblers (*Oreothlypis celata sordida*) and separate the demographic effects of density from those of rainfall. Our study population breeds on Santa Catalina Island, off the coast of southern California, and winters in coastal California and Baja California, Mexico (Dunn and Garrett 1997). We predicted that both density-dependent processes and rainfall would affect the demography of this population, and we had several reasons to expect intraspecific competition to be important. First, as is typical for an insular community (MacArthur et al. 1972), the California Channel Islands have relatively few breeding bird species, and these reach higher population densities than in comparable mainland habitat (Yeaton 1974). Second, males in our study population maintain unusually high testosterone levels during breeding (Horton et al. 2010) and respond more strongly to experimental playback of conspecific songs than in a lower density mainland population (Yoon et al. 2012). Finally, the California Channel Islands experience substantial variation in annual rainfall, and our previous work showed that food abundance, clutch initiation dates, breeding season length, and clutch sizes of *O. c. sordida* were all correlated with the total amount of winter and spring rainfall during the

years of our study (Sofaer et al. *in review*). The relationship between precipitation and food abundance and the warblers' strong behavioral responses to variation in rainfall imply that resource limitation may have important demographic effects in this population.

To understand how density-dependent and density-independent processes shaped warbler demography, we modeled the effects of conspecific density and rainfall on fecundity and survival. Our survival analysis assessed the importance of rainfall and population density on both the breeding and wintering grounds, allowing us to quantify their effects on demography during multiple phases of the annual cycle. Our analysis of fecundity was designed to account for the observation that many breeding pairs in our study fledged no young in a given year, as is typical for avian fecundity data. We therefore applied zero-inflated models, which allowed us to separate effects on the number of young fledged from effects on the probability of fledging no young. We predicted that factors influencing clutch size and the frequency of double-brooding would affect the number of young fledged, while factors affecting nest survival would affect the probability of fledging no young. Our use of zero-inflated models improved our mechanistic understanding of warbler demography, but although these models are broadly applicable to studies of reproductive success and fecundity, their application within ecology has been focused on studies of distribution and abundance (Martin *et al.* 2005).

## METHODS

### *Field methods*

We studied breeding orange-crowned warblers in Bulrush Canyon (33°20'N, 118°26'W) on Santa Catalina Island, CA (hereafter, Catalina Island) each spring from 2003-2009. The *O. c. sordida* subspecies is endemic to the California Channel Islands and adjacent coastal chaparral

habitat in mainland southern California. Most adults within our 6.8 ha study area were captured in mist-nets using conspecific playback and given a unique combination of colored plastic leg bands and a numbered U.S. Geological Survey aluminum band. Each March, intensive surveys were conducted throughout the study plot and adjoining habitat to resight color-banded warblers for our survival analysis. Those individuals were then monitored every 1-3 days throughout the breeding season to: (1) map territory boundaries relative to a 25x25m grid system, and (2) locate and monitor all nesting attempts, including renesting and double-brooding (see also Sofaer et al. *in review*). From 2003-2009, the number of territorial pairs in our study plot ranged from 23.4 (3.4 territories per ha) to 43.1 (6.3 territories per ha), and for each pair we used our mapping data to calculate the distance to the nearest neighbor (m), based on the center of each territory.

### *Fecundity and Nest Survival*

We collected longitudinal data on 181 breeding warbler pairs to characterize annual fecundity in our study area. We limited our fecundity analysis to pairs that either successfully fledged young or had an active, monitored nest after April 15<sup>th</sup>; these criteria excluded pairs that may have had an undetected renesting attempt. In 2007, an extreme drought led most pairs to skip breeding (Langin et al. 2009), so for that year we included closely monitored pairs that did not have any active nests. The average number of pairs included each year was 26 (range: 13 - 33 pairs). We calculated annual fecundity of each pair as the total number of young fledged from all nesting attempts in a given year.

Before analyzing our fecundity data, we visually inspected spatial plots and variograms to evaluate the degree of spatial autocorrelation in fecundity across our study area. A bubble plot of fecundity was created using the ggplot2 package in R (Wickham 2009; R Development Core

Team 2011), and showed no evidence of variation in the distribution of fecundity across space (Figure S1). In addition, variograms produced by combining data from all years (Figure S2), as well as those based on each year alone, showed little to no increase in the semivariance with increasing distance. Variograms were produced using the *geoR* package in R (Diggle and Ribeiro 2007). Because these plots showed only weak evidence of spatial autocorrelation in fecundity, we proceeded with analyses assuming independence between pairs.

We analyzed fecundity using zero-inflated models (see Martin *et al.* 2005), as 52% (95 of 181) of pairs fledged no young over the course of a breeding season. We used zero-inflated Poisson regression, which assumed fecundity was a mixture of two processes: one that inflates the probability of a zero (i.e. no successful reproduction), and one that affects the count (i.e. the number of young fledged). While zeros can arise from the count-side process, the zero-side process models effects leading to a higher proportion of zeros than would be expected from a Poisson distribution. For example, a Poisson distribution with a mean of 2.9 (the mean number of young fledged by successful pairs; see below) should yield data with 5.5% zeros, whereas over half of our observations were zeros. The probability of a zero was modeled as a binomial distribution with a logit link, while the count was modeled as a Poisson distribution with a log link.

We evaluated how precipitation and breeding density (the number of territorial pairs per ha) affected both the zero-side and count-side processes. We calculated precipitation as the total rainfall from November through April at a weather station located in Middle Ranch, Catalina Island (33°21'N, 118°26'W). This measure of precipitation was positively correlated with the primary food source for the warblers (insect larvae), clutch size, and, breeding season length, and negatively correlated with clutch initiation dates (Sofaer *et al. in review*). To account for the

shared density and rainfall values for pairs in the same year, we fit a normally distributed random effect of year on both the zero and count sides of the model; these random effects were assumed to be uncorrelated. However, in the full model (see below) the random effect of year on the count side of the model was estimated at zero, so we fit all models with the random effect only on the zero side.

In our statistical analysis of fecundity, we considered the following four fixed-effect model structures: intercept only, a precipitation effect, a breeding density effect, and an additive model with both precipitation and breeding density. We fit all combinations of these four model structures on both the count-side and zero-side processes, for a total of 16 possible models (Table 2.1), but did not have sufficient statistical power to consider interactions between breeding density and rainfall. For model selection, we used Akaike's information criteria adjusted for small sample sizes ( $AIC_c$ ; Burnham and Anderson 2002). All models were fit using the NLMIXED procedure in SAS (SAS Institute 2008).

Because results from our zero-inflated models indicated breeding density affected the probability of fledging no young, we analyzed daily nest survival probability to evaluate the effects of breeding density, precipitation, date, and nest site and territory attributes on nest predation rate. Because we were interested in factors affecting nest predation, rather than all sources of nest failure, we limited our analysis to nests that either fledged young or were depredated (as opposed to failure due to abandonment, weather, or starvation). We checked nest contents and observed adult behavior to unambiguously assign a nest fate to all nests included in our analysis. For each breeding pair in each year, we included the earliest successful or depredated nest in which at least one egg was laid ( $n = 142$  nests). Following Rotella et al. (2004, 2007), we modeled daily nest survival using a generalized linear mixed model assuming a

binomial distribution. Each day a nest was known to be active and each interval over which a nest failed contributed one survival interval to our analysis ( $n = 1983$  intervals). All models included a normally distributed, random effect of year to account for the lack of independence between breeding density and precipitation values within a year, and all models were fit with a logit link function. We built models including all additive combinations of the following five fixed effects: precipitation, date, nest height (Peluc et al. 2008), breeding density, and nearest neighbor distance (Table S2.1). Nearest neighbor distance was used to assess the effects of local density, whereas the breeding density covariate quantified plot-level density effects (these two measures of density were not highly correlated;  $r = -0.28$ ). We used Akaike's information criteria adjusted for small sample sizes ( $AIC_c$ ) for model selection. All models were fit using the NLMIXED procedure in SAS (SAS Institute 2008) and we calculated standard errors and confidence intervals based on the delta method (Powell 2007; Cooch and White 2012).

### *Adult Survival*

We fit Cormack-Jolly-Seber models (Lebreton et al. 1992) to estimate annual apparent survival ( $\phi$ ) and recapture ( $p$ ) probabilities of territorial adults ( $n = 197$ ). We used recapture and resighting data to model apparent survival from March to the following March. We calculated an index of winter density based on Christmas Bird Count data (hereafter CBC; National Audubon Society 2010). The CBC is a one-day count that occurs between mid-December and early January. Volunteers follow designated routes within 24-km radius count circles and record all birds observed that day; the location of each count circle is consistent between years. Groups of participants, known as parties, search for birds, and each party covers a different route within each count circle. Search effort is measured as the total number of party-hours (Dunn et al.



2005). We summarized data from count circles in the regular wintering range of *O. c. sordida*, which includes coastal habitats in northern Baja California and five southern California counties: Los Angeles, Orange, San Diego, Santa Barbara, and Ventura (K. Garrett, pers. comm.). We included count circles where at least one orange-crowned warbler was detected in all years between the winters of 2003-04 and 2009-10 ( $n = 19$  count circles). CBC data did not identify warblers to the subspecies level, and counts likely included subspecies other than *O. c. sordida* (Dunn and Garrett 1997). As morphological differences between subspecies are relatively slight (Gilbert et al. 2010), we assumed that these subspecies were ecologically equivalent during the non-breeding season and averaged the number of *O. celata* seen per party hour across all counts to generate an index of winter density in each year. The use of CBC data necessarily entails several simplifying assumptions (reviewed in Dunn et al. 2005), and our use of the number of birds per party hour as an index of density assumed a linear relationship between effort and the resulting count (Link and Sauer 1999). However, this assumption appeared justified as the count data used in our analysis showed no evidence of reaching an asymptote with increasing effort.

We evaluated how apparent survival was influenced by conditions across the annual cycle by considering models with effects from both the breeding and non-breeding seasons. We considered all possible additive combinations of the following factors on apparent survival ( $\phi$ ): sex, breeding density, November-April precipitation (described above), winter density, and winter precipitation on the mainland (Table S2.2). Winter precipitation was calculated by averaging the total November to February rainfall at Western Regional Climate Center ([www.wrcc.dri.edu](http://www.wrcc.dri.edu)) weather stations ( $n = 14$ ) that had complete data and were located in same five California counties as the CBC counts. Wintering densities on the mainland were correlated with mainland precipitation during the survival interval ( $r = -0.75$ ), so we did not build models

that included both potential winter-season covariates. All models included effects of sex and year on the resighting probability,  $p$ , and were fit using a logit-link function in Program MARK (White et al. 1999) and ranked based on  $AIC_c$ .

## RESULTS

### *Fecundity and Nest Survival*

Mean annual fecundity ( $\pm 1$  SE) was  $1.40 \pm 0.12$  young fledged per pair per breeding season ( $n = 181$  pairs). Excluding 2007, when no birds bred successfully, resulted in a mean annual fecundity estimate of  $1.55 \pm 0.13$  young per pair ( $n = 163$  pairs). Birds that successfully fledged at least one offspring had a mean annual fecundity of  $2.94 \pm 0.11$  young per pair ( $n = 86$  pairs). Our understanding of the processes affecting fecundity was improved by the use of zero-inflated models, which found weak effects on the number of offspring fledged (Fig. 2.1a,b) but strong effects of both rainfall (Fig. 2.1c) and density (Fig. 2.1d) on the probability of fledging no offspring. Birds were more likely to be unsuccessful (i.e. fledge zero young) in drier years (Fig. 2.1c) and in years with higher breeding density (Fig. 2.1d); removing each of these effects from the top model increased the  $AIC_c$  value by 7.61 and 8.23, respectively (Table 2.1). However, we found less support for effects of rainfall and breeding density on the count side of the model (i.e. on the number of offspring fledged; Table 2.1). The top model contained a breeding density effect on the count side, but a model without this effect received equivalent support ( $\Delta AIC_c = 0.48$ ; Table 2.1). Furthermore, the confidence interval for the count-side breeding density parameter ( $\pm 1$  SE) included zero ( $\beta = -0.14 \pm 0.09$ ; 95% CI: -0.36, 0.07), and support for this effect appeared to be influenced by one year of data (Fig. 2.1b). Similarly, a model including an effect of precipitation on the count side also received equivalent support ( $\Delta AIC_c = 0.56$ ; Table

2.1), although the confidence interval for this parameter also included zero ( $\beta = 0.006 \pm 0.005$ ; 95% CI: -0.006, 0.018). We therefore concluded that while support for effects of breeding density and rainfall on the zero-side process was strong, we had only weak evidence suggesting these variables influenced the count-side process.

Nest survival showed a strong pattern of density dependence, as survival was lower in years with higher breeding density (Fig. 2.2;  $\beta = -0.67 \pm 0.18$ ; 95% CI: -1.13, -0.20). Removing breeding density from the top model increased the AIC<sub>c</sub> value by 7.45 (Table S2.1). By contrast, we found little support for an effect of rainfall on daily nest survival (Table S2.1). Nest survival also declined as the season progressed ( $\beta = -0.03 \pm 0.01$ ; 95% CI: -0.05, -0.01) and increased with nest height, although zero was included near the boundary of the 95% confidence interval ( $\beta = 0.20 \pm 0.11$ ; 95% CI: -0.09, 0.50). Model selection showed less support for the effects of nearest neighbor distance (Table S2.1;  $\beta = -0.02 \pm 0.02$ ; 95% CI: -0.06, 0.02) and precipitation (Table S1;  $\beta = -0.01 \pm 0.01$ ; 95% CI: -0.03, 0.01). Daily nest survival rate ( $\pm 1$  SE) was  $0.974 \pm 0.004$  based on our top model and mean breeding density, date, and nest height values. Estimates, standard errors, and confidence intervals are from the top model in which each variable appears (Table S2.1).

### *Adult Survival*

We found little evidence to suggest that precipitation or population density during either the breeding or wintering seasons affected annual apparent adult survival, as the model with only a sex effect had equivalent statistical support as models containing these effects (Table S2.2). In addition, confidence intervals included zero for the effects of breeding density ( $\beta = -0.53 \pm 0.44$ ;

95% CI: -1.39, 0.34), wintering density ( $\beta = -1.79 \pm 1.68$ ; 95% CI: -5.07, 1.50), November – April precipitation prior to the survival interval (precip x-1;  $\beta = 0.01 \pm 0.01$ ; 95% CI: -0.00, 0.03), and November – February precipitation during the survival interval (precip x;  $\beta = 0.01 \pm 0.01$ ; 95% CI: -0.01, 0.03). Estimates, standard errors, and confidence intervals are from the top model in which each variable appears (Table S2.2). Estimated annual survival probability was higher for males ( $0.68 \pm 0.03$ ; 95% CI: 0.62, 0.73) than females ( $0.56 \pm 0.05$ ; 95% CI: 0.47, 0.66).

## DISCUSSION

We found that warblers were less likely to successfully reproduce as precipitation decreased and as breeding density increased (Fig. 2.1c,d). We documented breeding densities that were as high as 6.3 pairs/ha, four times higher than the maximum recorded breeding density on the mainland (1.5 pairs/ha; Gilbert et al. 2010). Breeding density had only a weak effect on the number of young produced (Fig. 2.1b), and was not correlated with annual adult survival (Table S2.2). Instead, the decline in fecundity with increasing breeding densities was due to density-dependent nest survival (Fig. 2.2), which was surprising because we had predicted competition for food was a more likely mechanism through which density-dependence would act in this island study system. These results provide a rare passerine example of density-dependent nest survival leading to density-dependent fecundity, and imply that this process contributes to population regulation.

Our understanding of the mechanisms by which rainfall and breeding density affected fecundity was improved by the use of zero-inflated models, which partitioned how these factors influenced the probability of fledging zero young (i.e. the zero side) from effects on the number

of young produced by successful pairs (i.e. the count side). We found that the probability of fledging zero young was higher in drier years and at high breeding densities (Fig. 2.1c,d), whereas precipitation and density were not strongly correlated with the number of young fledged (Fig. 2.1a,b). We therefore evaluated how both rainfall and breeding density affected the probability of fledging no young (i.e. reproductive failure) via their influence on nest survival rates and on the behavioral responses of breeding birds to ecological variation.

Three major processes determine whether an individual will reproduce successfully in a given year. First, a bird must breed, rather than skip breeding for a year, and species with slower life history strategies are more likely to regularly forgo reproduction (Jouventin and Dobson 2002). Second, the probability of nest survival can depend on attributes of the parent, nest site, and predator community (reviewed in Cresswell 1997), as nest predation is the major source of nest failure for breeding birds (Ricklefs 1969). Third, following nest failure, birds must either renest or suspend breeding and enter the non-breeding period, and this decision process repeats with each failed reproductive attempt. The propensity to renest depends on the timing of failure and may be affected by food availability or the energetic reserves of the breeding adult (e.g. Arnold et al. 2010; Caldwell et al. *in review*). Below, we evaluate how the effects of rainfall and breeding density may have been mediated via these three sources of reproductive failure.

The effects of rainfall on the probability of reproductive failure were likely driven by effects on the propensity to initiate breeding and to renest after nest failure. Indeed, the importance of rainfall was observed during a severe drought in the winter of 2006-2007, when the vast majority of territorial pairs did not attempt to breed and not a single pair successfully fledged young (Fig. 2.1c at 9cm of rainfall; see also Langin et al. 2009). Increased rainfall was also associated with longer breeding seasons with later clutch initiation dates (Sofaer et al. *in*

*review*), suggesting that the relationship between rainfall and food abundance led birds to increase their probability of reneating as precipitation increased. Taken together, the effects on both the probability of initiating breeding and the probability of reneating after failure provide a mechanism for how rainfall affected the probability of fledging no young. Rainfall was not correlated with daily nest survival probability (Table S2.1). However, it is surprising that rainfall did not have a stronger effect on the number of young fledged (Fig. 2.1a), as birds in this population lay larger clutches in wetter years (Sofaer et al. *in review*).

Density-dependent nest predation appeared to be the primary mechanism underlying the decline in reproductive success at high breeding densities in our study population (Fig. 2.1d, 2.2). Density was not correlated with the probability of breeding, as all pairs attempted to breed in the year with the highest observed conspecific density. Breeding density also did not influence breeding season length; a post-hoc analysis of breeding season length found that the addition of breeding density to a simple linear model including precipitation increased the AIC value by 1.74, and the confidence interval on the density effect included zero. Breeding density therefore was unlikely to affect the probability of reneating after nest failure.

Our observation that nest predation was density-dependent suggests that nest predators exhibited functional or numeric responses (Holling 1959) to increasing warbler density. The major nest predators in our study population are snakes and small mammals, as the island lacks avian nest predators such as jays (Peluc et al. 2008). The means by which these predators locate nests and allocate foraging effort are poorly understood (Weatherhead and Blouin-Demers 2004), but our results imply that at least one of the island's predators does not simply find nests incidentally. To date, no consensus exists about how differences in the type, diversity, and density of predator and prey species influence the likelihood of detecting density-dependent nest

predation, which has been found in several systems (Andersson and Wiklund 1978; Martin 1996; Lariviere and Messier 1998; Schmidt and Whelan 1999; Gunnarsson and Elmberg 2008) but not in others (Zimmerman 1984; O'Reilly and Hamon 1989; Reitsma 1992; Ackerman et al. 2004; Sillett and Holmes 2005). However, few previous studies documenting density-dependent nest predation in natural populations have been able to assess whether nest predation regulates the focal population (Arcese et al. 1992; Tapper et al. 1996). We found that density-dependent nest predation appears to be an important regulatory mechanism for *O. c. sordida* on Catalina Island.

Density-dependent nest predation has implications not only for population demography, but also for the evolution and expression of nest site selection. When a nest predator's functional response includes specializing on a set of nest site characteristics, individuals may benefit by nesting in less used sites, and this process may affect community composition and the evolution of nest site selection (Martin 1988, 1996), although not all studies have found support for predator specialization (Reitsma and Whelan 2000; Rangen et al. 2001). Our result raises the possibility that density-dependent nest predation could also favor the diversification of nesting sites within a population, rather than solely between species. *O. c. sordida* exhibits an unusual amount of variation in nest height and nest site location relative to other *O. celata* subspecies and many other members of this genus, which are ground nesters. On Catalina Island, individuals choose nest substrates that range from concealed ground nests in grasses and forbs that experience relatively high nest predation, to off-ground nests in shrubs and tree canopies that have higher nest success (Peluc et al. 2008). Future studies are needed to evaluate nest predators' search methods and functional responses, whether high breeding densities could have favored specialization by predators, and if warblers gain any selective advantage from choosing atypical nest-site locations.

## *Conclusions*

Predation has generally been generally found to limit, rather than regulate, avian populations (reviewed in Newton 1993, 1998). It is therefore surprising that although our study population breeds at relatively high densities on an island where intraspecific competition for food resources was expected to be strong, density-dependent nest predation appeared to be the major mechanism of population regulation (Fig. 2.2). Our understanding of the mechanisms by which variation in population density and rainfall affected fecundity was improved by the use of zero-inflated models. These models not only provide a statistically appropriate method for accounting for a relatively high proportion of zeros in our data, but also allowed us to separate the ecological factors affecting the count-side process (i.e. the number of young fledged) from those affecting the zero-side process (i.e. the probability of fledging no young). Although fecundity data are often likely to be zero-inflated, these methods have rarely been applied to studies of demography, and we suggest that their broader use will improve ecological inference.

## RECOGNITION

This work was supported by The Nature Conservancy, the Smithsonian Institution, and Colorado State University. HRS was supported by Colorado State University, NSF-IGERT Grant DGE-#0221595 (administered by the PRIMES program at Colorado State University) and NSF DEB-0846175 to CKG. The Catalina Island Conservancy provided logistical support and access to housing and vehicles. We thank the many field biologists who helped with data collection, particularly J. Coumoutso, H. Montag, S. Peluc, and J. Yoon. V. Bakker, P. Chapman, and J. Rotella provided statistical advice, and C. Webb provided helpful comments on the manuscript.



TABLES AND FIGURES

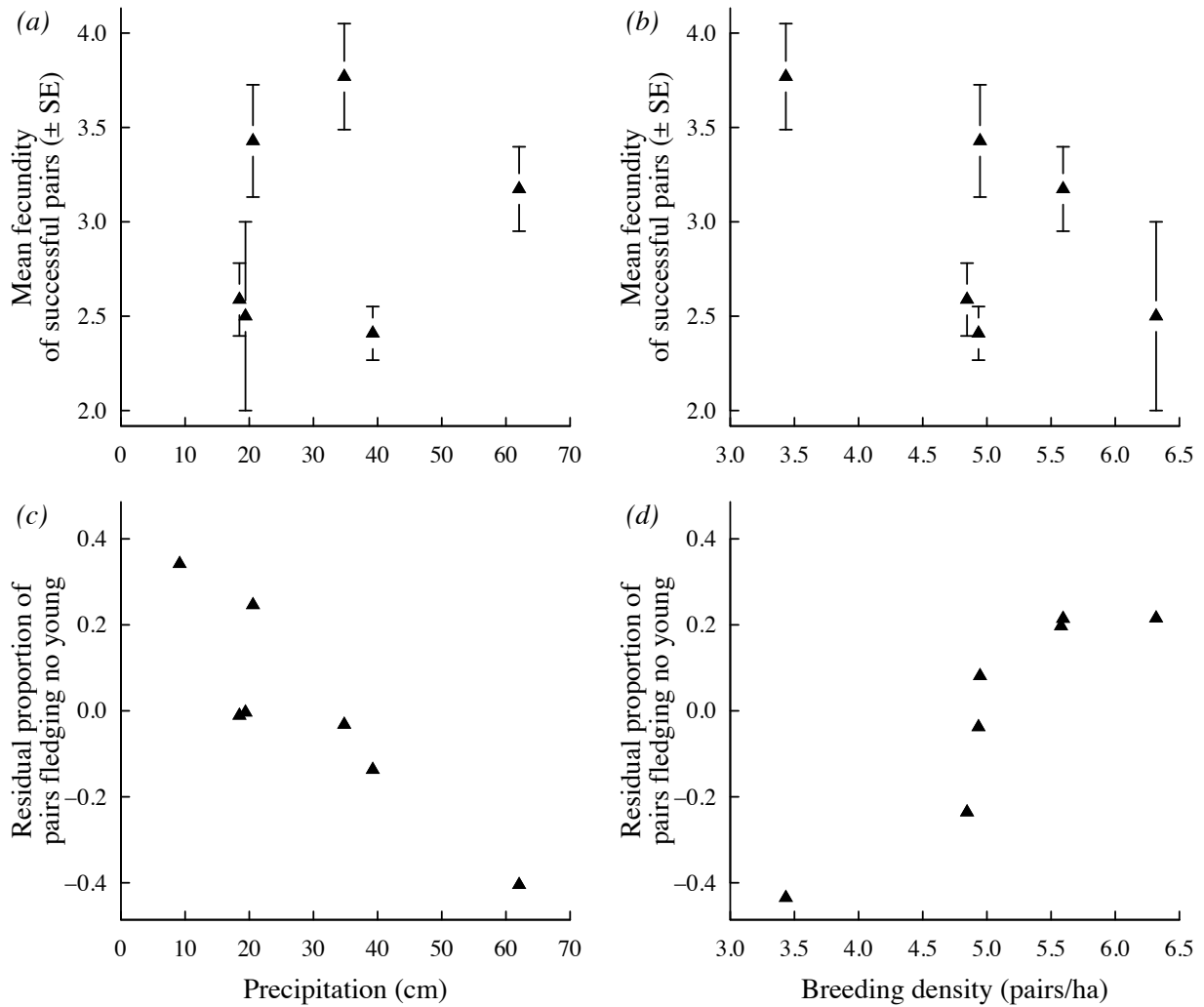


Figure 2.1: The fecundity of pairs that successfully fledged young was (a) not affected by precipitation and (b) weakly affected by breeding density. The proportion of pairs fledging no young in each year was strongly affected by both (c) precipitation and (d) breeding density. In (c) the y-axis coordinates are the residuals from a simple linear regression of the effects of density on the proportion of unsuccessful pairs, while in (d) they are the residuals from a simple linear regression of the effects of rainfall on the proportion of unsuccessful pairs. See text for formal zero-inflated analysis of fecundity.

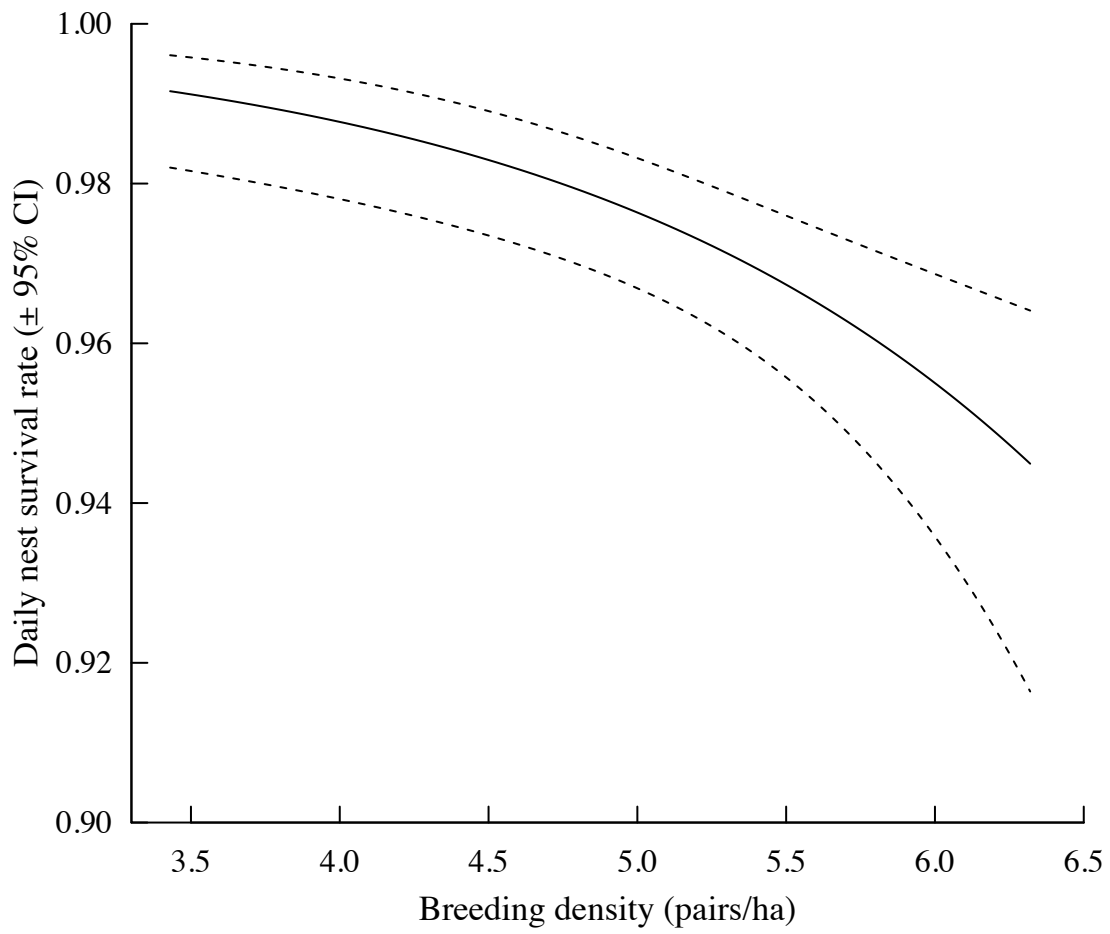


Figure 2.2: Daily nest survival rate declined with increasing breeding density.

Table 2.1. Model selection results for zero-inflated mixed models of fecundity showed strong support for the effects of breeding density (bd) and precipitation (precip) on the probability of fledging zero young. We considered all possible additive model structures on both the count-side and zero-side, including intercept-only (.) fixed-effect structures. All models contained a normally-distributed random effect of year on the zero side of the model.

Count-side	Zero-side	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	weight	-2log(L)	k
bd	bd + precip	464.02	0	0.33	451.53	6
.	bd + precip	464.50	0.48	0.26	454.16	5
bd + precip	bd + precip	464.58	0.56	0.25	449.93	7
precip	bd + precip	466.24	2.22	0.11	453.76	6
bd	bd	471.63	7.61	0.01	461.29	5
bd + precip	bd	471.65	7.63	0.01	459.17	6
.	bd	472.06	8.04	0.01	463.84	4
bd	precip	472.25	8.23	0.01	461.90	5
bd + precip	precip	472.98	8.96	0	460.50	6
.	precip	473.34	9.32	0	465.11	4
precip	bd	473.57	9.55	0	463.23	5
bd	.	474.84	10.82	0	466.61	4
bd + precip	.	475.07	11.05	0	464.72	5
precip	precip	475.15	11.13	0	464.81	5
.	.	475.54	11.52	0	469.41	3
precip	.	477.16	13.14	0	468.93	4

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APPENDIX II

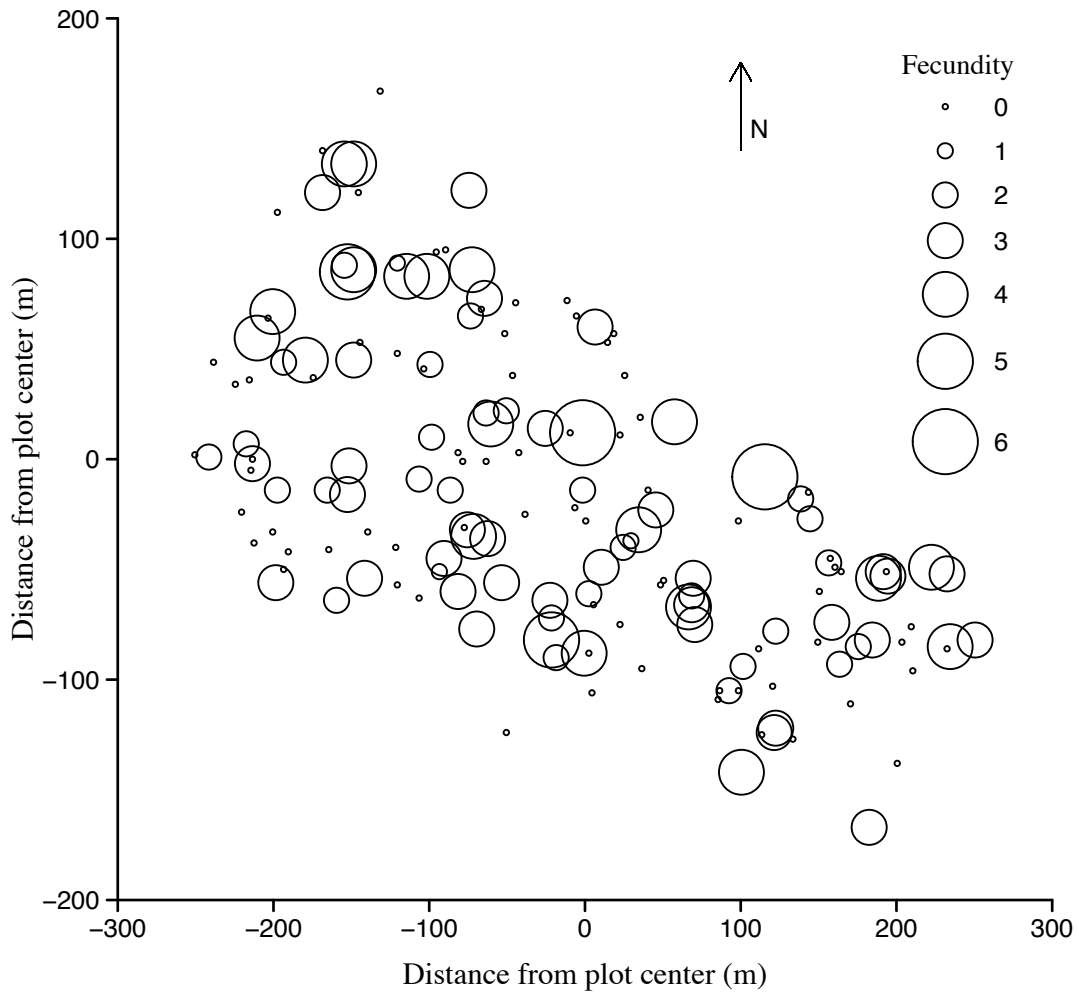


Figure S2.1: A bubble plot of the annual fecundity of warbler pairs in our study area showed no variation in the distribution of fecundity across space. An annual fecundity of 5-6 young was achieved via double brooding. Data are shown from all years except 2007, when a severe drought caused all monitored pairs to fledge no young.

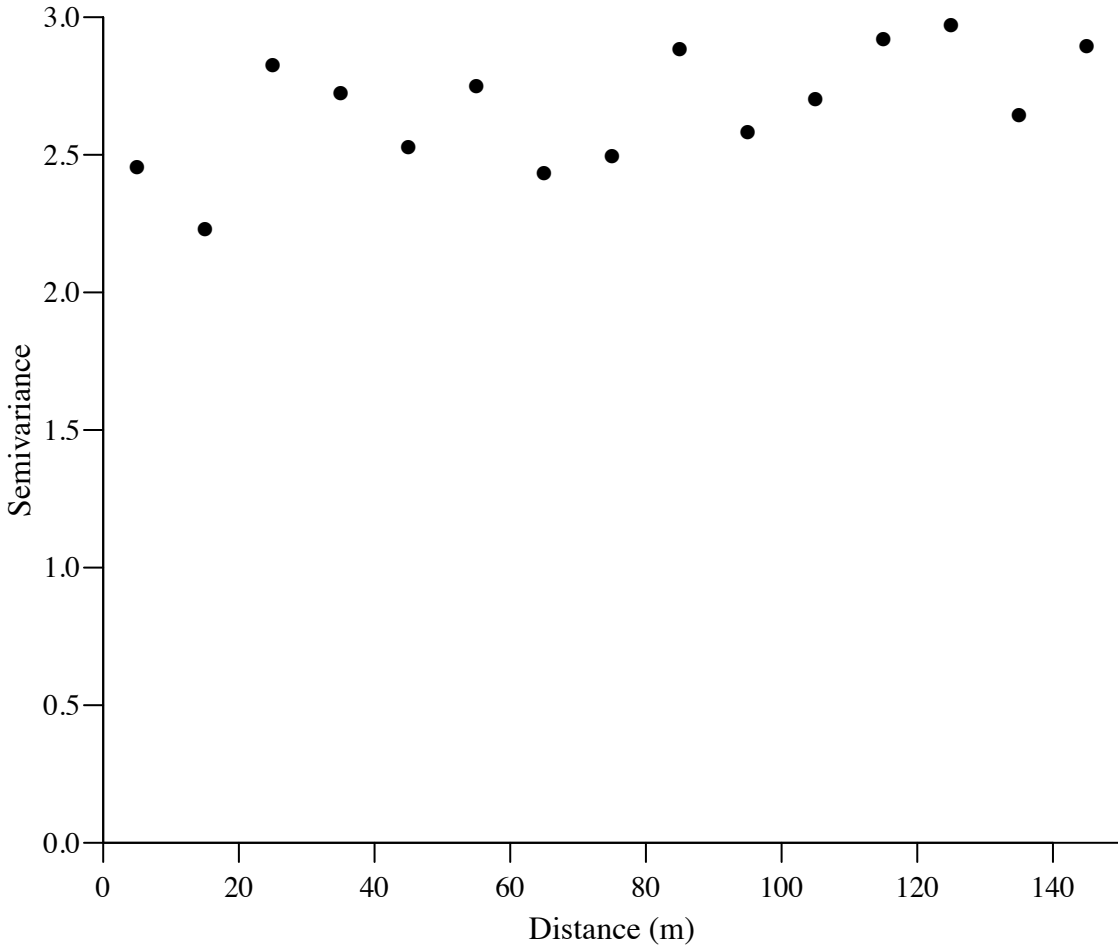


Figure S2.2: A variogram of fecundity showing weak evidence of spatial autocorrelation within our study area. The number of pairs per spatial interval ranged from 69-563 pairs. Data are shown from all years except 2007, when a severe drought caused all monitored pairs to fledge no young.

Table S2.1: Our generalized mixed models showed strong support for density-dependent effects on daily nest survival; at higher breeding densities (bd) daily nest survival was lower. We considered an intercept-only model (.) and those with all additive combinations of five fixed effects: breeding density, date, height (ht), precipitation (precip; equivalent to precip x-1 in Table 3) and nearest neighbor distance (nn). All models included a normally distributed random effect. Models with  $\Delta AIC_c > 15$  are not shown, with the exception of the intercept only model.

<b>Fixed-effect model</b>	<b>AIC<sub>c</sub></b>	<b><math>\Delta AIC_c</math></b>	<b>weight</b>	<b>-2log(L)</b>	<b>k</b>
bd + date + ht	548.02	0.00	0.24	537.99	5
bd + date + ht + nn	548.85	0.83	0.16	536.80	6
bd + date + ht + precip	549.15	1.14	0.13	537.11	6
bd + date + nn	549.42	1.40	0.12	539.39	5
bd + date	549.62	1.60	0.11	541.60	4
bd + date + ht + precip + nn	549.92	1.90	0.09	535.86	7
bd + date + precip + nn	550.44	2.43	0.07	538.40	6
bd + date + precip	550.75	2.73	0.06	540.71	5
date + ht	555.46	7.45	0.01	547.44	4
date	555.85	7.83	0	549.83	3
date + nn	556.75	8.73	0	548.73	4
date + ht + nn	556.93	8.91	0	546.90	5
date + ht + precip	557.03	9.01	0	547.00	5
date + precip	557.37	9.35	0	549.35	4
date + precip + nn	558.31	10.29	0	548.28	5
date + ht + precip + nn	558.52	10.50	0	546.47	6
bd + ht	562.46	14.45	0	554.44	4
.	572.06	24.04	0	568.05	2

Table S2.2. Model selection results for the top ten Cormack-Jolly-Seber mark-recapture models. The model structures included effects of: sex (s), breeding density (bd), wintering density (wd), precipitation during the winter prior to the March-March survival interval (precip x-1), and winter precipitation during the March-March survival interval (precip x). All models included sex and time effects on the resighting probability ( $p$ ).

<b>Model</b>	<b>AIC<sub>c</sub></b>	<b><math>\Delta</math>AIC<sub>c</sub></b>	<b>weight</b>	<b>-2log(L)</b>	<b>k</b>
$\phi(s + \text{precip } x-1)$	643.26	0.00	0.11	622.68	10
$\phi(s)$	643.28	0.02	0.11	624.80	9
$\phi(s + \text{bd} + \text{precip } x-1)$	643.74	0.48	0.09	621.04	11
$\phi(s + \text{bd})$	644.06	0.80	0.07	623.48	10
$\phi(s + \text{wd} + \text{precip } x-1)$	644.26	1.00	0.07	621.56	11
$\phi(s + \text{precip } x + \text{precip } x-1)$	644.39	1.13	0.06	621.68	11
$\phi(s + \text{bd} + \text{wd} + \text{precip } x-1)$	645.00	1.74	0.05	620.17	12
$\phi(.)$	645.23	1.97	0.04	628.85	8
$\phi(s + \text{precip } x)$	645.34	2.08	0.04	624.76	10
$\phi(s + \text{wd})$	645.38	2.13	0.04	624.80	10

CHAPTER 3:  
VARIATION IN NESTLING GROWTH TRAJECTORIES WITHIN AND BETWEEN  
POPULATIONS OF ORANGE-CROWNED WARBLERS: AN ANALYSIS BASED ON  
NONLINEAR MIXED MODELS<sup>3</sup>

SUMMARY

Understanding variation in growth rates has been the focus of many studies in avian biology. However, analyses of avian growth curves have not taken advantage of two statistical approaches that are useful for studying variation within and between populations. First, random effects can evaluate whether there are consistent differences between individuals and groups of siblings within a population, and also account for the lack of independence between data points. Second, nonlinear fixed effect functions can be altered to explicitly test for differences between groups or populations. We illustrate the advantages of these approaches by using nonlinear mixed models to study nestling growth rates of orange-crowned warblers (*Oreothylpis celata*). Specifically, we quantify the sources of variation within populations, analyze the effects of asynchronous hatching on growth trajectories, and test for a difference in the growth rates of two populations at the northern and southern limits of the breeding distribution. We found no evidence that the growth rate constant of a logistic model varied within populations, but we did find support for a difference in the growth rate constant between populations, and mixed models

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provided stronger support for this difference than models with only fixed effects. Our results provide a rare example of an intraspecific difference in a passerine growth rate and highlight statistical methods that can improve our understanding of intraspecific variation in growth and development. These methods can be applied to any taxonomic group and adjusted to fit any nonlinear function, and we provide code to facilitate their use in future studies.

## INTRODUCTION

An organism's growth rate is a fundamental life history trait that is often closely correlated with fitness and a suite of other traits (Haywood and Perrins 1992, Roff 1992, Stearns 1992). Variation in vertebrate growth rates is thought to reflect adaptive evolution to different ecological conditions (reviewed in Case 1978, Arendt 1997, Starck and Ricklefs 1998). Avian growth rates have been the focus of considerable research, as studies have highlighted the roles of ecological conditions such as food availability, sibling competition, and nest predation risk in creating variation in growth rates within and between species (Ricklefs 1968, Ricklefs 1976, Nilsson and Svensson 1996, Royle et al. 1999, Remes and Martin 2002). Within a species, growth trajectories can be sensitive to a variety of genetic and environmental factors, potentially leading to variation at multiple hierarchical levels: between individuals, between family groups, and between populations (Ricklefs and Peters 1981, Badyaev and Martin 2000, McCarty 2001). Accurately quantifying variation at each of these levels is therefore critical for understanding the ecological and evolutionary processes that shape growth and development.

Studies of growth face several fundamental methodological challenges. First, field studies generally track the growth of related individuals through time, leading to a lack of independence between data points. This occurs at two levels: at the nest level, because siblings share genetic

backgrounds and environmental conditions, and at the nestling level, because of repeated measurements of individuals. Second, the nonlinear nature of growth curves limits the types of statistical analyses that can be easily applied, so studies interested in identifying the sources of variation in growth have often used a multistep process to analyze their data. For example, passerine growth trajectories are usually analyzed by fitting a logistic function, which has three fixed parameters: the asymptotic mass, the inflection point, and the growth rate constant (Ricklefs 1967). To understand the factors affecting variation in the growth rate constant within a species, studies have divided their data and fit separate curves to different populations, sexes, nests, or treatment groups (Bancroft 1984, Gard and Bird 1992, Barrett 1996, Kaiser and Lindell 2007), or to each individual nestling (Best 1977, Ricklefs and Peters 1981, Blancher and McNicol 1988, Emms and Verbeek 1991, Badyaev et al. 2001, Searcy et al. 2004, Tilgar and Mand 2006, Tjorve and Underhill 2009). This provides a separate estimate of the growth rate constant for each group or individual, and these estimates are then used as the dependent variable in subsequent analyses that aim to identify how growth rates respond to variation in ecological conditions, parental behavior, or genetics.

The standard method of studying intraspecific variation by dividing datasets, fitting separate curves, and using parameter estimates in subsequent analyses has several drawbacks. First, it requires either the exclusion of groups or individuals with insufficient data to adequately estimate a curve, or use of inaccurate estimates based on little data. Second, it places equal weight each parameter estimate, although these are often generated from different amounts of data. For example, even if one individual was weighed a dozen times and another only six times, the estimated growth rate constant of each bird would be treated equally in any subsequent analyses, ignoring the larger standard error of the estimate based on fewer data. Third, it does not

provide an explicit estimate of group or individual-level variation in the parameter estimates. Finally, this method does not allow for accurate tests of differences in the growth rate constant between treatment groups or populations. Instead, studies that compare estimated growth rate constants from separate curves can overstate the difference between groups, because ignoring sibling relationships or repeated measures can lead to underestimated standard errors (Brisbin et al. 1987).

Traditional statistical approaches can be extended in two ways to address the methodological problem of related data points and to more directly test biological hypotheses of interest. First, the lack of independence between siblings and between repeated measurement of the same individual can be accounted for through the inclusion of random effects, which estimate the amount of variation between groups and/or individuals (Laird and Ware 1982, Pinheiro and Bates 2000). Mixed models are therefore particularly useful for studies interested in understanding the sources of variation within populations (Bolker et al. 2009). Rather than fitting a separate curve to each individual or group, they base fixed-effect parameter estimates on all the data, accounting for the structure dictated by the random effects. Extensive research during the past two decades has led to the development of theory, approximation methods, and software for nonlinear mixed models, and these models have become widely used (Lindstrom and Bates 1990, reviewed in Davidian and Giltinan 2003). For example, nonlinear mixed models of growth are used for fisheries research, where understanding individual variation in growth trajectories provides more accurate estimation of future harvest yields (Pilling et al. 2002, Alos et al. 2010, Shelton and Mangel 2012). Second, fixed-effect structure can be altered to directly test hypotheses of interest. As in any statistical model, nonlinear fixed-effect functions can be extended to explicitly test for differences between populations, experimental treatments, or other

groups, or to determine how growth rates are affected by variation in continuous variables such as provisioning rates, climate, or parasite loads (Ritz and Streibig 2008). Here, we illustrate how the application of these methods can improve biological inference, and include implementation advice to make these methods more accessible.

### *Variation in orange-crowned warbler growth trajectories*

We applied nonlinear mixed models to orange-crowned warbler (*Oreothlypis celata*) growth trajectories to understand patterns of variation between individual nestlings and groups of nestmates, to quantify the effects of asynchronous hatching on growth trajectories, and to test for differences in the growth curves of populations breeding in Alaska and California. We used random effects to address our first goal and to produce more accurate standard errors in all our analyses. Our second and third goals were accomplished by extending the logistic equation to include fixed effects that tested for differences between asynchronously hatched young and between populations. Below, we explain how our statistical methods addressed each goal.

We assessed the amount of variation between birds in different nests and between individuals by including nest and nestling-level random effects in our models. We first evaluated whether faster growing birds, or birds that reached their inflection points earlier, achieved a higher asymptotic mass. Next, because random effects estimated the amount of variation in each parameter at the nest and nestling levels, and because we expected variation to increase with the strength of competition (Ricklefs 1968; Rodenhouse et al. 1997), we used the random effect estimates to evaluate whether competition between siblings or between pairs was stronger in Alaska or California. If sibling competition increases with brood size, there should be more nestling-level variation in Alaska. At the nest level, greater variation in territory quality and food

delivery rates could increase variation between nests. Birds in California breed at a high density on an island, respond strongly to simulated territorial intrusions, and maintain higher testosterone levels during the nestling period than birds in Alaska (Horton et al. 2010, Yoon et al. 2012), suggesting stronger competition for high quality territories in that population. Therefore, we predicted the amount of variation between nests would be higher in California.

We then tested whether birds that hatched after their nestmates (i.e. asynchronously) differed in their growth rate constant or their asymptotic mass. Birds often hatch on different days when parents initiate incubation before all eggs are laid (Clark and Wilson 1981, Ricklefs 1993), and younger nestlings often show slower growth (reviewed in Krebs 1999) and may reach a smaller size (e.g. Bryant and Tatner 1990) than their siblings. Lower nestling mass and condition can negatively affect fitness (Magrath 1991, Linden et al. 1992), but to attain the same size, younger nestlings either have to grow for a longer time period (Krebs 1999, Johnson et al. 2003) or grow at a faster rate, which is rarely observed in birds (Starck and Ricklefs 1998) and which can have negative long-term effects on fitness (Metcalf and Monaghan 2001). We were interested in testing whether younger nestling reached the same asymptotic mass as their older siblings and whether they differed in their growth rate constant. This test was only carried out in the population in Alaska, as asynchronous hatching was less common in California.

Finally, we tested for differences between the growth curves of warblers breeding in California versus Alaska. Previous intraspecific comparisons of growth rates in passerine birds have found mixed results, as several studies have found little evidence for consistent variation between intraspecific populations (Hussell 1972, King and Hubbard 1981, Nisbet et al. 1995, McCarty 2001), but other work shows that geographically separated populations can have heritable differences in their growth rates (Starck et al. 1995). Comparisons between species

have shown that birds at higher latitudes often have faster growth rates (Ricklefs 1976, McCarty 2001, Remes and Martin 2002, Schekkerman et al. 2003), leading to the prediction that nestlings in Alaska should grow more quickly than those in California.

## METHODS

### *Data collection*

We collected data on the growth of orange-crowned warblers in Fairbanks, Alaska (*O. c. celata*) from 2007-08, and on Santa Catalina Island, California (*O. c. sordida*) from 2008-09. We weighed 210 nestlings or fledglings (dependent juveniles that had left the nest) from 49 nests in Alaska, and 64 individuals from 24 nests in California; the median number of days on which we weighed each individual was 3 in both Alaska (range: 1-6 days) and California (range: 1-8 days). Birds were individually marked with non-toxic permanent marker on their toenails, and were generally weighed daily or every other day, starting on hatch day or when the nest was located. Weights were taken to the nearest 0.01g using a My Weigh MX-50 digital scale. Some growth trajectories were incomplete due to nest failure. We weighed nestlings until flight feathers emerged from feather sheaths, which occurred on nestling day 6 in Alaska and day 7 in California (hatch day = day 0); we also banded birds on this day to identify individual fledglings.

We captured fledglings to accurately estimate asymptotic mass. When data collection ends before the asymptotic mass is attained, the estimated asymptotic mass may be biased low, leading to an inflated estimate of the growth rate constant (Austin et al. 2011). In Alaska we caught 26 birds on the day they left their nests, either day 9 or 10 post-hatch. This included two fledglings that fledged from nests that were not monitored. The feather development, behavior, and mobility of these birds indicated they had fledged within the past day, and they were

included in the dataset as 10 days old. California birds had longer nestling periods, so we measured 10 nestlings on day 10, and 7 birds on their natural fledge day, day 13-14. We found no evidence of bias in our estimates of asymptotic mass, which were within a single standard deviation of the mean mass ( $\pm 1$  SD) of adults in each population (Alaska:  $9.32 \pm 0.44$  g,  $n = 209$  adults; California:  $9.49 \pm 0.66$  g,  $n = 802$  adults).

### *Analysis of variation in growth trajectories within populations*

We modeled the growth curves of each study population with a logistic function, as is typical for passerine studies (Starck and Ricklefs 1998):

$$w = \frac{A}{1 + e^{(K(I-t))}}, \quad (1)$$

where  $w$  = average mass (g),  $A$  = asymptotic mass (g),  $K$  = growth rate constant,  $t$  = nestling age (days), and  $I$  = the inflection point of the growth curve (days).

Our model estimated the amount of variation between sibling groups and individuals by including two levels of random effects, nest and nestling. The nest effects accounted for the lack of independence between nestmates due to a shared genetic background (full or half siblings), maternal effects, and a common level of parental care. The nestling effects modeled repeated measurements on individuals. We included random effects for one or more of the three parameters in the model,  $K$ ,  $A$ , and  $I$ , allowing the parameter estimates to vary between each nest or nestling. For the  $k^{\text{th}}$  measurement on the  $j^{\text{th}}$  nestling in the  $i^{\text{th}}$  nest the mass was:

$$w_{ijk} = \frac{A + A_i + A_{ij}}{1 + e^{((K+K_i+K_{ij})(I+I_i+I_{ij}-t_{ijk}))}} + \epsilon_{ijk} \quad (2)$$

In all models, the random nest effects,  $(A_i, K_i, I_i)$ , the random nestling effects,  $(A_{ij}, K_{ij}, I_{ij})$ , and the random errors,  $\epsilon_{ijk}$ , were normally distributed with mean zero. Within each set of three

random effects for each nest or nestling, the effects were not assumed to be independent of each other. This potential dependence allowed, for example, for an earlier inflection point to be correlated with a higher asymptotic mass. Between nests and nestlings, effects were assumed to be independent of each other, as were the random errors. We report the estimated standard deviation of each random effect, which describes the variation around the population mean (i.e. the fixed-effect estimate) between groups of nestmates or the magnitude of individual variation around the mean of its nestmates. The fixed-effect estimates from our mixed models represent the subject-specific estimates, which are those for a typical (i.e. median) nestling in a typical nest, rather than the population average (Hu et al. 1998). For the fixed effects we report the standard error.

We built models that included a single random-effect level (nest or nestling) on one or more parameters as well as models that included both nest- and nestling-level random effects. We first applied the same random-effect structure at the nest and nestling levels, but when an estimated correlation between parameters in a top model was near zero, we also fit a reduced model without a correlation. If a model failed to converge, if the estimated random effect standard deviation was zero, or if the absolute value of the correlation between two random effects was 0.9 or higher (often 1 or 0.99), we concluded that the model was overparameterized (Pinheiro and Bates 2000) and discarded the model from further consideration.

We used an information-theoretic approach based on Akaike's information criterion (AIC) to select a random-effect structure (Burnham and Anderson 2002). AIC values can be used for mixed models, but may be biased to favor simpler random-effect structures (Molenberghs and Verbeke 2005, Bolker et al. 2009, Greven and Kneib 2010). Therefore, when AIC values are very close, support for the more complex random-effect structure is stronger than indicated. We



fit all models using maximum likelihood in the nlme package of R (Pinheiro et al. 2011, R Development Core Team 2011). Throughout our work, we compared mixed models to models that lack random effects to show how mixed models provided a better fit to our data and to highlight differences in the biological inferences based on each approach. Models without random effects were fit using nlme's gnl function, while mixed models were fit using the nlme function. We did not use the lme4 package (Bates et al. 2011) because it does not allow mixed models and models with only fixed effects to be directly compared, but we include example syntax for implementation in lme4 in our code.

To visualize the amount of variation within a population, we calculated intervals encompassing 95% of variation at the nest and nestling levels (Fig. 3.1). The interval encompassing 95% of the variation between nests was calculated as  $\pm 1.96$  times the nest-level standard deviation, while the 95% interval encompassing variation between both nests and nestlings was calculated as  $\pm 1.96$  times the square root of the sum of the nest- and nestling-level variances. Although the magnitude of nestling-level variation around the asymptotic mass was nearly equivalent to nest-level variation (see results), the joint 95% interval is only slightly bigger than the nest-only interval because of the rarity with which an extreme nestling would be found within an extreme nest.

#### *Incorporating asynchronous hatching into the analysis of growth trajectories*

We modified our nonlinear fixed-effect function to test for effects of asynchronous hatching on the growth trajectories in Alaska, where 23 of 49 nests were known to have hatched asynchronously; only six of 24 nests hatched asynchronously in California. We defined younger individuals (hereafter referred to as runts) as those that had not yet hatched on the first nest visit

when other nestmates had hatched. We estimated the difference in the inflection point,  $I_r$ , which quantified how far to the right the entire growth curve was shifted for younger nestlings, compared to their older siblings. We therefore did not have to assume that all nestlings in a nest were the same age or that runts were a full day younger. We also modified our fixed-effect function to include parameters that estimated how runts differed in their growth rate constant,  $K_r$ , and asymptotic mass,  $A_r$ ;  $x_r$  was an indicator variable with a value of 1 for younger nestlings:

$$w = \frac{A + A_r x_r}{1 + e^{((K + K_r x_r)(I + I_r x_r - t))}} \quad (3)$$

While model (3) shows only fixed effects, random effects of nest,  $(A_i, K_i, I_i)$ , and nestling,  $(A_{ij}, K_{ij}, I_{ij})$ , were also included, as in model (2). Following Zuur et al. (2009), we used model selection to select the random-effects structure with the most support, and then used hypothesis testing to evaluate the fixed effects based on our top model.

#### *Comparison of growth trajectories between two populations*

We tested for differences in the growth curves of Alaskan and Californian birds by adding a fixed site effect to each of the three parameters in the logistic function. The full fixed-effects model also included a shift in the inflection point for younger nestlings:

$$w = \frac{A + A_{pop} S}{1 + e^{((K + K_{pop} S)(I + I_r x_r + I_{pop} S - t))}} \quad (4)$$

where  $S$  was an indicator variable for the Alaskan population, and  $A_{pop}$ ,  $K_{pop}$ , and  $I_{pop}$  were the differences between sites. As before, while model (4) shows only fixed effects, we included nest- and nestling-level random effects. We included a runt effect on the inflection point, and assumed that this effect did not differ between sites, as the estimated shift in the inflection point of Alaskan runts was within one standard error of the estimate when the model was fit to

Californian birds. To evaluate how the use of mixed models affected our inferences, we compared the parameter estimates and statistical significance of the differences between sites from models with and without random effects.

## RESULTS

### *Analysis of variation in growth trajectories within populations*

We found unequivocal support for the inclusion of random effects in models of Alaskan birds. The top models included random effects of nest and nestling on the asymptotic mass and the inflection point, while other models fit comparatively poorly, with  $\Delta\text{AIC}$  values over 50 (Table S3.1). We found no support for random effects on the growth rate constant, indicating that neither nests nor individuals consistently varied in this parameter.

Next, we determined that birds that reached the inflection point of their growth curve earlier did not show consistent differences in their asymptotic mass. The estimated correlation between these two random effects at the nest level was zero ( $r = 0.05$ ; 95% CI: -0.66, 0.71), and the confidence interval on the nestling-level correlation also included zero ( $r = -0.28$ ; 95% CI: -0.64, 0.18). We therefore based our inference on the model with no correlations between random effect parameters, as this model had stronger or equivalent statistical support than the models with one or both correlations (Table S3.1). Neither the fixed-effect estimates nor the random effect standard deviations qualitatively differed between these top models.

Nests and individuals varied in their asymptotic masses and inflection points (Fig. 3.1). The estimated random effect standard deviations on the asymptotic mass at the nest and nestling levels were 0.55g (95% CI: 0.39, 0.78) and 0.51g (95% CI: 0.40, 0.64), while the estimated standard deviations on the inflection point were 0.33 days (95% CI: 0.23, 0.46) and 0.40 days

(95% CI: 0.33, 0.48), respectively. Fixed-effect estimates were similar in the top mixed model and the model without random effects, but the standard error of the growth rate constant was smaller in the mixed model ( $0.565 \pm 0.008$ ) than in the model with only fixed effects ( $0.569 \pm 0.016$ ), likely because the mixed model accounted for variation at the nest and nestling levels.

Results from the population in California also showed strong support for random effects on the inflection point and the asymptotic mass, but not on the growth rate constant. For models with the same random-effect structure at the nest and nestling levels, three had equivalent support ( $\Delta\text{AIC}$  values  $< 1$ ; Table S3.2), likely because nest-level effects on the asymptotic mass and the inflection point were highly correlated, although this estimate was imprecise ( $r = 0.80$ ; 95% CI: 0.02, 0.97). We therefore built two models with nest-level random effects on only the asymptotic mass and nestling-level random effects on both the asymptotic mass and the inflection point; one model estimated the correlation between the nestling-level random effects and the other constrained the correlation to be zero. These models avoided overfitting by eliminating highly correlated parameters. Support was strongest for the model in which nestling-level random effects were uncorrelated (Table S3.2). The asymptotic mass consistently varied between nests and individuals; random effect standard deviations were 0.55g (95% CI: 0.27, 1.13) and 0.52g (95% CI: 0.32, 0.85), respectively. Fixed effect estimates were not qualitatively affected by the inclusion of random effects.

#### *Incorporating asynchronous hatching into the analysis of growth trajectories*

We found that younger nestlings did not differ in their growth rate constant ( $K_r = 0.013 \pm 0.022$ ;  $t_{459} = 0.62$ ;  $P = 0.54$ ) or their asymptotic mass ( $A_r = -0.42 \pm 0.28$  g;  $t_{459} = -1.49$ ;  $P = 0.14$ ). However, altering the inflection point ( $I_r = 0.63 \pm 0.12$  days;  $t_{459} = 5.18$ ;  $P < 0.0001$ ) to shift the

growth curve to the right for younger nestlings greatly improved the fit of our model ( $\Delta\text{AIC} = 96.6$  for the top model without effects of asynchronous hatching). Including the difference in the inflection point for younger nestlings incorporated variation in hatching time into the fixed effect structure, whereas in our first model this variation was incorporated into the nestling-level random effect on the inflection point. Therefore, the estimated random effect standard deviation for the inflection point was lower in the model with the runt effects (0.14 days; 95% CI: 0.08, 0.26) than in the model without them (0.40 days; 95% CI: 0.33, 0.48). Model selection again supported nest and nestling-level random effects on the inflection point and asymptotic mass (Table S3.3). The top model constrained both random effects correlations to be zero, indicating birds that reached their inflection point earlier were not expected to attain a higher asymptotic mass.

#### *Comparison of growth trajectories between two populations*

Random effects substantially improved the fit of a model testing for population differences in the growth trajectories ( $\Delta\text{AIC} = 561.4$  for the model with only fixed effects; Table S3.4). By accounting for additional sources of variation, random effects made the difference in the growth rate constant highly significant ( $t_{627} = 3.26$ ,  $P = 0.001$ ) rather than marginally significant in the model with only fixed effects ( $t_{900} = 1.81$ ,  $P = 0.071$ ; Table 3.1). The difference in the inflection point was significant in the mixed model ( $t_{627} = -3.47$ ,  $P = 0.0006$ ) and in the model without random effects ( $t_{900} = -3.91$ ,  $P = 0.0001$ ), while neither model supported a difference in asymptotic mass between populations ( $t_{627} = 0.52$ ,  $P = 0.603$  and  $t_{900} = 0.43$ ,  $P = 0.663$ , respectively; Fig. 3.2). The intervals shown in Fig. 3.2 are much smaller than in Fig. 3.1 because these represent 95% confidence intervals on the estimated growth trajectory in each

population, whereas those in Fig. 3.1 show 95% of the variation between nests and nestlings within the Alaskan population. Our top model included random effects of nest and nestling on the inflection point and the asymptotic mass (Table S3.4).

## DISCUSSION

Identifying the ecological and evolutionary factors that underlie variation in growth rates has been a central goal of many avian studies. By including random effects and extending the logistic function to test specific hypotheses of interest, we were able to understand the sources of variation in growth (Fig. 3.1) and directly compare the growth trajectories of younger nestlings and of birds in two populations (Fig. 3.2). In each of our analyses, mixed models provided a substantially better fit to our data than models without random effects (Tables S3.1-S3.4). Below, we summarize our results and highlight how our extensions of standard methods improved our biological understanding of our study system.

### *Interpretation of random effects*

Within each population, we found consistent variation in the asymptotic mass and the inflection point (Fig. 3.1), but not in the growth rate constant. This latter result corroborates the longstanding hypothesis that the growth rate constant varies little within populations (e.g. Ricklefs 1968). We based our inferences on the strength of support for the inclusion of random effects on each parameter (Tables S3.1-S3.2) and on the magnitude of the random effect standard deviations, and the use of mixed models allowed us to partition variation between the nest and nestling levels. We predicted that there could be more variation between individual nestlings in Alaska and between nests in California. Instead, we found that these two populations had a

similar amount of variation in the asymptotic mass at each level; each random effect standard deviation was approximately half a gram in both populations. This half-gram difference is likely to be biologically meaningful, as these warblers weigh less than ten grams. The similarity of these estimates also implies that the strength of competition between siblings may be similar in these populations, and surprisingly, suggests that competition between pairs may either not act via nestling provisioning rates or may also have a similar strength in these two populations.

We were also interested in assessing whether nestlings that reached their inflection point earlier attained a higher asymptotic mass, and to do so we used the estimated correlation between random effect parameters, which measures whether group- or individual-level deviations around one fixed effect are related to deviations around other fixed effects. We found that variation in the inflection point was not correlated with variation in the asymptotic mass, as models in which this correlation was constrained to be zero received more support both in California and in Alaska. We saw the same pattern between populations, as birds in Alaska reached their inflection point earlier, but the two populations did not differ in asymptotic mass.

### *Interpretation of fixed effects*

Instead of fitting separate growth curves to different groups or individuals, we extended the logistic model to explicitly test for effects of asynchronous hatching on growth trajectories, and also to test for differences between populations. We found no differences in the growth rate constant or the asymptotic mass between younger and older nestlings, indicating that asynchronous hatching did not substantially affect growth trajectories. The contrast between our results and previous work (reviewed in Krebs 1999) may reflect the low rates of starvation and relatively small differences in hatching time in our study population.

Our comparison between populations showed that Alaskan nestlings grew more quickly than Californian birds and reached the inflection point of their growth curve approximately half a day earlier; the two populations did not differ in their asymptotic mass (Fig. 3.2). Mixed models provided qualitatively stronger support for a difference in the growth rate constant compared with a model with only fixed effects (Table 3.1), likely because the random effects explained additional variation within populations and thereby highlighted differences between populations that previously had been masked by within-group variation. Few previous studies have found strong evidence for intraspecific variation in a passerine bird (e.g. Starck et al. 1995), and these demonstrations are particularly important in light of past work suggesting that passerine growth rates may be maximized and should therefore not vary between populations (Ricklefs 1969, Werschkul and Jackson 1979, King and Hubbard 1981). We found that although growth rate constants varied little within populations, they were not physiologically constrained to be equivalent between populations. These results highlight the need for studies that test whether the ecological factors that are thought to underlie variation in growth between species can also lead to adaptive variation between intraspecific populations.

Comparative studies of avian growth have focused on the growth rate constant, which can be compared between species that differ in their asymptotic mass (Starck and Ricklefs 1998), whereas few studies have considered variation in the inflection point. We show inflection points can differ between populations, and suggest that future work could evaluate whether the inflection point is under selection and shaped by ecological factors such as breeding season length and nest predation risk. Alaskan birds reached their inflection point nearly half a day earlier and also had shorter nestling periods (mean  $\pm$  1 SD:  $9.5 \pm 0.8$  days,  $n = 39$  nests) than Californian birds ( $12.0 \pm 1.1$  days,  $n = 42$  nests), but the relative effects of faster growth rates,



earlier inflection points, and differences in the developmental stage at fledging have not been integrated to understand the factors underlying variation in avian nestling period lengths.

### *Conclusions*

We suggest that future studies of avian growth should consider the two types of model extensions we illustrate here: the inclusion of random effects and the alteration of the fixed-effect function to explicitly test hypotheses of interest. Random effects quantify variation within populations and account for the lack of independence between data points, leading to more accurate estimates of parameters and their standard errors. Not only are these features useful for intraspecific studies, but because comparative methods that control for phylogeny can now incorporate estimates of intraspecific variation (Ives et al. 2007), future interspecific studies will also benefit. More generally, mixed models are appropriate tools for ecological research because they can partition the sources of variation in a dataset and because unbalanced designs, missing data, and varied measurement intervals do not increase the complexity of implementation (Vonesh and Carter 1992). Therefore, studies should consider individually marking nestlings to allow for the inclusion of both nest and individual-level random effects, although analyses of existing data can likely improve model fit by including at least nest-level random effects (e.g. Table S3.1). An increased use of models with both random effect levels would allow for comparisons of how the relative amount of variation explained at each level is affected by breeding ecology or life history strategy. For example, a greater relative importance of nest-level effects would indicate that shared genes, maternal effects, and/or a relatively even distribution of parental care overwhelm differences between nestmates. By contrast, when starvation of one or more young is common or nestmates vary considerably in mass, more variation should be

captured by individual-level effects.

To understand the ecological factors that underlie intraspecific variation in growth trajectories, we suggest that studies directly incorporate tests of relevant hypotheses into the nonlinear fixed effect function. Previous methodological suggestions for studies of avian growth have largely focused on the appropriateness of different nonlinear functions (e.g. logistic, Gompertz, von Bertalanffy, and Richards functions; Starck and Ricklefs 1998, Brown et al. 2007, Tjorve and Tjorve 2010), but have not discussed how these functions may be altered to test specific hypotheses. Our study illustrates how to incorporate parameters that estimate the difference between two groups in the growth rate constant, asymptotic mass, or inflection point. Similar extensions of the fixed-effect function could be used to incorporate continuous covariate data, for example to test how variation in provisioning rate affects nestlings' growth rate constant or asymptotic mass. Because of their flexibility, nonlinear mixed models are also widely applicable beyond the study of growth curves, and we encourage the wider use of these methods.

## RECOGNITION

Our research was supported by the The Nature Conservancy, the Smithsonian Institution, an American Ornithologists' Union Graduate Research Award, and a Frank M. Chapman Memorial Grant from the American Museum of Natural History. HRS was supported by NSF-IGERT Grant DGE-#0221595 (administered by the PRIMES program at Colorado State University) and NSF Grant DEB-#846175 to CKG. The Catalina Island Conservancy provided logistical support. We thank users of the R mixed effect models message board for advice. Comments from B.R. Noon, K.M. Pepin, and C.T. Webb improved the manuscript.

TABLES AND FIGURES

Table 3.1: Fixed-effect parameter estimates ( $\pm 1$  SE) from models testing for differences between populations in growth trajectories. We compare the model without random effects to the best-supported mixed-model, which contained random effects of nest and nestling on the inflection point and asymptotic mass. Parameters with the *pop* subscript estimate the difference in the Alaskan population compared with the Californian population;  $\beta$  estimates the shift in the inflection point for younger nestlings. The mixed model provided stronger statistical support for a difference in the growth rate constant between populations.

Model	$K$	$K_{pop}$	$A$	$A_{pop}$	$I$	$I_{pop}$	$\beta$
No random effects	0.534 $\pm$ 0.019	0.041 $\pm$ 0.023 <sup>^</sup>	9.35 $\pm$ 0.16	0.09 $\pm$ 0.20 <sup>NS</sup>	3.67 $\pm$ 0.09	-0.44 $\pm$ 0.11 <sup>***</sup>	0.93 $\pm$ 0.05 <sup>***</sup>
Nest: $A$ and $I$	0.525 $\pm$ 0.012	0.048 $\pm$ 0.015 <sup>**</sup>	9.31 $\pm$ 0.23	0.14 $\pm$ 0.26 <sup>NS</sup>	3.67 $\pm$ 0.10	-0.42 $\pm$ 0.12 <sup>***</sup>	0.77 $\pm$ 0.05 <sup>***</sup>

<sup>^</sup> indicates a *p*-value between 0.10 and 0.05; <sup>\*\*</sup> indicates significance at the 0.01 level; <sup>\*\*\*</sup>

indicates significance at the 0.001 level; NS indicates a *p*-value greater than 0.10. The

significance of  $K$ ,  $A$ , and  $I$  is not noted, as it is unreasonable to expect these parameter estimates to be zero.

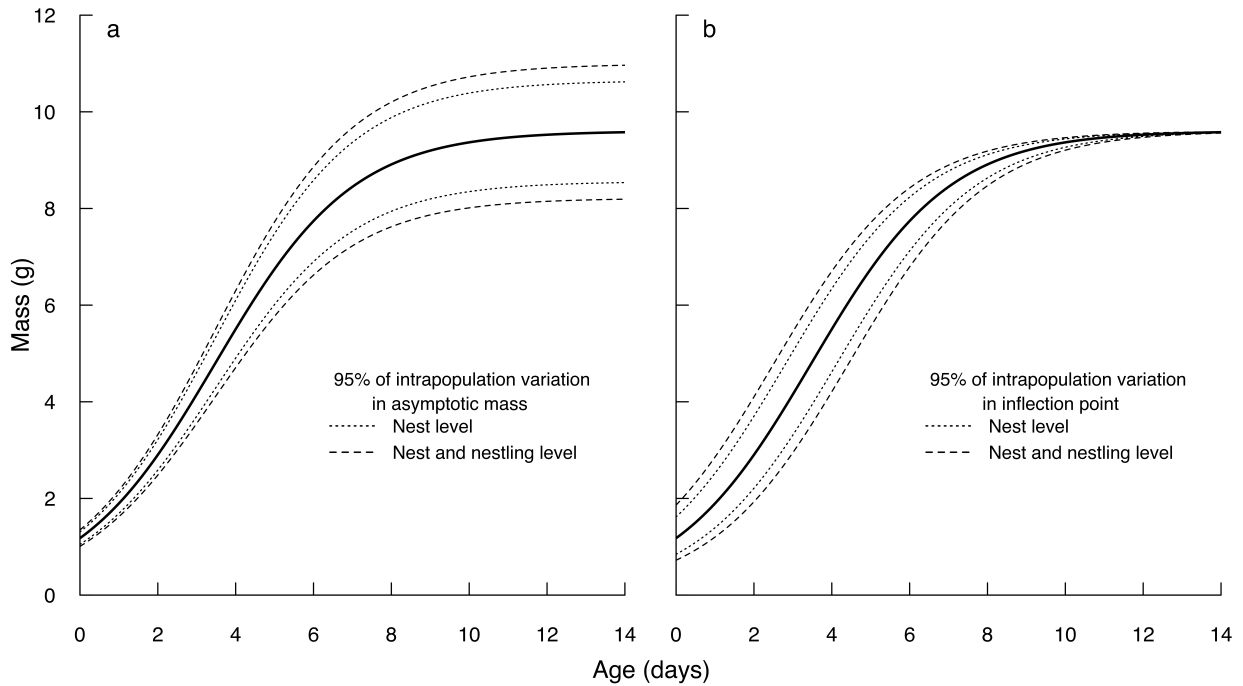


Figure 3.1: Variation within the Alaskan orange-crowned warbler population: (a) variation between nests and individuals in the asymptotic mass while holding the inflection point constant, and (b) variation in the inflection point given a constant asymptotic mass. This model included uncorrelated nest- and nestling-level random effects on the asymptotic mass and the inflection point. The fixed-effect structure was a three-parameter logistic function, and the solid lines show the growth trajectory of a typical nestling.

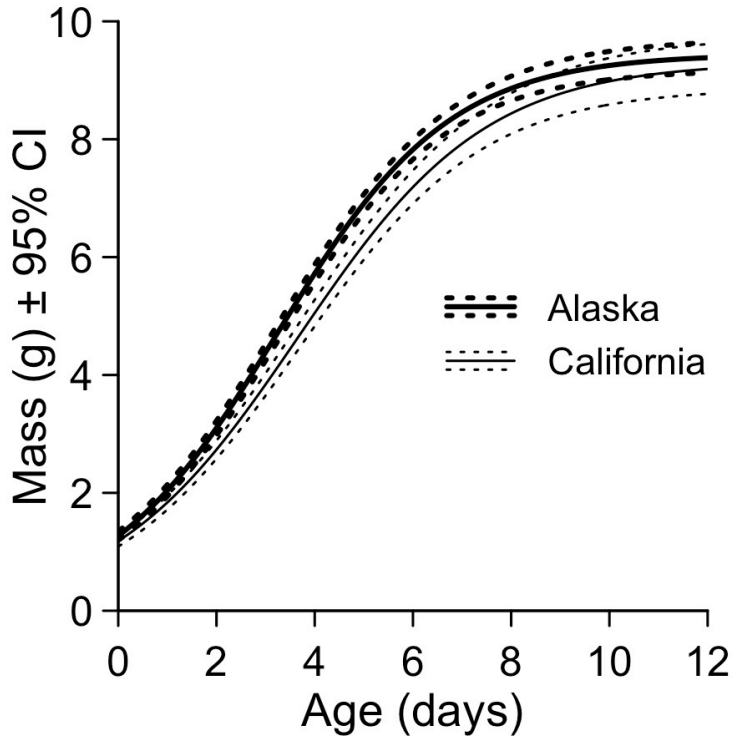


Figure 3.2: Comparison of estimated growth trajectories in the Alaskan and Californian populations. Alaskan birds reached their inflection point earlier and had a higher growth rate constant. The populations did not differ significantly in their asymptotic mass.

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APPENDIX III

Table S3.1: Model selection results showing models with different random-effect structures for the Alaskan population. The fixed-effect structure was a three parameter logistic model. In the top models, the correlation between random effects within the nest and/or nestling level was constrained to be zero; this constraint is indicated with an asterisk.

Random effect structure	$\Delta$ AIC	AIC	$\log(L)$	Total number of parameters	Number of random-effect parameters
Nest*: <i>A</i> and <i>I</i> Nestling*: <i>A</i> and <i>I</i>	0.00	825.53	-404.76	8	4
Nest*: <i>A</i> and <i>I</i> Nestling: <i>A</i> and <i>I</i>	0.26	825.79	-403.90	9	5
Nest: <i>A</i> and <i>I</i> Nestling: <i>A</i> and <i>I</i>	2.33	827.86	-403.93	10	6
Nestling: <i>A</i> and <i>I</i>	55.72	881.25	-433.62	7	3
Nest: <i>I</i> Nestling: <i>I</i>	96.8	922.33	-455.17	6	2
Nestling: <i>I</i>	138.87	964.40	-477.20	5	1
Nest: <i>A</i> Nestling: <i>A</i>	152.33	977.86	-482.93	6	2
Nestling: <i>A</i>	202.74	1028.27	-509.13	5	1
Nest: <i>A</i> , <i>I</i> , and <i>K</i>	362.32	1187.85	-583.93	10	6
Nest: <i>A</i> and <i>I</i>	365.62	1191.15	-588.57	7	3
Nest: <i>I</i>	374.59	1200.12	-595.06	5	1
Nest: <i>A</i>	404.42	1229.95	-609.97	5	1
Nest: <i>K</i>	651.08	1476.61	-733.30	5	1
Nest: <i>K</i> Nestling: <i>K</i>	653.07	1478.60	-733.30	6	2
No random effects	657.59	1483.12	-737.56	4	0
Nestling: <i>K</i>	659.59	1485.12	-737.56	5	1

Table S3.2: Model selection results for the Californian population for models with different random-effect structures. The fixed effect structure was a three-parameter logistic model. In the top model the correlation between the two nestling-level random effects was constrained to be zero, as indicated by an asterisk.

Random effect structure	$\Delta$ AIC	AIC	$\log(\mathcal{L})$	Total number of parameters	Number of random-effect parameters
Nest: <i>A</i> Nestling*: <i>A</i> and <i>I</i>	0.00	381.23	-183.61	7	3
Nest: <i>A</i> Nestling: <i>A</i> and <i>I</i>	1.77	383.00	-183.50	8	4
Nestling: <i>A</i> and <i>I</i>	3.70	384.93	-185.47	7	3
Nest: <i>A</i> Nestling: <i>A</i>	4.49	385.72	-186.86	6	2
Nest: <i>A</i> and <i>I</i> Nestling: <i>A</i> and <i>I</i>	4.54	385.77	-182.89	10	6
Nestling: <i>A</i>	6.57	387.80	-188.90	5	1
Nestling: <i>A</i> and <i>K</i>	10.58	391.81	-188.91	7	3
Nestling: <i>A</i> , <i>K</i> , and <i>I</i>	22.93	404.16	-192.08	10	6
Nestling: <i>I</i>	30.55	411.78	-200.89	5	1
Nest: <i>I</i> Nestling: <i>I</i>	31.05	412.28	-200.14	6	2
Nest: <i>A</i>	40.37	421.60	-205.80	5	1
Nest: <i>A</i> and <i>K</i>	42.76	423.99	-205.00	7	3
Nest: <i>A</i> and <i>I</i>	43.05	424.28	-205.14	7	3
Nest: <i>K</i> and <i>I</i>	45.81	427.04	-206.52	7	3
Nest: <i>I</i>	53.44	434.67	-212.34	5	1
No random effects	86.21	467.44	-229.72	4	0
Nest: <i>K</i>	86.62	467.85	-228.93	5	1
Nestling: <i>K</i>	88.16	469.39	-229.69	5	1
Nest: <i>K</i> Nestling: <i>K</i>	88.62	469.85	-228.92	6	2

Table S3.3: Model selection results for the Alaskan population, where all models included fixed differences in each parameter between younger and older nestlings. In the top models, the correlation between random effects within the nest and/or nestling level was constrained to be zero; this constraint is indicated with an asterisk.

Random effect structure	$\Delta$ AIC	AIC	$\log(\mathcal{L})$	Total number of parameters	Number of random-effect parameters
Nest*: <i>A</i> and <i>I</i> Nestling*: <i>A</i> and <i>I</i>	0	728.93	-353.47	11	4
Nest*: <i>A</i> and <i>I</i> Nestling: <i>A</i> and <i>I</i>	1.89	730.82	-353.41	12	5
Nest: <i>A</i> and <i>I</i> Nestling*: <i>A</i> and <i>I</i>	1.94	730.87	-353.44	12	5
Nest: <i>A</i> and <i>I</i> Nestling: <i>A</i> and <i>I</i>	3.80	732.73	-353.37	13	6
Nest: <i>A</i> and <i>K</i> Nestling: <i>A</i> and <i>K</i>	62.24	791.18	-382.59	13	6
Nestling: <i>A</i> and <i>I</i>	69.98	798.91	-389.46	10	3
Nest: <i>A</i> Nestling: <i>A</i>	89.32	818.25	-400.13	9	2
Nest: <i>I</i> Nestling: <i>I</i>	123.18	852.11	-417.06	9	2
Nestling: <i>A</i>	145.39	874.32	-429.16	8	1
Nestling: <i>I</i>	168.68	897.61	-440.8	8	1
Nest: <i>A</i> and <i>I</i>	229.85	958.78	-469.39	10	3
Nest: <i>I</i>	250.93	979.87	-481.93	8	1
Nest: <i>A</i>	267.38	996.31	-490.15	8	1
Nest: <i>K</i>	529.64	1258.57	-621.29	8	1
Nest: <i>K</i> Nestling: <i>K</i>	531.64	1260.57	-621.28	9	2
No random effects	544.80	1273.73	-629.86	7	0
Nestling: <i>K</i>	546.80	1275.73	-629.86	8	1

Table S3.4: Model selection results for models testing for fixed differences in the growth rate constant, the inflection point, and the asymptotic mass between populations breeding in Alaska and California. All models included a fixed effect that shifted the inflection point for younger nestlings; this effect did not differ between populations.

Random effect structure	$\Delta$ AIC	AIC	$\log(\mathcal{L})$	Total number of parameters	Number of random-effect parameters
Nest: <i>A</i> and <i>I</i> Nestling: <i>A</i> and <i>I</i>	0.00	1125.58	-548.79	14	6
Nest: <i>A</i> Nestling: <i>A</i>	63.34	1188.92	-584.46	10	2
Nestling: <i>A</i> and <i>I</i>	85.48	1211.06	-594.53	11	3
Nestling: <i>A</i>	132.38	1257.96	-619.98	9	1
Nestling: <i>A</i> and <i>K</i>	136.38	1261.96	-619.98	11	3
Nest: <i>I</i> Nestling: <i>I</i>	155.62	1281.20	-630.60	10	2
Nest: <i>A</i> and <i>I</i>	199.88	1325.46	-651.73	11	3
Nest: <i>K</i> and <i>I</i>	202.15	1327.73	-652.87	11	3
Nestling: <i>I</i>	214.19	1339.77	-660.88	9	1
Nest: <i>A</i> and <i>K</i>	230.68	1356.26	-667.13	11	3
Nest: <i>A</i>	235.24	1360.82	-671.41	9	1
Nest: <i>I</i>	240.91	1366.49	-674.24	9	1
Nest: <i>K</i>	545.11	1670.69	-826.34	9	1
Nest: <i>K</i> Nestling: <i>K</i>	547.10	1672.68	-826.34	10	2
No random effects	561.42	1687.00	-835.50	8	0
Nestling: <i>K</i>	563.42	1689.00	-835.50	9	1



## CHAPTER 4:

# NESTLING PROVISIONING RATES, GROWTH RATES, AND FOOD QUALITY ACROSS LATITUDES: REVISITING LACK'S HYPOTHESIS<sup>4</sup>

## SUMMARY

Resource abundance can have major effects on reproductive investment, and variation in food availability has long been thought to be a major factor driving the evolution of the latitudinal gradient in avian clutch sizes. Yet despite over sixty years of research, few studies have quantified how total and per-nestling provisioning rates vary with latitude or tested whether the relationship between nestling provisioning and growth rates is consistent between populations. Here, we exploit life history variation between orange-crowned warbler (*Oreothlypis celata*) populations breeding in Alaska and California to test whether variation in food delivery could explain the larger clutch and brood sizes in Alaska. Using 24-hour recordings of parental behavior at nests, we show that while total provisioning rates increased with brood size, per-nestling provisioning rates were higher in small broods in California. In addition, we weighed nestlings before and after each 24-hour video to show that per-nestling food delivery had a positive effect on nestling growth only in the Alaskan population, suggesting that nestlings in these populations may allocate energy and nutrients differently. Finally, we found that insects collected in Alaska contained fewer calories, a higher percentage of protein

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and minerals, and a lower percentage of fat than those collected in California, rejecting the assumption that food quality is consistent between populations. Our study shows that the relationship between brood sizes and provisioning rates can differ between populations and highlights the need to understand variation in nestling growth strategies and individual quality.

## INTRODUCTION

Understanding the ecological factors driving variation in fecundity, survival, and growth is a central challenge for studies of life history evolution (Roff 1992; Stearns 1992). Life histories can be shaped by environmental factors that affect age-specific mortality rates, such as predation and parasitism (Williams 1966; Law 1979; Michod 1979; Abrams and Rowe 1996; Agnew et al. 2000), and by variation in resource quantity and quality and the intensity of intraspecific competition (Lack 1947; Ashmole 1963; Brockelman 1975; Reznick et al. 2000; Bassar et al. 2010). Because food availability affects the pool of resources available for allocation to maintenance, growth, and fecundity (Williams 1966; van Noordwijk and de Jong 1986), its effects on the evolution and expression of life histories have received considerable attention in taxa including vertebrates (Martin et al. 1987; Wiehn and Korpimäki 1997; Grether et al. 2001; Mueller and Diamond 2001), invertebrates (Glazier 1992; Boggs and Ross 1993; Awmack and Leather 2002; Messina and Fry 2003), and plants (Grime 1977, Chapin et al. 1987). Yet, it has been difficult to evaluate the relative importance of variation in food availability for explaining differences in reproductive investment between populations, particularly for species with parental care, where the resources available to each offspring depend on parental behavior.

Studies of birds have been central to developing and testing life history theory owing to the influential work of David Lack, who argued that the amount of food available to parents shaped the evolution of avian clutch sizes (Moreau 1944; Ricklefs 2000; Ricklefs and Wikelski 2002; Martin 2004). Lack (1947) suggested clutch sizes should evolve to reflect the maximum number of young parents could provision without compromising offspring condition. He therefore predicted that variation in food availability and parents' ability to provision their offspring could explain geographic variation in avian clutch sizes, as well as variation within single populations (1947, 1968). For over sixty years, Lack's hypothesis has been the focus of extensive testing in birds and in other taxa (Godfray et al. 1991). Studies of birds have found food availability can explain variation in clutch size between individuals (Hogstedt 1980; Pettifor et al. 1988, 2001; Bolton et al. 1993), within and between years (Boyce and Perrins 1987; Winkler and Allen 1996; Korpimaki and Wiehn 1998; Grant et al. 2000; Sofaer et al. *in review*), and between different sites or habitats (Hussell and Quinney 1987; Blondel et al. 1993), leading to a strong consensus that resource availability contributes to variation in fecundity (Klomp 1970; Drent and Daan 1980; Martin 1987; Ricklefs 2010). However, birds appear capable of provisioning more nestlings than the number in their natural broods (VanderWerf 1992), likely reflecting both costs during other reproductive stages (Monaghan and Nager 1997; Russell et al. 2004; Tarwater and Brawn 2010) and trade-offs between current reproduction and future fitness (Dijkstra et al. 1990; Stearns 1992; Ghalambor and Martin 2001). Therefore, while food availability alone cannot explain all variation in avian clutch sizes or other life history traits (Martin 2004), progress in understanding avian life histories will depend on identifying the components of life history variation that can or cannot be attributed to variation in resource availability.

Lack made several important assumptions and predictions that few studies have tested, particularly regarding the quantity and quality of food delivered to each nestling. First, Lack (1947) predicted that total food delivery rates should be higher at northern latitudes, where longer day lengths enable birds to provision their broods for more hours each day. Yet, while birds breeding at high latitudes can feed their young for over 20 hours per day (Karplus 1952; Sanz 1999), the role of day length in driving variation in clutch size is unclear because few comparisons between latitudes have examined provisioning rates over a 24-hour period (Hussell 1972).

Second, Lack's hypothesis assumed that investment in each nestling would not differ between latitudes because clutch and brood sizes should be adjusted to food availability. However, more recent life history theory has emphasized the trade-off between fecundity and per-offspring investment (Roff 1992). In particular, competitive environments can favor higher per-offspring investment if larger offspring size or higher physiological quality can increase competitive ability and fitness (Brockelman 1975; Sinervo 1990; Bashey 2008). The trade-off between offspring quality and quantity has traditionally received little attention in birds, but there is an increasing recognition that birds breeding at lower latitudes may invest more in their young (Young 1996), particularly during the post-fledging period (Tarwater et al. 2010). Higher per-nestling investment may also occur during the nestling period, as per-nestling food delivery rates during the morning hours were shown to be higher in subtropical populations than in temperate populations (Martin et al. 2000). Comparing 24-hour per-nestling investment between populations that experience differences in the strength of intraspecific competition can therefore provide an important test of whether variation in offspring quality contributes to the latitudinal gradient in clutch size.

Third, Lack (1968) recognized that differences in growth rate could affect the relationship between brood size and food delivery, as slower-growing individuals may require less food per day. He suggested that by raising larger broods of slower-growing nestlings, birds could increase their fecundity without increasing their total daily provisioning rates. Yet studies have suggested that passerine growth rates may either be maximized in most populations (Ricklefs 1969; Werschkul and Jackson 1979; King and Hubbard 1981), or may be faster at high latitudes (Ricklefs 1976; Starck et al. 1995; Remes and Martin 2002). However, it is not clear whether slower passerine growth rates at lower latitudes reflect variation in food delivery, metabolic rates (Wikelski et al. 2003; Robinson et al. 2010), or offspring quality (Arendt 1997).

Finally, the prediction that food delivery rate should be proportional to brood size assumes that the energetic and nutritional quality of the food fed to nestlings is consistent between populations. Passerine growth and development are sensitive to dietary quality (Boag 1987; Johnston 1993; Wright et al. 1998), but no studies have tested for large-scale geographic variation in food quality or incorporated measures of food quality into comparative studies of provisioning rates between latitudes.

We compared populations of orange-crowned warblers (*Oreothlypis celata*) breeding near their northern limit in Fairbanks, Alaska, and their southern limit on Santa Catalina Island, California to test Lack's hypothesis. These populations differ in their life history strategies, as preliminary analyses indicated that birds in Alaska lay larger clutches and have lower annual survival rates than those in California (Horton et al. 2010). Rapid development is frequently seen in populations with fast life history strategies (Roff 1992), and nestlings in Alaska have a faster growth rate and reach the inflection point of their growth curve earlier than those in California (Sofaer et al. *in revision*). In addition, these populations differ in the ecological conditions they

experience, and because our study population in California breeds on an island, breeding densities in that population average eight times higher than in Alaska (Yoon et al. 2012). These differences in breeding density are consistent with stronger intraspecific competition in California, and could favor higher per-nestling investment in that population (Brockelman 1975).

We tested Lack's predictions and assumptions to assess whether variation in food quantity or quality could explain life history differences between our study populations. First, we confirmed that birds in Alaska had larger clutch and brood sizes, and compared nestling period lengths between these populations. Second, we directly tested Lack's central predictions by comparing total and per-nestling food delivery between nests in Alaska and California using 24-hour video data. Third, Lack assumed that the relationship between per-nestling investment and offspring fitness should be consistent between populations. We tested this assumption by comparing the relationship between per-nestling provisioning rates and nestling mass gain, tarsus growth, and feather growth in Alaska and California. Finally, we tested the assumption that food quality was constant by comparing the energetic and nutritional content of insect larvae collected in our study areas. Collectively, our analyses provide a test of whether variation in food quality and availability can explain the most striking pattern in avian life histories: the latitudinal gradient in clutch size.

## METHODS

### *Avian field methods and video data*

We studied the reproductive investment and behavior of orange-crowned warblers in Fairbanks, Alaska (64°47'N, 147°53'W) and on Santa Catalina Island, California (33°20'N, 118°26'W). Our study populations are located near the northern and southern ends of the

breeding range of this species, and represent different subspecies (*O. c. celata* and *O. c. sordida*, respectively; see Horton et al. 2010; Yoon et al. 2012). We studied birds in Alaska from May-July of 2006-2008 and in California from March-May or June of 2003-2009. Most breeding adults in our study populations were individually marked with color bands, and we monitored between 25-131 nesting attempts in each season except for 2007, when individuals on Catalina Island did not breed because of drought (Langin et al. 2009). We observed parental activity at nests every 1-3 days and checked nest contents to determine clutch and brood sizes.

To quantify provisioning rates and compare parental behavior across latitudes, we collected digital video recordings at nests over an entire 24-hour period from 2007-08 in Alaska and 2008-09 in California. We placed small camouflaged cameras (Swann Inc.) beside the nest site and video recorders (Archos Inc.) and custom battery packs (Batteries Plus Inc.) 10-20m away. Cameras were set up a minimum of half an hour before recording began, and we observed parental behavior to ensure cameras were accepted. Most recordings were from noon until noon the following day, but data are presented from midnight to midnight for ease of interpretation.

We recorded 62 24-hour videos of parental behavior, and designed our video data collection to control for developmental differences between our study populations. Nestlings' flight feathers generally emerge from their sheaths on nestling day six in Alaska and on nestling day seven in California (hatch day = day 0), reflecting the more rapid growth and development of Alaskan nestlings (Sofaer et al. *in review*). We therefore videotaped nests on nestling day 5-6 in Alaska (n = 17 videos; n = 2 on day 6-7), and in California we recorded nests at both at the same age (nestling day 5-6; n = 9 videos) and at the same developmental stage (nestling day 6-7; n = 16 videos). In addition, we videotaped nests in both populations near the age of fastest growth, on nestling day 2-3 (AK: n = 8 videos, CA: n = 10 videos; Sofaer et al. *in review*)

We transcribed nest videos to quantify the number of active feeding hours, the number of feeding trips, and the mean food load size from each video. We recorded the time of each arrival and departure and defined food load size as the size of the food item relative to the parent's bill size (e.g. 1.5 times the bill size). Nine videos were between 20-24 hours long, with missing time during midday. For these videos, we scaled the number of feeding trips by dividing by the proportion of active feeding time that was actually recorded; this scaled number of total feeding trips was used in all subsequent analyses. In addition, in some videos from Alaska ( $n = 4$ ) and California ( $n = 14$ ) the food load size could not be seen in over two-thirds of the feeding trips. For these videos, we predicted the missing food load values. Because of the potential for a trade-off between feeding rate and food load size, we modeled food load size as a function of the number of feeding trips, nestling age, and brood size, and included a random effect for nest identity to account for multiple videos from each nest. Each population was modeled separately. None of the effects were significant in the Alaskan population, and we replaced missing food load sizes with the population mean. Feeding rate and nestling age had significant effects on food load size in California, and were used to predict missing food load sizes in that population. To ensure missing hours and food load sizes did not qualitatively affect our results, we also analyzed total and per-nestling provisioning rates using only complete data.

To quantify the relationship between provisioning and growth rates, we weighed and measured nestlings before and after our 24-hour video recordings. We individually marked nestlings using non-toxic permanent marker on their toenails, allowing us to calculate the growth of each bird over a 24-hour period. Nestlings were weighed to the nearest 0.01g, and we measured the tarsus and the length of the first primary feather from where it exited the skin to the tip of either the feather sheath or the feather, if it had emerged from its sheath. We weighed and



measured 54 nestlings from 11 nests on day 5 and day 6 in Alaska, and 23 nestlings from 9 nests on day 5, 6, and 7 in California. To ensure the handling of nestlings was complete by half an hour before the start of each video, in California we recorded nests from 11am-11am on day 5-6, weighed and measured nestlings just after the end of the video, and videotaped again from noon to noon on day 6-7.

#### *Clutch size, brood size, and nestling period length*

We compared the clutch sizes of birds breeding in Alaska ( $n = 77$ ) and California ( $n = 341$ ) using a generalized linear model. Because clutch sizes were underdispersed relative to a Poisson distribution (i.e. the variance was less than the mean), we modeled clutch size using a quasi-Poisson distribution, in which the variance was  $\phi\mu$  (see Ver Hoef and Boveng 2007). Our estimate of the dispersion parameter,  $\phi$ , was 0.11, indicating that the variance was approximately one-tenth of the mean, and justifying our use of the quasi-Poisson distribution. We modeled clutch size as a function of population, clutch completion date, and the interaction between population and clutch completion date. Clutch completion date was included to account for the seasonal decline in clutch sizes. We performed an identical analysis to test for differences in brood sizes between Alaska ( $n = 67$ ) and California ( $n = 240$ ); our estimate of the dispersion parameter,  $\phi$ , for the analysis of brood sizes was 0.21.

We compared the length of the nestling period based on a subset of nests whose contents were checked daily around hatching and fledging (AK:  $n = 39$ ; CA:  $n = 39$ ). We used Pearson's chi-squared test to test for differences between populations. Observed nestling period lengths ranged from 8-14 days, but to reduce the number of low expected cell counts and avoid violating the assumptions of Pearson's chi-squared test, we excluded nests that fledged in only eight days

( $n = 3$  in Alaska) and a single nest in California that fledged in 14 days. When including only nestling period lengths from 9-13 days (AK:  $n = 36$ , CA:  $n = 38$ ), two expected cell counts were between 4 and 5. Clutch size, brood size, and nestling period length data were analyzed in R (R Development Core Team 2012). Descriptive statistics are given as mean  $\pm$  1 SD throughout this paper.

### *Provisioning patterns and 24-hour food delivery rates*

We summarized patterns of nestling provisioning in Alaska and California, including the mean number of active feeding hours per day, the number of feeding trips, and the mean food load size in each population. Videos from which two-thirds or more of the food load sizes could not be seen were excluded from the overall population mean for the food load size variable. To test the hypothesis that the differences in clutch and brood sizes between birds in Alaska and California reflected variation in food availability, we tested for a difference between populations in total and per-nestling food delivery over 24 hours. Total food delivery during each video was defined as the number of feeding trips multiplied by the mean food load size, and this value was divided by brood size to calculate per-nestling food delivery. For each of these two variables, we tested for a difference between populations using linear mixed models, which included a random effect of nest identity because some nests were videotaped at multiple ages (AK:  $n = 4$  of 24 nests; CA:  $n = 9$  of 20 nests). For each variable we fit a model with fixed effects of population, nestling age, brood size, and a brood size by population interaction. Initially, we also tested for a population by age interaction because of differences in the rate of development between populations, but excluded this effect because it did not have a significant effect on total provisioning ( $t = -0.79$ ,  $P = 0.59$ ) and had only a marginal effect on per-nestling provisioning ( $t$

= 1.70,  $P = 0.07$ ). Models were fit in the lme4 package in R (Bates et al. 2012; R Development Core Team 2012), and we generated  $P$ -values based on Markov chain Monte Carlo sampling using the languageR package (Baayen 2011); we present both the  $t$ -values from lme4 and  $P$ -values from languageR.

### *Nestling growth*

For each nestling, we calculated the increase in mass (g), tarsus length (mm), and primary feather length (mm) over the 24-hour period that was recorded. In Alaska, mass gain was positively correlated with tarsus growth ( $r = 0.65$ ) and feather growth ( $r = 0.43$ ), and feather and tarsus growth were also positively correlated ( $r = 0.48$ ). Similar correlations were observed in California ( $r = 0.57$ ,  $r = 0.46$ ,  $r = 0.30$ , respectively). We modeled the relationship between each measure of growth and per-nestling provisioning rates using linear mixed models. We included a random effect of nest to account for sibling relationships and shared per-nestling provisioning rates for birds in each nest at each age. In addition, we included a random effect of nestling because all 23 nestlings in California had data from both day 5-6 and day 6-7. The nestling random effect did not explain any variance for nestling mass gain or feather growth, so was removed from these models but retained in the model of tarsus growth. Our models included fixed effects of population, brood size, nestling age, whether or not the nestling hatched asynchronously (i.e. was younger than its siblings), per-nestling provisioning rate, and an interaction between population and per-nestling provisioning rate. As in the previous analysis, models were fit in lme4 and  $p$ -values were obtained using the languageR package.

### *Energetic and nutritional content of insect larvae*

Insect samples were collected in Bulrush Canyon, Catalina Island in March 2010 and in Fairbanks, Alaska in June 2010. Our study sites were delineated by a 25m x 25m grid system, and we randomly selected 18 grid points in California and 37 grid points in Alaska (reflecting the larger study area) as center points for each sample of insects. Insects were collected from oak trees (*Quercus* spp.) in California, which is the primary foraging substrate for warblers in that population. In Alaska, we collected insects from alder (*Alnus* spp.), willow (*Salix* spp.), poplar (*Populus* spp.), and spruce (*Picea* spp.). We collected insects by beating the vegetation and catching them in a beating sheet (BioQuip Products Inc.). In addition, we opened clumps of dead oak leaves in California and collected the larvae inside, as we have observed orange-crowned warblers foraging within these leaves. All analyses were conducted on insect larvae, which were dominated by Lepidoptera species but also included sawfly (Symphyta) larvae in Alaska. Video data showed birds in both populations primarily feed larvae to their young. Because analyses of the nutritional quality of larvae required larger samples than we collected at each sampling point, we grouped larvae according to plant species. After grouping, we had five samples from oaks trees in California and seven total samples from Alaska: three from alder, two from willow, one from poplar, and one from spruce, reflecting both the relative abundance of each plant species and the larvae on these substrates.

We assayed the samples of insect larvae for gross energy content (i.e. caloric content), protein content, fat content, and ash content at the Nutrition Laboratory of the Smithsonian National Zoological Park. Samples were oven-dried at 60° C for 24-hours prior to all analyses. Adiabatic bomb calorimetry was used to determine caloric content of insect samples (Model 1241, Parr Instruments, Moline IL). Total nitrogen (TN) content was measured using a CHN

elemental gas analyzer (Model 2400, Perkin-Elmer, Norwalk, CT), and percent crude protein was calculated as  $100 \times \text{TN} \times 6.25$  (Merrill and Watt 1973). Fat content was measured using the Soxhlet procedure, in which lipid is extracted from samples using hot petroleum ether, the ether is collected into aluminum pans and then evaporated off leaving the lipid. Ash (the total mineral content of each sample) was measured by combusting the samples in a muffle furnace at  $500^\circ \text{C}$  for 5 hours.

For each insect sample, assays of caloric density (AK:  $n = 7$ , CA:  $n = 4$ ), percent fat (AK:  $n = 5$ , CA:  $n = 4$ ), and percent ash (AK:  $n = 5$ , CA:  $n = 3$ ) were done in duplicate and protein was analyzed in triplicate (AK:  $n = 7$ , CA:  $n = 4$ ). We used the mean value in our statistical analyses. Sample sizes differed between analyses because not all insect samples had sufficient mass for all analyses, and two samples collected from willows in Alaska were combined for the analysis of fat and ash.

## RESULTS

### *Clutch size, brood size, and nestling period length*

Birds breeding in Alaska laid significantly larger clutches (Fig. 4.1a;  $4.96 \pm 0.75$  eggs, mode = 5 eggs,  $n = 77$ ) than those breeding in California ( $3.15 \pm 0.68$  eggs, mode = 3 eggs,  $n = 341$ ;  $t_{414} = -22.65$ ,  $P < 0.0001$ ). There was a significant seasonal decline in clutch size ( $t_{414} = -5.01$ ,  $P < 0.0001$ ), and this decline was steeper in the Alaskan population, reflecting its shorter breeding season (population by day of year interaction:  $t_{414} = 2.74$ ,  $P < 0.006$ ). Similarly, brood sizes were significantly larger in Alaska (Fig. 4.1b;  $4.63 \pm 1.15$  nestlings,  $n = 67$ ) than in California ( $2.93 \pm 0.80$  nestlings,  $n = 240$ ;  $t_{303} = -15.01$ ,  $P < 0.0001$ ), but there was no seasonal decline in brood size ( $t_{303} = -1.14$ ,  $P = 0.25$ ) nor was there a significant population by date

interaction ( $t_{303} = -0.38$ ,  $P = 0.70$ ). Nestling period length was significantly shorter in Alaska (Fig. 4.1c;  $9.54 \pm 0.82$  days,  $n = 39$ ) than in California ( $12.26 \pm 0.68$  days,  $n = 39$ ;  $\chi^2_{df=4} = 65.01$ ,  $P < 0.0001$ ).

#### *Provisioning patterns and 24-hour food delivery rates*

Warblers breeding in Alaska fed their young for approximately six more hours per day than those in California (Table 4.1). Birds in Alaska also brought more food per feeding trip, but despite their longer feeding hours, they averaged approximately 50-60% fewer feeding trips over a 24-hr period than individuals breeding in California (Table 4.1). These patterns were maintained for both young and old nestlings, but at each age, we also observed substantial variation in feeding rates within populations (Table 4.1; Fig. 4.2).

Our mixed model of total food delivery showed that birds brought more food to older nestlings ( $t = 6.24$ ,  $P = 0.0001$ ) and to larger broods (Fig. 3a;  $t = 3.23$ ,  $P = 0.0014$ ). The main effect of population was not significant ( $t = -0.07$ ,  $P = 0.87$ ), and the interaction between population and brood size was marginally significant ( $t = -1.68$ ,  $P = 0.085$ ). Results based on perfect data (i.e. nests videotaped for 24 hours in which over two-thirds of the food load sizes could be estimated) were qualitatively similar except the brood size effect was marginal ( $t = 2.00$ ,  $P = 0.05$ ) and the population by brood size interaction was not significant ( $t = -1.12$ ,  $P = 0.33$ ).

Per-nestling provisioning rates increased with nestling age ( $t = 6.87$ ,  $P = 0.0001$ ), and we found a strong interaction between population and brood size ( $t = -4.44$ ,  $P = 0.0001$ ), with birds in California feeding larger broods at a lower per-nestling rate (Fig 4.3b). The main effects of population ( $t = -0.91$ ,  $P = 0.24$ ) and brood size ( $t = -0.32$ ,  $P = 0.75$ ) were not significant. Results

based on perfect data were similar, as age and the interaction between population and brood size were highly significant (both  $P = 0.0001$ ), and the main effects of population and brood size were not significant (both  $P > 0.5$ ).

### *Nestling growth*

Nestlings in Alaska gained an average of  $1.4 \pm 0.4$  grams on day 5-6 ( $n = 54$  nestlings) and those in California gained an average of  $1.4 \pm 0.6$  grams on day 5-6 ( $n = 23$  nestlings) and  $1.3 \pm 0.3$  grams on day 6-7 ( $n = 23$  nestlings). The tarsus grew by an average of  $1.7 \pm 0.4$  mm on day 5-6 in Alaska and by  $1.8 \pm 0.3$  mm on day 5-6 and  $1.5 \pm 0.3$  mm on day 6-7 in California. The first primary feather grew by an average of  $4.9 \pm 0.7$  mm on day 5-6 in Alaska and by  $4.2 \pm 0.7$  mm on day 5-6 and  $4.0 \pm 0.6$  mm on day 6-7 in California. Sample sizes for tarsus and feather growth were identical to those given for mass gain.

We found a significant positive effect of per-nestling provisioning rate on mass gain ( $t = 2.05$ ,  $P = 0.021$ ), and we also found a significant interaction between population and per-nestling provisioning that reduced the slope for nestlings in California ( $t = -2.19$ ,  $P = 0.015$ ). The net result of these two effects was to have a positive effect of per-nestling provisioning rate in Alaska but no effect in California (Fig 4.4a). The main effect of population was not significant ( $t = -0.29$ ,  $P = 0.80$ ), nor was the effect of age ( $t = -0.76$ ,  $P = 0.50$ ) or whether an individual hatched asynchronously ( $t = 1.53$ ,  $P = 0.16$ ).

Tarsus growth increased with per-nestling provisioning rate ( $t = 2.39$ ,  $P = 0.0030$ ), but an interaction between population and per-nestling provisioning rate ( $t = -2.42$ ,  $P = 0.0018$ ) acted to make the effect of food delivery effectively zero in the California population (Fig. 4.4b). There was no significant main effect of population ( $t = 0.55$ ,  $P = 0.35$ ), but tarsus growth was lower on

day 7 than on day 6 ( $t = -5.37$ ,  $P = 0.0006$ ), and was higher for asynchronously hatched young ( $t = 2.55$ ,  $P = 0.017$ ), likely reflecting their younger age.

Feather growth was faster for nestlings in Alaska ( $t = -3.74$ ,  $P = 0.0001$ ), and increased with per-nestling provisioning rate ( $t = 2.90$ ,  $P = 0.0024$ ). However, as with the results for mass gain and tarsus growth, there was a significant interaction between population and per-nestling provisioning rate ( $t = -2.84$ ,  $P = 0.0040$ ), which led to a positive overall effect of per-nestling provisioning in Alaska but no overall effect in California (Fig. 4.4c). Neither nestling age ( $t = -0.69$ ,  $P = 0.56$ ) nor whether a bird hatched asynchronously ( $t = -1.17$ ,  $P = 0.22$ ) affected feather growth.

#### *Energetic and nutritional content of insect larvae*

Larvae collected on deciduous plants (i.e. excluding the single sample from spruce) in Alaska averaged approximately 10% fewer calories per gram (AK:  $5314 \pm 109$  cal/g,  $n = 6$ ; CA:  $5902 \pm 99$  cal/g,  $n = 4$ ) because samples from Alaska contained nearly 50% less fat (Fig. 5; AK:  $12.3 \pm 1.0$  percent fat,  $n = 5$ ; CA:  $23.2 \pm 1.4$  percent fat,  $n = 4$ ). By contrast, the percentage of protein and ash was higher in Alaska ( $57.4 \pm 1.6$  percent protein,  $n = 6$ ;  $7.5 \pm 0.4$  percent ash,  $n = 5$ ) than in California ( $52.0 \pm 0.6$  percent protein,  $n = 4$ ;  $4.8 \pm 0.3$  percent ash,  $n = 3$ ). However, the composition of the single sample of larvae collected from spruce trees in Alaska, which was only large enough to measure caloric and protein content, was more similar to the larvae collected in California than to larvae collected from deciduous trees in Alaska (Fig. 4.5).

Our measures of larval nutritional composition were highly correlated; excluding the single spruce sample, caloric density was positively correlated with percent fat ( $r = 0.93$ ) and negatively correlated with percent protein ( $r = -0.95$ ) and percent ash ( $r = -0.95$ ). We therefore



used a t-test assuming unequal variances to compare the energetic content (cal/g) of larvae collected in Alaska and California, rather than conducting a multivariate analysis. Based on all samples, larvae collected in Alaska had significantly lower energetic content than those collected in California (AK  $\pm$  1 SD:  $5398 \pm 244$  cal/g,  $n = 7$ ; CA:  $5902 \pm 99$  cal/g,  $n = 4$ ;  $t_{8.5} = -4.82$ ,  $P = 0.001$ ); excluding the single spruce sample from Alaska increased the difference between the population means ( $t_{7.0} = -8.85$ ,  $P < 0.0001$ ).

## DISCUSSION

Our study tested Lack's assumption that the relationships between brood size, nestling provisioning rates, and nestling growth rates were consistent between two populations that differed in their breeding latitudes. Warblers breeding in Alaska had faster life history strategies, with larger clutch and brood sizes and shorter nestling periods than birds breeding in California (Fig. 4.1). Within Alaska, parental investment conformed to Lack's predictions, as total food delivery increased with brood size (Fig. 4.3a) and per-nestling provisioning rates were consistent across the range of natural brood sizes (Fig. 4.3b). By contrast, birds in California showed relatively little increase in total provisioning rates with increasing brood size (Fig. 4.3a), so that per-nestling provisioning rates were much lower in larger broods (Fig. 4.3b). These different relationships between brood sizes and provisioning rates in Alaska versus California indicate that variation in food availability alone cannot explain differences in clutch and brood sizes between these populations. We also found that nestlings that received more food grew more quickly in Alaska but not in California, and that the energetic and nutritional quality of food differed between populations. The degree to which variation in food quality affects growth in these populations remains speculative, but the different relationships between nestling provisioning

and growth rates suggest nestlings in these populations differ in their allocation to growth and development. Our results therefore challenge fundamental assumptions of Lack's hypothesis, and highlight gaps in our understanding of both the causes and the consequences of variation in parental investment.

*Patterns of nestling provisioning: day length, feeding rate, and food load size*

Variation in day length was an important component of Lack's hypothesis (1947, 1968), and he predicted that parents should take advantage of longer days to raise more offspring. Yet little is known about the ways in which feeding rate (i.e. trips per hour), food load sizes, and total feeding time per day vary between populations to determine 24-hour provisioning rates. As expected under Lack's hypothesis, birds breeding in Alaska did feed their young for approximately 19 hours per day, six hours more than birds breeding in California (Table 4.1). During each hour, parents in Alaska made fewer trips to the nest (Fig. 4.2a), but brought more food on each trip (Table 4.1). The net result of these hourly differences was that birds in California brought an equivalent amount of food per hour per brood as their counterparts in Alaska (Fig. 4.2b). Because of their smaller brood sizes, birds in California therefore had higher rates of per nestling food delivery during their active hours (Fig. 4.2c), and higher average per-nestling provisioning rates (Table 4.1). Collectively, these results show that while birds in Alaska did feed their nestlings for more hours per day, the longer day length they experienced was not the primary factor that enabled them to raise more young because per-nestling provisioning rates over 24-hours were not consistent between populations.

In addition to day length, other ecological and evolutionary factors also influence how frequently parents feed their young. Parents with higher extrinsic adult mortality rates should be

more willing to invest in their current brood at the expense of adult self-maintenance (Williams 1966; Mauck and Grubb 1995; Ghalambor and Martin 2001). On average, birds in Alaska did bring more total food to the nest (Table 4.1), and increased their total provisioning rates more steeply as brood size increased. However, it is difficult to assess the relative costs of provisioning young in these two environments, and comparisons of field metabolic rates would be needed to determine the costs of higher feeding rates, which we observed in California, versus larger food load sizes, which we observed in Alaska. In addition, rather than reflecting variation in adult mortality, the different provisioning strategies we observed may reflect the absence of any visually oriented nest predators in the insular community in which our California study population breeds (Peluc et al. 2008). The lack of constraint by visually oriented nest predators could have allowed birds in California to make many feeding trips while bringing small food loads (Skutch 1949; Martin et al. 2000; Eggers et al. 2005; Sofaer et al. *in review*).

Finally, testosterone has frequently been shown to have a negative effect on provisioning rates (e.g. Silvernin 1980; Ketterson et al. 1992), and may provide a mechanistic explanation for differences between populations. Yet, the high nest visitation rates and per-nestling provisioning rates we observed in California are counter to predictions based on hormonal variation because these males have higher testosterone levels during the nestling period than males in Alaska (Horton et al. 2010). These results highlight the potential for different physiological mechanisms to underlie variation in parental care within versus between populations, and suggest that additional comparisons of the relationship between hormonal levels and provisioning rates between populations are needed (Lynn 2008).

### *Variation in per-nestling provisioning rates*

Lack predicted that brood sizes would be evolutionarily adjusted to match food delivery rates, so that per-nestling provisioning rates would be relatively constant within and between populations. Instead, the magnitude of the difference in total food delivery between populations was smaller than the differences in clutch and brood sizes, leading to lower average per-nestling provisioning rates in Alaska (Table 4.1). We also observed a striking decline in per-nestling provisioning rates within our study population in California but not within the population in Alaska (Fig. 4.3b). Comparisons across the range of natural brood sizes show that in broods of four young, per-nestling provisioning rates did not differ between populations (Fig. 4.3b). However, while larger broods in Alaska were fed at approximately the same per-nestling rate, per-nestling provisioning rates in the smallest broods in California were up to three times higher (Fig. 4.3b). Lower per-offspring provisioning rates in larger broods have frequently been observed in avian populations (Lack 1947; Klomp 1970; Nur 1984; Grundel 1987; Moreno 1987; Rytönen et al. 1996), but the factors underlying this decline remain poorly understood.

Lack (1947) suggested that the decline in per-nestling feeding rates in larger broods reflected the limited ability of parents to provision their offspring, and he pointed to this pattern in support of his hypothesis that food availability limits clutch size. However, while Lack envisioned that an optimum clutch size would apply to an entire population, more current models of reproductive investment emphasize the potential for variation in resource acquisition between individuals within populations (van Noordwijk and de Jong 1986; Reznick et al. 2000). Therefore, differences in clutch size within a population are often interpreted as reflecting variation in individual or territory quality (Hogstedt 1980; Pettifor et al. 1988), such that individuals with access to more food are able to invest in larger clutch sizes without incurring

any fitness costs. These models predict that birds laying larger clutches should have higher total provisioning rates, as we saw within Alaska. However, in this context it is less clear why some individuals in California should raise more young but provision them at a lower per-nestling rate, or assuming the lower rate is sufficient, why other individuals in California should raise fewer young while provisioning them at a higher rate.

Several other hypotheses to explain higher per-nestling food delivery in smaller broods cannot account for the pattern we observed within California. For example, the costs of thermoregulation may be higher for birds in small broods (Royama 1966; Nur 1984), but cannot explain higher per-nestling provisioning rates on nestling day 2-3, when altricial young are effectively ectothermic (reviewed in Visser 1998). Similarly, optimality models suggest high per-offspring investment can be favored in small broods when an additional offspring could not be raised without substantially decreasing offspring quality (Charnov 1995a,b). However, this hypothesis cannot explain why there was a relatively weak correlation between total provisioning rate and brood size within California (Fig. 4.3a), and per-nestling provisioning rates in the smallest broods were up to three times higher than those in the largest broods (Fig. 4.3b).

The trade-off between offspring quantity and quality has been invoked to explain why per-nestling provisioning rates are lower in large broods, even within single populations (Nur 1984; Smith et al. 1989). However, studies have not tested for mechanisms that could favor and maintain variation in per-offspring investment between individuals in a single population. For example, variation in the strength of intraspecific competition between years can favor genetic divergence between individuals, such that individuals raise either high-quality or low-quality young (Sinervo et al. 2000). Under this scenario, different per-offspring investment strategies could be favored in different years, thereby maintaining variation in per-offspring investment

within a single population. Interestingly, we have observed substantial variation in breeding densities in California (Sofaer et al. *in prep.*), suggesting that annual variation in the strength of intraspecific competition could affect post-fledging survival and recruitment. However, this possibility requires further testing, and a fluctuating intensity of competition may be an unlikely general explanation for the decline in per-nestling feeding rates within populations.

Differences in parents' allocation towards current versus future reproductive effort could also help explain our results. Warblers breeding in California have slower life history strategies than those breeding in Alaska, with smaller clutches (Fig. 4.1a) and higher adult survival rates (Horton et al. 2010; Sillett et al. unpub. data). Individuals in this population may therefore be relatively unwilling to increase their reproductive investment as brood size increases, whereas birds breeding in Alaska may prioritize investment in current reproduction (Williams 1966; Ghalambor and Martin 2001). We found that total provisioning rates were relatively weakly correlated with brood size in California, but increased with brood size in Alaska (Fig. 4.3a), supporting this hypothesis. Although the interaction in our models was only marginally significant, this likely reflects the relatively small overlap in brood sizes between populations, and visual inspection of the data does support the interaction. Therefore, the relatively small increase in total provisioning rate with brood size that we observed within California could indicate that reproductive effort was relatively fixed in that population, and that nestlings, rather than parents, bear the costs of the increasing demands for food associated with larger brood sizes (Mauck and Grubb 1995). This hypothesis predicts that birds with slower life histories should be less willing to increase their feeding rates in response to brood enlargement experiments, and it assumes that the lower per-nestling provisioning rates in larger broods in California do have some negative fitness consequences for those young. However, it remains unclear why

individuals in California should lay an additional egg if they were unable or unwilling to increase their provisioning rates to the brood.

#### *Per-nestling provisioning and growth rates*

Higher food delivery rates are expected to result in faster growth, but we found that higher per-nestling provisioning had a positive effect on the growth of nestlings only in Alaska, and had no effect on nestling growth in California (Fig. 4.4). The lack of a correlation between per-nestling provisioning and growth rates within California is surprising, as food limitation is thought to cause most variation in nestling growth rates within populations (Ricklefs 1976; Price 1985; Konarzewski et al. 1996; Schew and Ricklefs 1998; Konarzewski and Starck 2000; Searcy et al. 2004; Killpack and Karasov 2012). In addition, nestlings in Alaska had a substantially shorter nestling period (Fig. 4.1c), and our previous work shows they also have a faster overall growth rate (Sofaer et al. *in review*). Therefore, variation in growth between populations was also in an unexpected direction because birds in Alaska did not have higher per-nestling food delivery rates (Fig. 4.3b, Table 4.1) but did grow more quickly.

The surprising results we observed, that food delivery was not related to nestling growth either within California or between populations, could be explained if the selective pressures shaping growth and development have led nestlings in these populations to allocate energy and nutrients differently. For example, rapid growth appeared to be favored in Alaska, and nestlings in that population did invest any additional resources on mass gain (Fig. 4.4a), tarsus growth (Fig. 4.4b), and feather growth (Fig. 4.4c). In addition, birds in Alaska allocated more resources towards feather growth compared with birds in California, and their feathers grew more quickly even at the same per-nestling provisioning rate (Fig. 4.4c). Previous studies have shown

differential allocation towards feather growth within single populations in response to pressure to leave the nest site (Saino et al. 1998; Miller 2010), suggesting that temporal constraints can favor the decoupling of feather and body growth, and raising the possibility that a short breeding season in Alaska has favored rapid growth and development in that population.

Fast growth rates, such as those we observed in Alaska, are thought to be costly because they may decrease individual quality (Arendt 1997; Metcalfe and Monaghan 2003; Dmitriew 2011). Studies of birds have found rapid growth during the embryonic or nestling period was correlated with decreased immune function (Ricklefs 1992; Mauck et al. 2005; Brzek and Konarzewski 2007; van der Most et al. 2011) and increased rates of aging (Ricklefs 2006). Therefore, nestlings in California may slow growth in order to prioritize investment in any physiological functions that could increase individual quality, as these birds have relatively high adult survival rates (Sofaer et al. *in prep*) and selection could favor investment in traits that could further increase longevity (Williams 1966). Alternatively, their slower growth may reflect higher maintenance costs. Distinguishing between these hypothesis will require a more nuanced understanding of nestling metabolic rates, digestive physiology, and patterns of energetic and nutrient allocation, as it is currently unclear how nestlings in California are allocating the high resource levels they appear to be receiving. However, we can reject Lack's suggestion that slow growth may be favored as a method of reducing nestlings' demand for food, because slow-growing nestlings in California did not receive less food.

Interestingly, our study is not the first to suggest that growth and provisioning rates may be decoupled. A comparison between species found that after controlling for phylogeny and body size, growth rate was not related to provisioning rate (Saether 1994). Similarly, a recent comparative study found faster growth was associated with lower per-nestling provisioning rates



(Martin et al. 2011), and a comparison between two populations of the same species found a difference in the growth rate but no difference in per-nestling provisioning rates (Ferretti et al. 2005). The latter two results were attributed to the effects of nest predation risk, which should favor both a reduction in the nest visitation rate and an increase in the nestling growth rate. However, nest predation is unlikely to account for the patterns we observed, as the population in Alaska had a lower nest predation rate than the population in California (Horton et al. 2010; Sillett et al. unpub. data). Instead, a short breeding season in Alaska could have favored allocation towards more rapid growth. However, although other intraspecific comparisons have shown that high-latitude passerine populations can grow more quickly (Starck et al. 1995) and have shorter nestling periods (Sanz 1999), no studies have isolated the evolutionary effects of breeding season length from those of nest predation risk and food delivery rates.

#### *Variation in food quality*

Lack focused on variation in food availability, and most tests of his hypothesis have assumed that food quality is constant within and between populations (e.g. Hussell 1972; Martin et al. 2000). We found that insect larvae collected in Alaska had higher protein and mineral content, while insects collected in California had higher caloric and fat content (Fig. 4.5). No previous studies have combined geographic comparisons of food delivery rates and food quality, and additional work is needed to understand how this variation in food quality may contribute to variation in nestling growth and development, as well as to differences in clutch sizes between populations.

Relatively little is known about whether avian growth is limited by overall caloric content or by specific nutrients, such as protein or minerals (Ricklefs et al. 1998). For example, a low-

protein diet did not appear to limit the growth rate of seabirds (Ricklefs et al. 1987) or frugivorous passerines (Ricklefs 1976), and insectivorous diets may have a surplus of protein (Ricklefs et al. 1998). However, one of the few experimental studies on a wild insectivorous passerine found that supplementing the diet with fat led to slower growth, a longer nestling period, and a smaller size at fledging (Johnston 1993). The implications of the variation in food quality we observed are therefore unclear, because although larvae collected in both populations contained over 50% protein, insects in California had higher levels of fat (Fig. 4.5b), and birds in that population grew more slowly (Sofaer et al. *in review*). In addition, feather growth requires a substantial amount of protein (Wylie and Hocking 1999; Urdaneta-Rincon and Leeson 2004), raising the possibility that the higher protein levels in Alaskan larvae could contribute to faster feather growth in that population. Finally, other nutrients or minerals may also limit growth, particularly calcium (Tilgar et al. 2004; Wilkin et al. 2009), and calcium limitation has also been proposed to explain geographic variation in clutch size (reviewed in Patten 2007). We found that ash (i.e. mineral) content was higher in Alaskan insect samples, supporting the assertion that the mineral composition of insects within and between latitudes deserves further study.

Quantifying variation in food quality is a promising avenue of research. Prey quality can vary both between plant species within a single location and over large geographic distances (Fig. 4.5), and may also vary seasonally (Arnold et al. 2010). Our observation that the energetic and nutritional content of insects varied between sites is particularly striking because we limited our analysis to Lepidoptera and Symphyta larvae, and populations that consume different types of insect prey likely experience more pronounced variation in food quality. Recent research in fish has shown that life history strategies can be correlated with variation in food quality, with populations with faster life histories consuming higher quality prey (Zandonata et al. 2011). These

results raise the possibility that variation in food quality may underlie variation in fecundity, growth, and other life history traits across a broad range of taxa.

### *Conclusions*

Our study compared provisioning and growth rates over 24-hours to provide a comprehensive test of Lack's predictions and assumptions, several of which we can reject. First, the relationship between brood size and provisioning rates was not consistent between populations, indicating that the higher clutch and brood sizes in the Alaskan population did not simply reflect higher food availability or longer day length. Second, per-nestling provisioning rates were much higher in small broods in California, raising the possibility that nestling quality varies between and within populations. Third, the consequences of variation in per-nestling provisioning rates differed between populations, as more food was associated with faster growth within Alaska but not within California. Fourth, birds in Alaska had faster feather growth than those in California, further supporting the hypothesis that patterns of allocation towards nestling growth and development differ between populations. Finally, the energetic and nutritional content of insect larvae differed between these populations, and quantifying how geographic variation in food quality contributes to variation in avian life history traits will be a productive avenue for future research. Collectively, our results highlight the need to understand patterns of total and per-offspring investment within and between populations. We suggest that this will require studies that quantify how variation in adult mortality interacts with food availability to affect total provisioning rates, as well as research that evaluates whether the trade-off between offspring quality and quantity contributes to variation in avian clutch size within and between populations.

## RECOGNITION

This work was supported by The Nature Conservancy, the Smithsonian Institution, an American Ornithologists' Union Graduate Research Award (HRS), and a Frank M. Chapman Memorial Grant from the American Museum of Natural History (HRS). HRS was supported by Colorado State University, NSF-IGERT Grant DGE-#0221595 (administered by the PRIMES program at Colorado State University), NSF DEB-0846175 to CKG, and by a Smithsonian Institution Predoctoral Fellowship. The Catalina Island Conservancy provided logistical support. We thank our field technicians and the undergraduate students who transcribed our nest videos for their hard work.

TABLES AND FIGURES

Table 4.1: Twenty-four hour provisioning patterns (mean  $\pm$  1 SD) of warblers feeding young and old nestlings in Alaska and California. Birds in Alaska were active for approximately six more hours per day but nevertheless made fewer total trips. At each age, total food delivery was higher in Alaska but per-nestling food delivery was higher in California. Food load sizes were estimated relative to bill size, with summary values limited to videos in which at least two-thirds of the food loads were seen.

Nestling age	Population	Active feeding hours	Total feeding trips	Food load size	Total food delivery	Food delivery per nestling
Young (day 3)	Alaska (n = 8)	19.4 $\pm$ 0.7	67.8 $\pm$ 17.7	3.1 $\pm$ 1.0 (n = 5)	196.4 $\pm$ 59.1	40.2 $\pm$ 11.0
	California (n = 10)	13.3 $\pm$ 0.4	116.3 $\pm$ 36.2	1.2 $\pm$ 0.5 (n = 3)	134.5 $\pm$ 15.9	53.8 $\pm$ 13.7
Old (day 6-7)	Alaska (n = 19)	19.3 $\pm$ 0.6	109.2 $\pm$ 30.3	2.7 $\pm$ 0.6 (n = 18)	290.8 $\pm$ 86.7	60.8 $\pm$ 14.1
	California (n = 25)	13.4 $\pm$ 0.5	212.6 $\pm$ 55.5	1.2 $\pm$ 0.5 (n = 18)	238.6 $\pm$ 87.3	91.8 $\pm$ 42.6

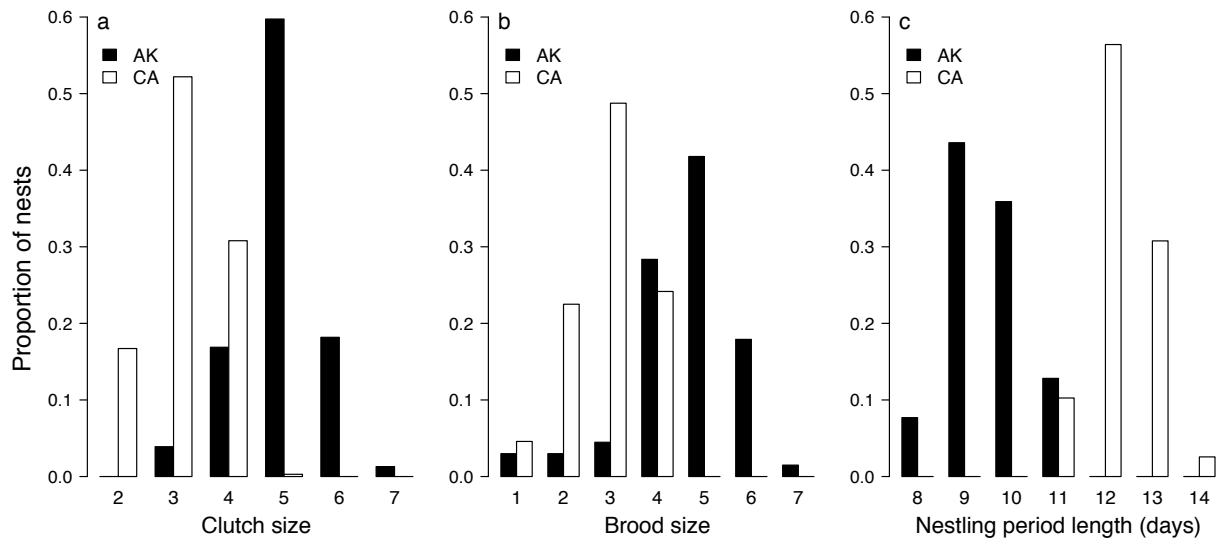


Figure 4.1: Birds breeding in Alaska had (a) larger clutch sizes, (b) larger brood sizes, and (c) shorter nesting periods than birds breeding in California.

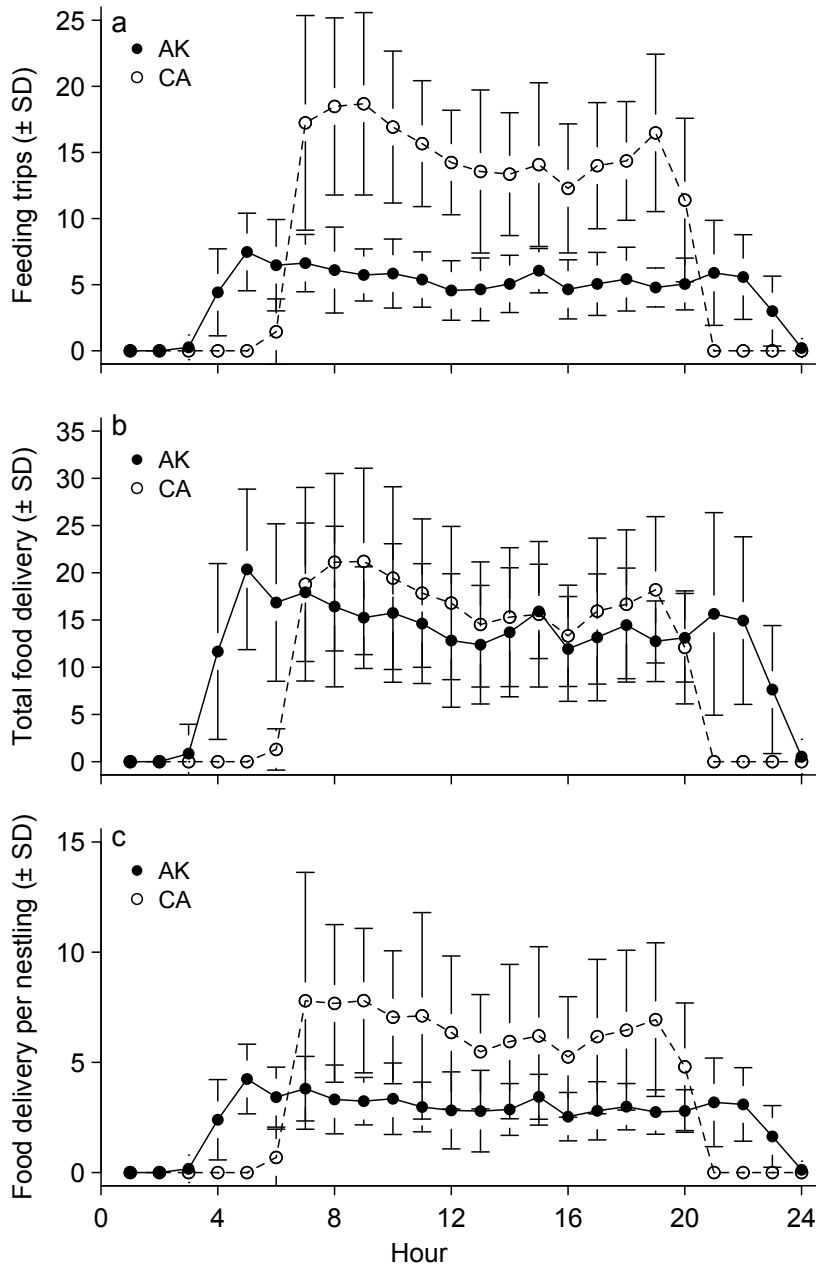


Figure 4.2: Twenty-four hour feeding patterns in Alaska and California. (a) Birds in California fed for fewer hours of the day but made more trips per hour. (b) Alaskan birds brought bigger food loads on each trip, making total hourly food delivery rates to their broods similar between populations. (c) During their active hours, food delivery per nestling was higher in California.

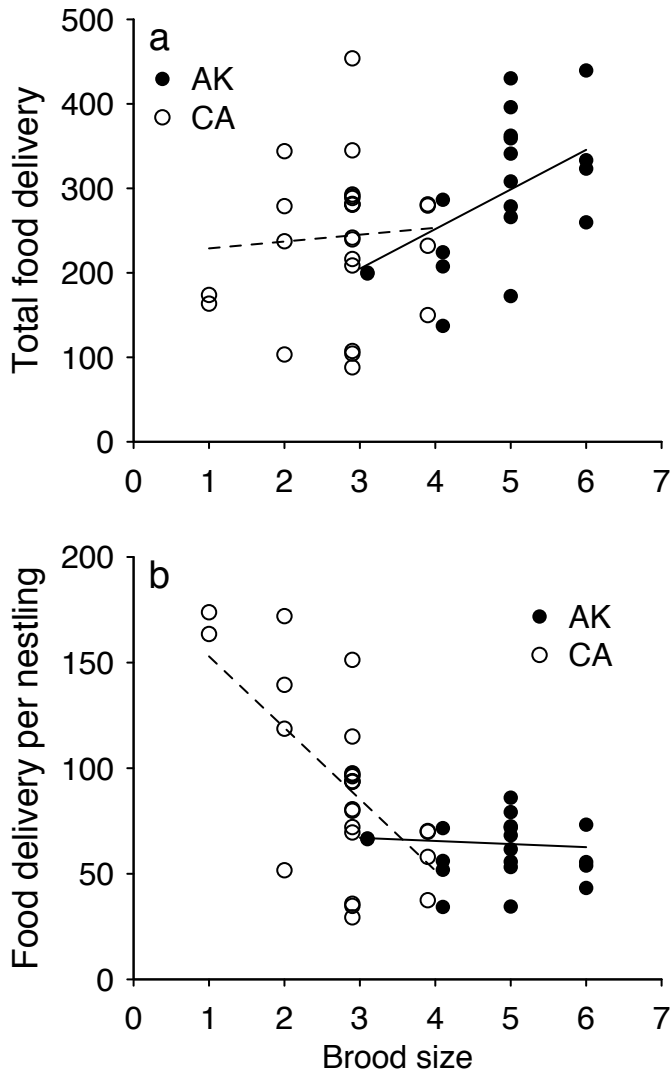


Figure 4.3: (a) Total provisioning rates increased with brood size; the interaction between brood size and population was marginally significant. (b) Per-nestling food delivery decreased sharply with brood size in California, but not in Alaska. Data are shown for video recordings from nestling days 5-6 and 6-7 in both populations. Each point represents a 24-hour period for a single nest, although some nests in California were recorded on subsequent days. For better visibility, points from each population were shifted horizontally where brood sizes overlap. Lines were fit based on estimates for each population and the mean age of plotted nests.



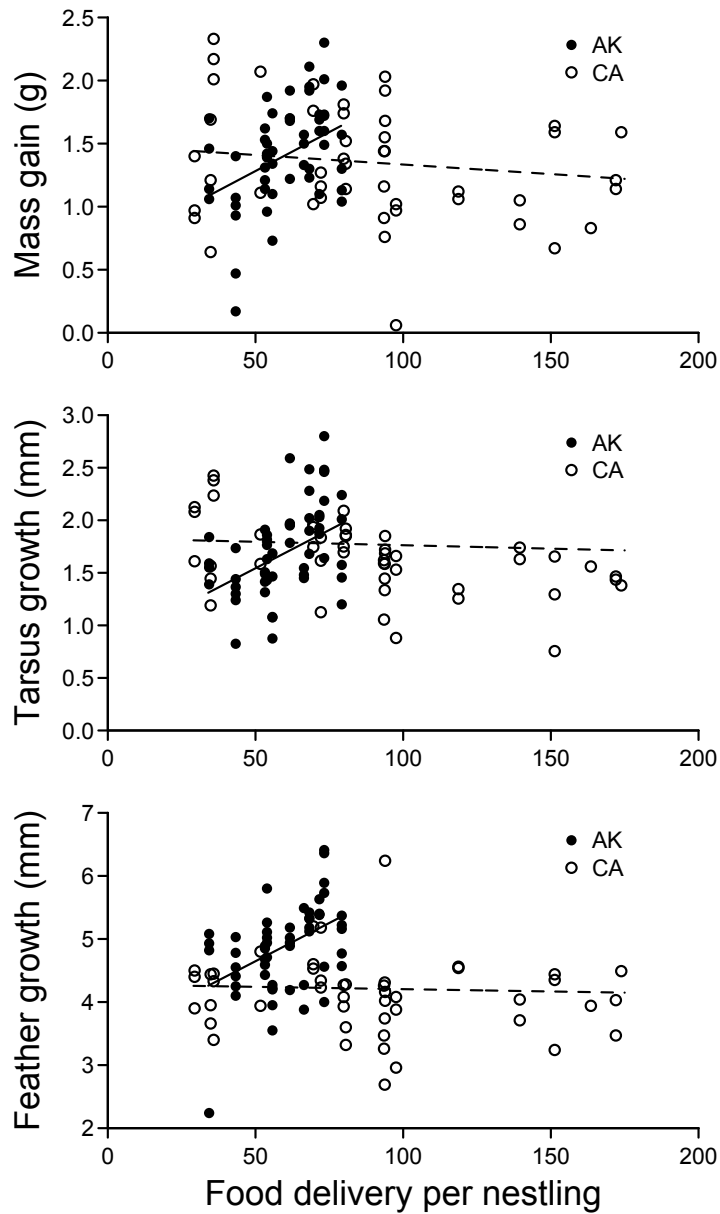


Figure 4.4: Over a 24-hour period, higher per-nestling provisioning rates were correlated with greater (a) mass gain, (b) tarsus growth, and (c) feather growth for nestlings in Alaska but not those in California. Each point represents a single nestling, and nestmates occur in vertical rows due to their shared per-nestling provisioning rate; our analysis included a random effect of nest to account for this lack of independence. Lines were fit based on model estimates for six-day-old nestlings in each population.

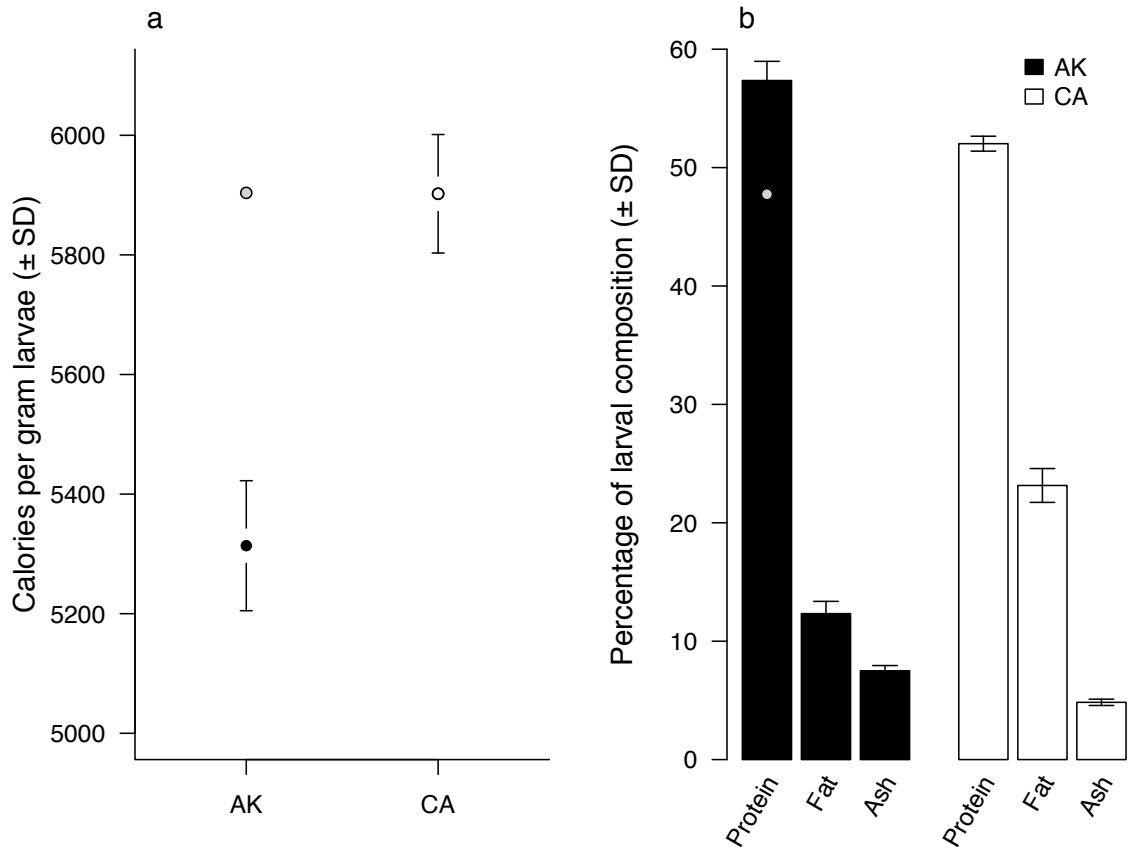


Figure 4.5: Insect larvae collected in Alaska had (a) lower energetic content and (b) higher protein content, lower fat content, and higher ash content than insects collected in California. The single sample collected on spruce trees in Alaska (denoted by a grey circle) was more similar in caloric and protein content to larvae collected in California; this sample was not included in the standard deviations shown for the Alaskan samples.

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