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Original Article

Differential effects of food availability and nest predation risk on avian reproductive strategies

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Spatial and temporal variation in resource abundance and predation risk can favor the evolution of phenotypic plasticity as a means of tracking changing environments. However, because food abundance and predation risk often covary in nature, few studies have separated their effects or tested whether different phenotypic traits respond to the same sources of environmental variation. We investigated patterns of parental investment and behavior over a 7-year period in 2 island populations of orange-crowned warblers (*Oreothlypis celata*) that showed little genetic divergence but experienced dramatic temporal variation in rainfall and spatial variation in nest predation risk. The amount of rainfall in each year was correlated with food abundance, and birds on both islands initiated breeding earlier and laid larger clutches in wetter years. In contrast, the rate at which parents visited their nests was not affected by rainfall but was negatively correlated with nest predation risk both within and between islands. Our results suggest that although the effects of food availability and nest predation have been viewed as mutually exclusive drivers of entire suites of life-history and behavioral traits, these traits can differ in their sensitivity to resource abundance or mortality risk, and traits that are often correlated can be decoupled under appropriate environmental conditions. *Key words:* breeding phenology, clutch size, life-history strategies, parental care, phenotypic plasticity. *[Behav Ecol]*

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, although studies of natural populations often find evidence for phenotypic plasticity in reproductive traits, it is difficult to establish which aspects of the environment these 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., Hogstedt 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. Like 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; Kleindorfer 2007; 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

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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 nest predation risk may often decrease with latitude, while food availability increases, latitudinal comparisons of avian life histories are often unable to separate the effects of these 2 ecological factors (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 (Martin et al. 2000; Ferretti et al. 2005). Instead, research indicates that 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 Island (hereafter Catalina) and Santa Cruz Island (hereafter Santa Cruz), 2 of the Channel Islands off the coast of southern California. Both islands have a Mediterranean climate that is subject to dramatic changes in annual rainfall associated with El Niño–driven dynamics (Cody and Mooney 1978; Polis et al. 1997). Catalina and Santa Cruz are approximately 150 km apart and have similar biotic communities (Schoenherr et al. 1999), but 2 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, where it breeds in the same oak-dominated habitats as the warblers. No jay species occurs on Catalina, and warblers there have no major visually oriented nest predators (Peluc et al. 2008). Second, despite large annual fluctuations in rainfall, Santa Cruz averages more rainfall per year than Catalina (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, and 3) across a gradient of nest predation risk within Santa Cruz. We also quantified the level of genetic divergence between warblers on these 2 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 compared with Catalina (Table 1). By contrast, higher rainfall and greater food availability on Santa Cruz 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 (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). 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 on Catalina from 2003 to 2009 in Bulrush Canyon (33°20′N, 118°26′W), and on Santa Cruz from 2006 to 2008 in Coches Prietos Canyon (33°58′N, 119°42′W) and from 2005 to 2006 in Islay Canyon (33°59′N, 119°43′W). 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, nest predator communities are similar on both islands (Schoenherr et al. 1999). We have observed gopher snakes (*Pituophis melanoleucus*) depredating nests on both islands, and other potential or observed nest predators include island foxes (*Urocyon littoralis*), deer mice (*Peromyscus maniculatus*), and on Catalina, 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. 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, whereas both parents feed the nestlings. We observed nests for activity at least every 3 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 3 h during the morning. Sample sizes of nests monitored were smaller on Santa Cruz (incubation: $n = 25$; nestling: $n = 12$) than on Catalina (incubation: $n = 44$; nestling: $n = 84$) due to the fewer

Table 1
Summary of the predicted effects of spatial and temporal variation in food abundance and nest predation risk

	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	–	–

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.

years of study and the extremely high nest predation rates on Santa Cruz (see below). Incubation videos were recorded on Catalina in 2004–2005 and 2008–2009 and on Santa Cruz 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 nonfeeding 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 posthatch, from 2004 to 2006 and 2008 to 2009 on Catalina and in 2005 and 2007 on Santa Cruz.

Genetic differences between islands

To quantify genetic divergence between warblers breeding on each island, we genotyped 198 adults from Catalina and 40 adults from Santa Cruz at 7 variable microsatellite loci. Five (Dpμ01, Dpμ16, LSWμ7, LSWμ18, and Pat43) were previously used in an orange-crowned warbler population genetics study (Bull 2005), and 2 were developed for Kirtland's warblers (DkiB12 and DkiD128; King et al. 2005). Blood (30–100 μL) 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 μL volumes for Dpμ01, Dpμ16, LSWμ7, LSWμ18, and Pat43, and 11 μL volumes for DkiB12 and DkiD128. Each contained 1 μL of genomic DNA (except LSWμ18, which contained 1.5 μL of DNA), 1 μL of dNTPs (1 mM deoxynucleotide triphosphates), 0.1 μL of 1× Taq buffer, 0.5 μL each of forward and reverse primers, and 1 μL of FlexiTaq polymerase (Promega Corp., Madison, WI). Dpμ01, Dpμ16, DkiB12, and DkiD128 were run with 1 μL of 25 mM $MgCl_2$, whereas LSWμ7, LSWμ18, and Pat43 were run with 0.9, 1.1, and 0.75 μL of $MgCl_2$, respectively. LSWμ7 was run with 0.15 μL of 2.5× bovine serum albumin (BSA), whereas DkiB12 and DkiD128 were run with 1 μL of BSA, and other loci were run without BSA.

PCR conditions consisted of initial denaturing at 94 °C for 3 min, followed by 30 cycles of denaturation at 94 °C for 30 s, annealing for 30 s, extension at 72 °C for 45 s, followed by a final extension at 72 °C for 5 min. The annealing temperature was 61 °C for Dpμ01, 55 °C for Dpμ16, 57.5 °C for LSWμ7, 53 °C for LSWμ18, 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, $P = 0.0454$), whereas alleles at LSWμ18 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 to 17 (Table S1). We calculated F_{ST} values using all 7 loci and also while excluding DkiB12 or LSWμ18.

We used the program STRUCTURE 2.3.2 (Pritchard et al. 2000) to compare the fit of models with $k = 1$ versus 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 Markov chain Monte Carlo repetitions. Each model was run 10 times, and we compared the likelihoods for 1 versus 2 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 survival modeling to those that were successful or depredated ($n = 506$ nests). We assumed nests were depredated when previously observed eggs or young nestlings were missing, and we conducted extensive observations of parental behavior when nestlings were near fledging. Predation was the primary source of nest failure on both islands. For failed nests in which at least 1 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 2 nests (<1%) failed due to starvation. We considered 5 a priori models of the factors affecting nest survival: a constant model (S_{Null}), an island effect (S_{Island}), a nest height effect (S_{Height}), an additive model with island and height ($S_{Island + Height}$), and a model with both additive effects and an island by height interaction ($S_{Island \times Height}$). 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 spatial and temporal variation in daily nest survival, we also estimated nest survival for each year on each island (Figure 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: $n = 519$ nests; Santa Cruz: $n = 97$ 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: $n = 478$ nests; Santa Cruz: $n = 87$ 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, the effects of high predation risk and high food abundance on incubation visitation rates could be confounded, whereas the effects of nest predation risk and food abundance on nestling visitation rates lead to opposing predictions (see Table 1). Incubation visitation rates were modeled as a linear function of island, ambient temperature, and day of year. With the exception of 3 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

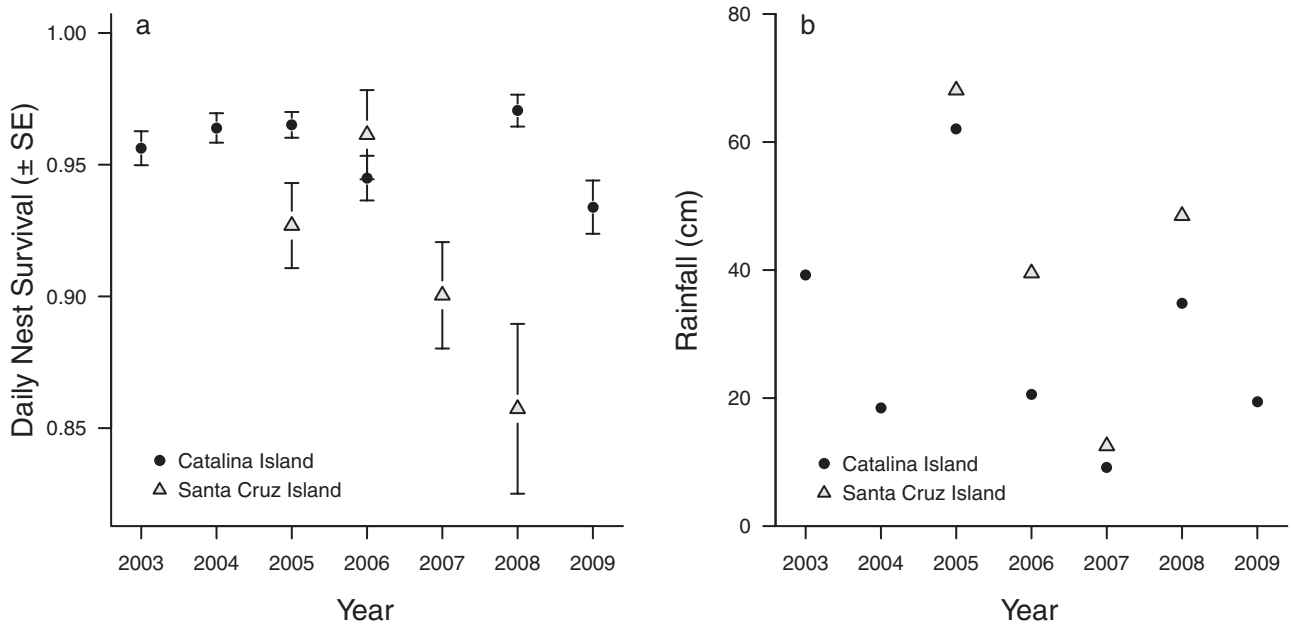

Figure 1
Spatial and temporal variation in daily nest survival and precipitation. (a) Daily nest survival was higher on Catalina Island than on Santa Cruz. (b) Total rainfall during winter and spring varied considerably between years, with Santa Cruz always receiving more rainfall in a given year than Catalina Island.

not individually color banded (15 unbanded males versus 35 unbanded females). However, male identity did not explain additional variation in the data, and this random effect was not included in our final model.

To evaluate how clutch size varied across space, we tested for a difference in clutch size between islands. In years 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 minimized any confounding of the effects of breeding season length and island, as birds were always followed to the end of the breeding season on Catalina, but not on Santa Cruz. 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 with 5 eggs (this nest was included in Figure 2b and in the analysis of clutch size vs. 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

We quantified spatial variation in scrub-jay abundance in Coches Prietos Canyon on Santa Cruz from 2007 to 2008 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 5-min surveys in each warbler territory. We placed survey points approximately 10 m 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 (±1 SE) number of scrub-jay surveys conducted in each territory in 2007 and 2008 was 18.5±0.9 and 26.1±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 1 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 7 days post-hatch at 5 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 from Western Regional Climate Center stations located within several kilometers of our field sites (Figure 1b; http://www.wrcc.dri.edu/). We sampled insects at 2-week intervals from 2003 to 2009 on Catalina Island and from 2006 to 2008 on Santa Cruz by collecting branch clippings from oak trees at 12 randomly generated grid locations in each study plot (Johnson and Sherry 2001); grid points were 25 m 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 more than 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

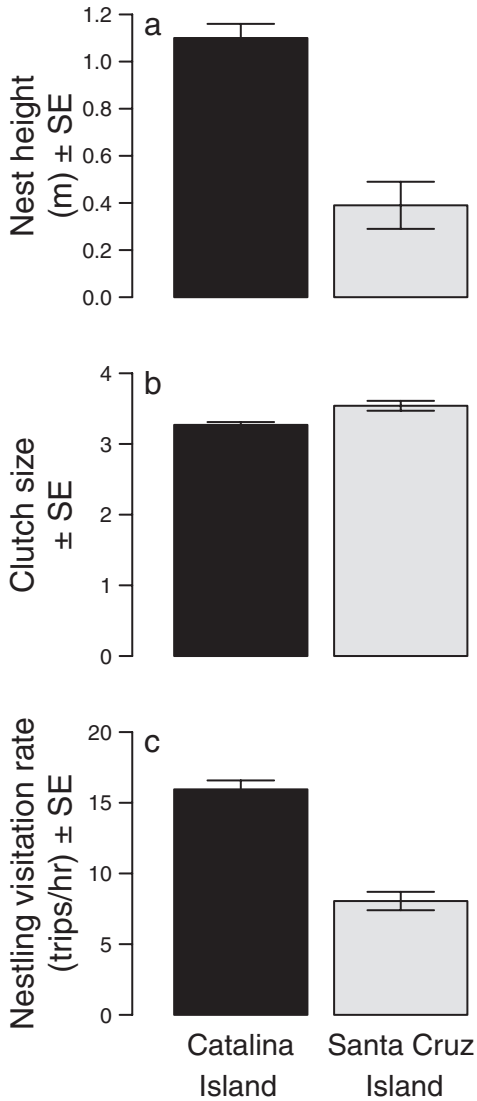

Figure 2
Divergence in reproductive traits between the 2 islands (±1 SE). (a) Mean nest height (meters; Catalina: $n = 519$ nests; Santa Cruz: $n = 97$ nests). (b) Mean clutch size (Catalina: $n = 273$ nests, mode = 3; Santa Cruz: $n = 59$ nests, mode = 4). (c) Mean nestling visitation rates (trips/hour; Catalina: $n = 84$; Santa Cruz: $n = 12$).

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 that grouped samples from each island in each year (i.e., each level of precipitation), and 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. The model was fit using the adaptive Gaussian quadrature method for maximum likelihood estimation (Pinheiro and Chao 2006). The shape of the relationship between date and larvae number varied considerably between years, but although 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. Therefore, we 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 was modeled as a simple linear function of rainfall; field crews could not consistently remain on Santa Cruz until the end of each breeding season. Breeding season length on Catalina 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 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 and accounted for the lack of independence of the nests in each group relative to the level of precipitation. Similarly, to test for an effect of rainfall on nestling feeding rates, we built a model with additive fixed effects of precipitation, day of year, and island. The 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 (Bates et al. 2012; R Development Core Team 2012), but because lme4 does not provide degrees of freedom for these models, we generated P values based on Markov chain Monte Carlo sampling using the languageR package (Baayen 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 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'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 was minimal. Including all loci, we found an overall $F_{ST} = 0.0037$. Our results were robust to excluding loci that violated test assumptions; without DkiB12, the $F_{ST} = 0.0039$, whereas without LSWμ18, the $F_{ST} = 0.0049$. Results from program STRUCTURE also provided 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 2 subpopulations. In addition, for models assuming $k = 2$, individuals from both islands were equally likely to be assigned to each of the 2 subpopulations. Collectively, these results suggest that birds on these 2 islands show little genetic divergence at these neutral loci. Because these islands have never been connected and birds from these islands winter on the mainland and willingly cross open water (Gilbert et al. 2010), this pattern likely reflects gene flow rather than a recent divergence.

Phenotypic variation between islands

Nest survival rates were higher on Catalina (where there are no scrub-jays) compared with Santa Cruz (Figure 1a) and increased with nest height on both islands. Based on our top model ($S_{Island + Height}$), estimated daily nest survival rates for a nest on the ground were 0.953 ± 0.004 (95% CI: 0.945, 0.960) on Catalina and 0.910 ± 0.011 (95% CI: 0.886, 0.929) on Santa Cruz. We found no support for an interaction between island and nest height, as the second-ranked model ($S_{Island \times Height}$) had one more parameter than the top model and had a ΔAIC_c value of 1.95 (Table S2).

Nest heights were significantly higher on Catalina compared with Santa Cruz ($t_{181.6} = -6.25$, $P < 0.0001$; Figure 2a). On Catalina, 28.2% of nests were built in grasses, leaf litter, ferns, or herbaceous plants, whereas 56.3% of nests on Santa Cruz were built in this class of vegetation. By contrast, 28.5% of nests on Catalina were built in oaks (of any height), whereas only 10.3% of nests on Santa Cruz were built in oaks; the vast majority of remaining nests on both islands were built in woody shrubs, and a few birds on Catalina 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 (±1 SE) were higher on Catalina (2.81 ± 0.17 trips/h, $n = 44$) compared with Santa Cruz (1.36 ± 0.06 trips/h, $n = 25$; island effect: $F_{1,62} = 36.83$, $P < 0.0001$; whole model: $F_{3,62} = 14.93$, $P < 0.0001$, $R^2 = 0.42$). Incubation visitation rate was also 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 had shorter on-bouts (16.43 ± 1.15 min, $n = 44$) and a lower percentage of attentiveness (67.23 ± 1.28, $n = 44$) than those on Santa Cruz (36.61 ± 2.44 min and 76.91 ± 1.26, respectively; $n = 25$).

Birds on Santa Cruz had lower nestling visitation rates but laid larger clutches than individuals on Catalina (Figure 2b,c). Nestling visitation rates were significantly lower on Santa Cruz (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 (Pearson $\chi^2_{2,n=331} = 9.45$, $P = 0.0089$).

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

Warblers on Santa Cruz exhibited a significant reduction in activity at the nest in response to spatial variation in relative nest predator abundance (Figure 3). Incubation visitation rate was negatively correlated with relative scrub-jay abundance (Figure 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 (Figure 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 (±1 SE) on-bout length was 31.5 ± 2.0 min in 2007 and 45.5 ± 5.1 min 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

Rainfall varied substantially on both islands during the course of this study (Figure 1b), and we found a positive relationship between rainfall and food abundance. The count side of our model showed that the number of larvae was positively correlated with rainfall ($t_9 = 2.90$, $P = 0.018$), was not affected by the mass of the branch clipping ($t_9 = 1.12$, $P = 0.29$), and was marginally higher on Santa Cruz ($t_9 = -1.91$, $P = 0.089$). The probability of a zero count

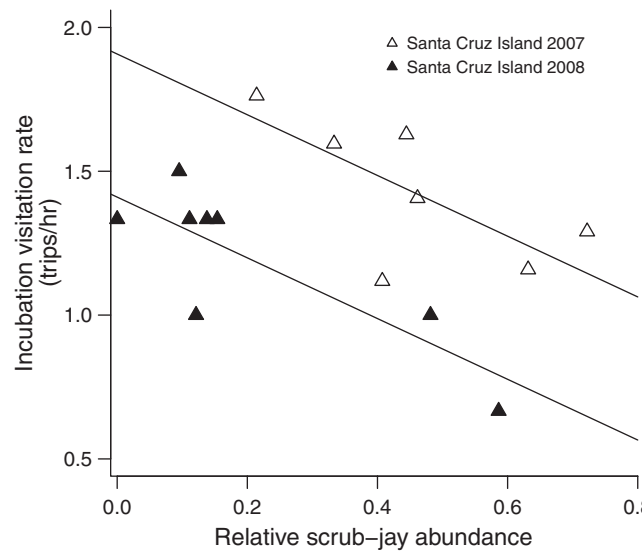

Figure 3
Nest visitation rates declined with increasing relative scrub-jay abundance. Nest visitation rates were significantly higher in 2007, a drought year, and there was no significant interaction between year and relative scrub-jay abundance.

decreased as leaf mass increased ($t_9 = -3.18$, $P = 0.011$), but was not affected by rainfall ($t_9 = -1.30$, $P = 0.23$) or island ($t_9 = -0.41$, $P = 0.69$).

Rainfall had strong effects on breeding phenology and clutch size (Figure 4), but did not affect parental behavior. Birds initiated breeding earlier in wetter years (Figure 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, 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. Clutch sizes were significantly larger on both islands in wetter years (Figure 4b; $F_{1,321} = 9.39$, $P = 0.0024$). We found no support for an additional island effect ($F_{1,321} = 0.65$, $P = 0.42$).

We found no support for an effect of precipitation on incubation attentiveness ($t = 0.27$, $P = 0.79$) or nestling feeding rates ($t = 0.14$, $P = 0.91$). Our model of incubation attentiveness supported an island effect ($t = 2.93$, $P = 0.018$), but not effects of ambient temperature ($t = 0.65$, $P = 0.48$) or day of year ($t = -0.79$, $P = 0.34$). An analysis of incubation visitation rates, rather than attentiveness, also failed to support a precipitation effect. Our model of nestling feeding rates found a significant effect of island ($t = -2.65$, $P = 0.020$) and a marginally significant effect of day of year ($t = 1.96$, $P = 0.089$).

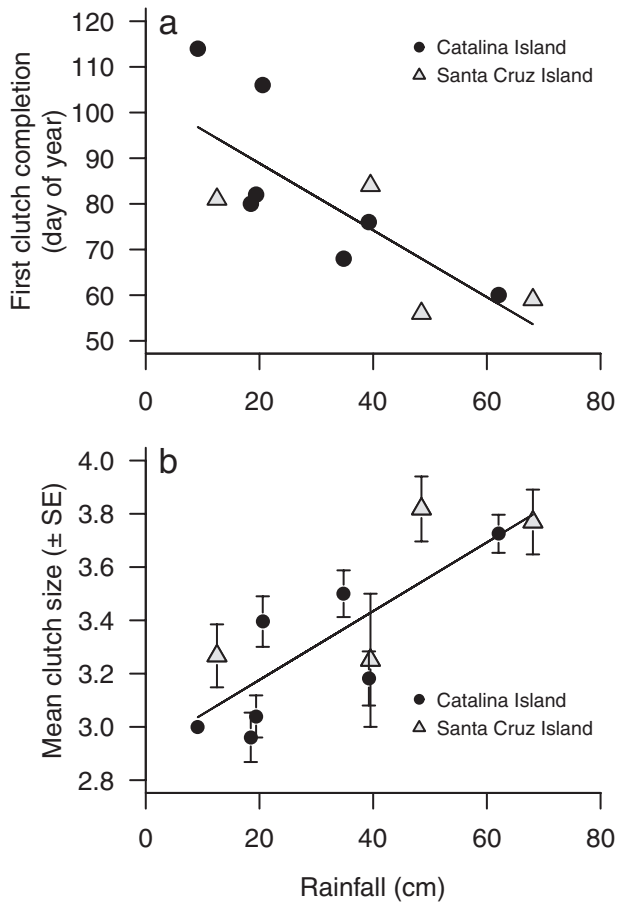

Figure 4
Birds on both islands responded similarly to annual variation in precipitation by (a) initiating breeding earlier and (b) laying larger clutches in wetter years.

DISCUSSION

Theory predicts that ecological variation should favor adaptive phenotypic plasticity as a means of tracking dynamic environments (Levins 1968; Moran 1992; Scheiner 1993; 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 experienced substantial spatial and temporal variation in nest predation risk (Figure 1a) and rainfall (Figure 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. Specifically, nest visitation rate (Figures 2c and 3) and nest height (Figure 2a) responded to variation in nest predation risk, whereas clutch size and breeding phenology were correlated with rainfall (Figure 4), and therefore with food abundance. Therefore, although 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 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; birds on Santa Cruz had larger clutches and lower nestling visitation rates (Figure 2b,c). This decoupling allowed predictions from both hypotheses to be supported. As Skutch predicted, variation in nestling visitation rates between islands (Figure 2c) and within Santa Cruz (Figure 3) likely reflected the constraint of visually oriented nest predators; however, as Lack predicted, birds on both islands laid larger clutches in wetter years (Figure 4b), when food was more abundant. Yet counter to their predictions (Table 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 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. Nevertheless, the different sensitivities of these traits to different types of ecological variation indicate that although 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, orange-crowned warblers began breeding earlier and laid larger clutches (Figure 4), likely reflecting their responses to variation in 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 (Sofaer 2012). In addition, studies in dry climates show that productivity and food availability for birds increase with rainfall (Noy-Meir 1973; Smith 1982; Boag and Grant 1984) and suggest 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 for these traits because, after accounting for the effect of rainfall, breeding phenology and clutch sizes did not differ between islands (Figure 4). Higher rainfall on Santa Cruz 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 interisland variation in clutch size reflects phenotypic plasticity, rather than fixed genetic differences.

Although 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, which were affected by relative nest predator abundance and were also higher in 2007, a drought year (Langin et al. 2009), than in 2008 (Figure 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, 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. Spatial and temporal variation in phenology, behavior, and clutch sizes has often been attributed 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 warblers on territories with a higher relative abundance of scrub-jays had lower visitation rates than other pairs breeding in the same study plot (Figure 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 and between islands mirror the plasticity observed within Catalina, where experimental presentations of scrub-jay taxidermic mounts led to lower nest placement and lower nestling visitation rates, despite the complete absence of jays on that island (Peluc et al. 2008). These insular endemic populations of orange-crowned warbler (*Oreothlypis celata sordida*) therefore show an exceptional degree of plasticity in nest height and in the vegetative strata used for nesting because nest placement is often evolutionarily conserved (Collias and Collias 1984). The lack of genetic differentiation between warblers on Catalina and Santa Cruz, coupled with the observations that corvids 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), suggests that the differences in visitation rates and nest placement we documented 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 were the warbler's main nest predator on Santa Cruz 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 warbler nests on Santa Cruz. In addition, lowering nest height may have been rendered less effective because overgrazing by feral livestock had substantially reduced understory vegetation on Santa Cruz. The last of these nonnative 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 how different ecological factors 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 (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 reveal 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. Although neither Lack's nor Skutch's hypothesis 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, 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.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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