



Original Article

Nest predation risk explains variation in avian clutch size

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Questions about the ecological drivers of, and mechanistic constraints on, productivity have driven research on life-history evolution for decades. Resource availability and offspring mortality are considered among the 2 most important influences on the number of offspring per reproductive attempt. We used a factorial experimental design to manipulate food abundance and perceived offspring predation risk in a wild avian population (red-faced warblers; *Cardellina rubrifrons*) to identify the mechanistic cause of variation in avian clutch size. Additionally, we tested whether female quality helped explain the extant variation in clutch size. We found no support for the Food Limitation or Female Quality Hypotheses, but we did find support for both predictions of the Nest Predation Risk Hypothesis. Females that experienced an experimentally heightened perception of offspring predation risk responded by laying a smaller clutch than females in the control group. Additionally, predation rates at artificial nests were highest where red-faced warbler clutch size was smallest (at high elevations). Life-history theory predicts that an individual should invest less in reproduction when high nest predation risk reduces the likely benefit from that nesting attempt and, indeed, we found that birds exhibit phenotypic plasticity in clutch size by laying fewer eggs in response to increasing nest predation risk.

Key words: elevational gradient, evolutionary constraints, offspring mortality, life-history evolution, phenotypic plasticity, predation risk manipulation, reproductive investment, resource availability.

INTRODUCTION

Resource allocation trade-offs are thought to produce life-history trait combinations best suited to environmental conditions (Roff 1992; Stearns 1992; Doughty and Shine 1997). Determining the selective pressures that limit reproductive output, and how the relative importance of these processes vary along environmental and geographic gradients, has motivated research on life-history evolution for decades, and led to the development of some of the central tenets of life-history theory. However, the relative importance of different ecological constraints in mediating these trade-offs and producing variation in life-history strategies remains a subject of debate (Martin 1995; Hatchwell and Komdeur 2000; Ricklefs and Wikelski 2002).

The number of offspring produced is not necessarily the maximum number that an individual has the time, energy and resources to produce or support, but instead reflects trade-offs between

offspring quantity and quality, current and future adult reproduction, and reproduction and survival (Bell 1980; Stearns 2000). Many hypotheses exist to explain why the outcome of those trade-offs vary within and between species. Commonly, explanations of variation in investment in offspring number invoke selective pressures caused by environmental variation in resource availability, offspring mortality, or parental quality (Martin 1987; Promislow and Harvey 1990; Reznick et al. 1996; Smith and Moore 2003).

Functional hypotheses that focus on offspring mortality suggest that an elevated risk of predation results in selection for fewer offspring per reproductive attempt in mammalian (Korpimäki et al. 1994; Creel et al. 2007), avian (Eggers et al. 2006; Zanette et al. 2011) and some fish (Mukherjee et al. 2014) species, but more and smaller offspring in guppies (*Poecilia reticulata*; Reznick and Endler 1982) and *Daphnia* (Stibor 1992). On the other hand, hypotheses that focus on resource availability suggest that increased food abundance results in selection for higher investment in offspring numbers. Indeed, studies on invertebrates (Stahlschmidt et al. 2013), reptiles (Olsson and Shine 1997), mammals (Doonan and Slade

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1995), and birds (Arcese and Smith 1988) have demonstrated that increased food abundance resulted in females producing more offspring per reproductive attempt. Likewise, hypotheses that focus on parental quality suggest that higher-quality adults invest more in offspring number than their counterparts. For example, larger and more experienced female mice produced more offspring than their smaller, younger conspecifics (Morris 1998), and individual differences in parental condition were positively correlated with clutch size in birds (Hochachka 1990; Winkler and Allen 1995). However, past studies have rarely tested predictions of all 3 of these functional hypotheses simultaneously. Doing so would help elucidate the relative importance of these different selective pressures at explaining why life histories often vary so much among species.

We utilized an elevational gradient in avian clutch size to test multiple experimental and correlative predictions of 3 hypotheses commonly proposed to explain variation in avian life histories. Red-faced warblers (*Cardellina rubrifrons*) lay a decreasing clutch size in association with increasing elevation: most females lay 5-egg clutches at the lower end of their elevational breeding range and 4-egg clutches at the upper end (a 20% average decline) (Figure 1; Dillon and Conway 2015). This elevational gradient in clutch size provides an ideal system in which to test functional hypotheses to explain the ecological constraints on annual fecundity; individuals at the highest elevations within a mountain range breed in relatively close proximity to those at the lowest elevations but lay fewer eggs per clutch.

Field studies often test only a single hypothesis to explain variation in life-history strategies. We used a factorial experimental design where we experimentally manipulated food and perceived risk of offspring predation. This design enabled us to test the effects of food abundance and nest predation risk on clutch size, as well as an interaction between these 2 variables. Additionally, we tested correlative predictions to evaluate 3 mechanistic hypotheses that are commonly invoked to explain variation in avian clutch size (Table 1). If our results lent support to a particular hypothesis, we tested additional predictions to help identify the explicit mechanism(s) by which that ecological process causes clutch size to vary with elevation (Table 2). Although these hypotheses are not mutually exclusive (Sofaer et al.

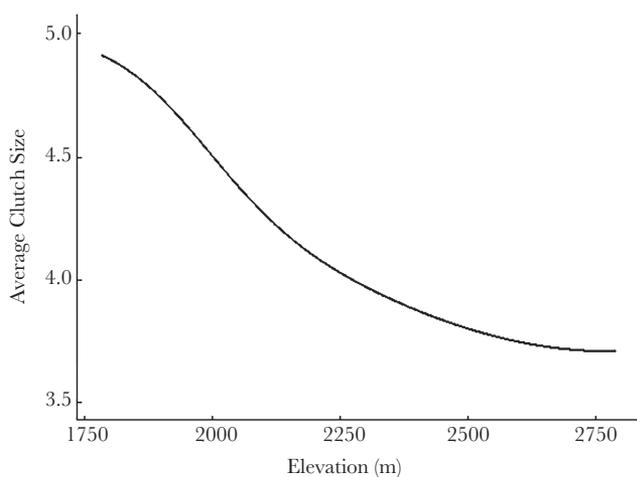


Figure 1
Average clutch size across red-faced warblers' elevational breeding range calculated as the sum of each clutch size multiplied by the probability of that clutch size at each elevation as predicted by a multinomial logistic regression model. Clutch size probabilities for the peak of the breeding season (5 June) were used for the calculation of average clutch size. Graph and associated statistical models originally published in Dillon and Conway (2015).

2013) and involve inherent tradeoffs, this is the first field study to test these hypotheses simultaneously in the same ecosystem. The results will help determine the relative importance of ecological processes commonly proposed to mediate complex life-history tradeoffs and help explain how individuals resolve allocation tradeoffs in response to changes in environmental conditions.

MATERIALS AND METHODS

Study site

We monitored red-faced warbler nests located between 1798 m and 2779 m a. s. l., encompassing the species' entire elevational breeding range in the Santa Catalina Mountains, Coronado National Forest, Pima County, Arizona. Nests were monitored throughout the red-faced warbler breeding season in 2011 and 2012: 27 April through 20 July. Red-faced warblers were an ideal study species to test the 3 hypotheses because their nests are relatively easy to locate and monitor, and occasional nest visitation by researchers does not increase the risk of nest predation (Kirkpatrick and Conway 2009). Red-faced warblers will renest after nest failure, but are not known to produce multiple broods in a breeding season (Martin and Barber 1995; Conway C, Dillon K, personal observation). Females breeding at the highest extreme of the species' elevational breeding range in the Santa Catalina Mountains (2750 m) initiate their first nests of the season approximately 18 days later than females breeding at the lowest extreme of the elevational breeding range (1750 m) (Dillon and Conway 2015).

We located and monitored 305 red-faced warbler nests during the study period. We found 187 of the 305 nests during the building stage and the remainder after building was complete, and monitored them daily until clutch completion and then every 2 to 4 days until fledge or failure. Fifty-five percent of the 187 nests that we found during the building stage did not succeed to clutch completion; 32.6% were abandoned prior to nest completion (i.e., before any eggs were laid) and 22.4% failed during the laying period. These early losses were expected; red-faced warblers will often build nonbreeding nests or abandon a partially built nest and then build another in a different location (Martin and Barber 1995; Dillon K, Conway, C, personal observation). Hence, 84 of the 187 nests yielded a complete clutch (advanced to the incubation stage) and were included in the analyses below (Table 3).

We assigned the nests that were located during the building stage to 2 experimental treatment groups (described below) in a randomized block design where the blocking factor was the segment of the elevation gradient in which birds were breeding. Hence, we randomly assigned these nests to one of 4 treatment combinations (increased predation risk and supplemental food, increased predation risk and ambient food, ambient predation risk and supplemental food, and ambient predation risk and ambient food) in a factorial experimental design. We used the methods below to test the 3 hypotheses.

The percentage of our experimental nests that we found during building that subsequently failed during the laying stage (23%) was slightly lower than the same percentage in the 2 subsequent years when we did not manipulate nests (32% in 2014 and 29% in 2015). Hence, we found no evidence that our experimental manipulations of food and perceived predation risk increased the likelihood of nest failure or abandonment, as further reflected by the lack of difference among treatments in percent of nests that survived until clutch completion (Table 3). All field methods described herein

Table 1
Predictions tested to evaluate 3 alternative hypotheses to explain the elevational gradient in avian clutch size^a

Predictions	Hypotheses					
	Nest Predation Risk		Food Limitation		Female Quality	
	Predicted Relationship	Observed Relationship	Predicted Relationship	Observed Relationship	Predicted Relationship	Observed Relationship
a) If the perception of nest predation risk is experimentally increased for a subset of females, those females should lay a smaller clutch than the control group.	Decrease	Decrease				
b) If nest predation is constraining clutch size at higher elevations, predation rates of artificial nests should increase with increasing elevation, mirroring the relationship between clutch size and elevation.	Positive	Positive				
c) If some females are provided supplemental food during nest-building and egg-laying, those females should lay a larger clutch than controls.			Increase	Decrease		
d) If food limitation constrains the number of eggs females are able to lay or nestlings they can feed, food abundance during peak egg-laying or nestling feeding, respectively, will be negatively correlated with elevation.			Negative	Positive		
e) If quality is constraining clutch size, female body condition will be negatively correlated with elevation.					Negative	No Change
f) If observed variation in clutch size reflects variation in inherent female body condition, we expect no change in, or reduced, nestling growth rates with increasing elevation because a female in worse condition likely remains in worse condition (relative to other females) for the entire nesting cycle, thus constraining provisioning of young.					No Change/ Negative	Positive

^aThese predictions were generated to help distinguish among 3 hypotheses commonly invoked to explain why clutch size varies among species and environmental gradients, but not necessarily between the mechanisms by which each hypothesis might constrain clutch size (Table 2). A “positive” or “negative” relationship indicates the predicted (or observed) relationship between that factor and elevation (e.g., The Nest Predation Risk Hypothesis predicts that predation rates at artificial nests should be positively correlated with elevation, if nest predation rates are constraining clutch size). An “increase” or “decrease” indicates the predicted (or observed) response of clutch size to the experimental treatment (e.g., The Food Limitation Hypothesis predicts that females that received supplemental food should increase their clutch size relative to controls, if food abundance constrains clutch size). Results that concurred with the relationship predicted by the hypothesis are indicated in bold type.

were in compliance with the Association for the Study of Animal Behavior guidelines for the treatment of animals in research and were approved by the University of Arizona Institutional Animal Care and Use Committee (protocol #11–265).

Field methods

Nest predation risk hypothesis

Nest predation can vary with elevation (Skutch 1985; Boyle 2008) and increased predation risk can favor smaller clutch size (Skutch 1949; Martin 1995; Ibanez-Alamo et al. 2015). Skutch (1949) proposed the Nest Predation Risk Hypothesis to explain latitudinal variation in clutch size (and variation in clutch size in general). Higher probability of nest predation can favor smaller clutch size via several mechanisms: 1) smaller broods require less parental activity at the nest due to fewer trips to feed nestlings, and fewer trips likely attract fewer predators (Parental Activity Mechanism, Table 2) (Skutch 1949, Conway and Martin 2000); 2) smaller broods are quieter

because nestlings are more satiated and less likely to beg for food, and less begging attracts fewer nest predators (Nestling Begging Mechanism, Table 2) (Skutch 1949, Slagsvold 1982, McDonald et al. 2009); and 3) females in areas with higher nest predation lay a smaller clutch as a bet-hedging strategy by which they might make a trade-off between current and future reproductive success (Bet-hedging Mechanism, Table 2) (Slagsvold 1982, Martin 1995). Indeed some, but not all, species appear capable of assessing predation risk and responding by reducing the number of offspring they produce per brood (Fontaine and Martin 2006; Zanette et al. 2011).

We introduced a cliff chipmunk (*Tamias dorsalis*) in a cage to the nests that were assigned to receive increased perception of nest predation risk. Cliff chipmunks are common throughout our study area and are one of the 2 primary predators of red-faced warbler nests on our study sites (Kirkpatrick and Conway 2010). However, chipmunks are typically not predators of adults birds (Venne 2004) and have not been documented as predators of adult red-faced warblers. We placed the chipmunk 5 m from the (perceived) risk-enhanced

Table 2**Predictions tested to evaluate the mechanisms by which nest predation might constrain clutch size^a**

Predictions	Mechanisms					
	Parental activity		Nestling begging		Bet-hedging	
	Predicted relationship	Observed relationship	Predicted relationship	Observed relationship	Predicted relationship	Observed relationship
a) Correlation between elevation and nest predation rates (real nests)	NR*	NR	NR	NR	Positive	NR
b) Correlation between elevation and nestling growth rates	NR	Positive	Positive	Positive	Positive	Positive

The predicted and observed relationships^a between elevation and a) nest predation rates of real nests, and b) nestling growth rates helped identify the most likely mechanism by which nest predation influences clutch size.

*NR = No Relationship.

^aResults that concurred with the relationship predicted by the hypothesis are indicated in bold type.

Table 3**The total number of nests assigned to each of 4 treatments and the total number that survived to clutch completion in each treatment^a**

	Chipmunk introduction		Control treatment for chipmunk introduction	
	Number of nests assigned to treatment	Number of nests that survived to clutch completion	Number of nests assigned to treatment	Number of nests that survived to clutch completion
Supplemental Food	44	20	48	15
Control Treatment for Supplemental Food	43	20	52	29
Totals	87	40	100	44

^aThe 4 treatments were supplemental food, chipmunk introduction, and a control group for each treatment. We used a randomized block design to assign 187 nests to the 4 treatments. We included data from 84 of the 187 nests in our analysis; 103 of the 187 nests did not reach incubation.

nests twice daily (two 30–45 min periods each day) from the time the nest was found until clutch completion ($\mu = 7$ days, range = 5–10 days). We placed a Styrofoam painted and feathered model goldfinch in a cage 5 m from the 100 control nests (those that were assigned to not receive experimental enhancement of perceived nest predation risk) with the same frequency. We randomly assigned each nest to an experimental treatment group when it was found (during the building stage). We randomized across space and time and thus the number of nests in each of the 4 treatment groups (across all elevations pooled) was similar but not identical.

We also systematically placed 462 artificial nests across the 1000-m elevational gradient during the 2012 breeding season. We used Midwest Design 8.255-cm (3.25-inch) Wild Grass Bird Nests, each with 3 eggs molded from Van Aken Plastalina, to resemble red-faced warbler nests with 3 eggs. At each randomly generated location within a known breeding site, we placed the artificial nest in the site most closely resembling a red-faced warbler nest site. We left artificial nests with eggs deployed for the average length of the red-faced warbler nesting cycle ($\mu = 19$, range = 16–21 days) and then collected and classified the nest as either predated or not predated based on the presence of teeth or beak marks in the eggs. We used artificial nests to test the prediction of the Nest Predation Hypothesis that ambient nest predation risk would be highest at high elevation, where clutch size is the smallest, if predation risk does indeed constrain clutch size. The inclusion of artificial nests, rather than just real nest success data,

was important to this study because some mechanisms by which predation may constrain clutch size predict that birds may lay a smaller clutch when faced with high nest predation risk in order to reduce the risk to their nest. If this were the case, we would not expect to see variation in actual red-faced warbler nest predation rates, as the birds have adjusted their reproductive effort appropriately, even though there would in fact be elevational variation in actual predation risk. Artificial nests have many shortcomings (e.g., different suites of predators at different elevations may be differentially attracted to artificial nests), but we did not rely solely on artificial nests, they were used as one of numerous predictions, and so we concluded that an artificial nest experiment (in combination with other predictions, including those with real nests) would provide invaluable insight to this study.

We examined the factors that influenced the risk of nest predation in red-faced warblers across the elevational gradient ($n = 176$ nests). Two mechanisms of the Nest Predation Risk Hypothesis (the Nestling Begging and Parental Activity Mechanisms) predict that birds are responding to high nest predation risk by reducing their clutch size (thereby reducing their nest predation risk). Thus, these mechanisms predict that altered life histories at high elevation may mask an elevational gradient in nest predation at real red-faced warbler nests but not at artificial nests (Fontaine et al. 2007). However, the third mechanism of the Nest Predation Risk Hypothesis (Bet-hedging Mechanism) predicts that females lay a smaller clutch to reserve energy for future reproductive investment

(i.e., a smaller clutch does not have a lower risk of nest predation). Therefore, the Bet-hedging Mechanism predicts a positive relationship between elevation and nest predation rates at real nests (as well as at artificial nests; Table 2, Prediction *a*).

Food limitation hypothesis

Food abundance might decline with increasing elevation (Lessard et al. 2011) and thereby constrain: 1) the number of eggs that females have the energy to lay (especially if females are primarily income breeders), or 2) the number of nestlings that parents have the resources to feed (Lack 1947; Martin 1987). Abundance and phenology of ambient food availability may vary across the elevational gradient and thereby constrain clutch size at some elevations. Some (Arcese and Smith 1988), but not all (Martin 1987), species of birds supplied with supplemental food during egg-laying laid a larger clutch than nonsupplemented females, suggesting that while food limitation during laying can constrain clutch size in some species it might not be as important as previously thought. Females may also use food availability during the laying period as a proximate cue of food availability during the nestling period (Lack 1947). Indeed, nestling energy requirements can limit the number of offspring that can be raised and food supplementation during the nestling period can increase fledging success (Martin 1987; Wiehn and Korpimäki 1997).

We assigned a random subset of the nests that were found during building to one of the 4 treatment groups, 2 of which included food supplementation (Table 3). We provided 50g of live wax moth larva—approximately 4 to 6 times the total mass of an adult red-faced warbler—per day at these nests throughout the nest building and laying stages ($\mu = 8$, range = 5–12 days) in a plastic-lined depression in the ground directly in front of the nest. We observed female red-faced warblers eating the larva provided at the nest each day, confirming that the larva were being eaten by female warblers and not escaping or being consumed by another species. Hence, we were confident that the female red-faced warblers knew that the larva were there and were willing to consume them ad libitum. For the nests assigned to the 2 treatment groups that did not include food supplementation, we filled a plastic-lined depression with pine needles and leaf debris each day as a control.

We measured ambient abundance of *Lepidoptera* larva, the primary food source for breeding red-faced warblers (Martin and Barber 1995), along 6 transects spanning the elevational breeding range of red-faced warblers. We measured larval abundance weekly at 8 systematically placed points along each transect. At each of the 48 points we cut, and counted larva on, the 25 cm terminus of a branch 4m above the ground. We sampled from the 4 closest maple or oak trees (*Acer grandidentatum*, *Quercus spp.*) and the 4 closest coniferous trees (*Abies concolor*, *Pseudotsuga menziesii*, *Pinus ponderosa*) to the survey point. Thus, we sampled all tree species that red-faced warblers use for foraging at all elevations (Martin and Barber 1995; Decker et al. 2012).

Female quality hypothesis

To explain the observed elevational gradient in clutch size, this hypothesis assumes that females breeding at higher elevations are in worse physiological condition and have a smaller optimal clutch size than females breeding at lower elevations. This intrinsic condition hypothesis assumes that females breeding at high elevation are in worse condition (Smith and Moore 2003) than their lower elevation conspecifics. For example, high elevation females may be late arrivers to the breeding grounds, who arrive in poor condition from migration. These individuals may settle

disproportionately at higher elevations because low-elevation territories are no longer available when they arrive and higher-elevation sites that were not suitable when early-arriving females settled territories (due to snow cover or phenology of food availability) are now available. Indeed, migratory American redstarts (*Setophaga ruticilla*) that arrived on the breeding grounds with larger stores of body fat had higher clutch size, egg volume, and nestling growth compared to individuals who arrived with smaller fat stores (Smith and Moore 2003).

We used mist nets to capture adult female red-faced warblers during the incubation and nestling stages. We measured body mass to the nearest 0.25 g, and wing chord and tarsus length to the nearest 0.5 mm. We used the residuals of mass regressed against the first principal component of wing chord and tarsus length as an index of body condition.

We measured wing chord, tarsus length, and mass of nestlings on days 3 and 6 of the nestling period. We calculated the average values of each of the 3 measured traits across all nestlings within each nest on each measurement day, and then calculated the slope between the measurements taken on day 3 and day 6 of the nestling period for each trait (i.e., the average nestling growth rate from day 3 to day 6 at each nest). We calculated a *z*-score for each of the 3 indices of nestling growth (mass, wing chord, tarsus length) obtained for each nest, and then averaged the 3 *z*-scores into a single, standardized, composite index of nestling growth rate. Standardization of the different nestling growth measurements into a *z*-score allowed us to use a single composite nestling growth rate measurement for analysis. Nestling growth rates were included in this study for 2 reasons: 1) as a test of the Female Quality Hypothesis, and 2) to distinguish between mechanisms of the Nest Predation Hypothesis. The Female Quality Hypothesis predicts that if smaller clutch sizes at high elevation are due to lower quality individuals there, we would expect to see no elevational variation in nestling growth rates or a negative relationship between nestling growth rates and elevation, rather than higher growth rates at higher elevation as might be expected given that the female has fewer offspring to provision (Table 1, Prediction *f*). In contrast, the Nestling Begging and Bet-hedging Mechanisms of the Nest Predation Hypothesis both predict a positive relationship between nestling growth rates and elevation, whereas the Parental Activity Mechanism predicts no relationship. If parental activity at the nest increases nest predation risk, thereby selecting for smaller clutches in high risk areas, then we would not expect high elevation breeders to feed their smaller clutch at a faster rate (as they might with a smaller clutch and no increase in predation risk). If, on the other hand, increased nestling begging increases nest predation risk, then we might expect high elevation breeders to provision their smaller clutch at a faster rate because they have the resources to do so and doing so would further serve to reduce begging noise at the nest. Moreover, nestling growth rates provide a way to determine whether there is a trade-off between offspring quantity and offspring quality along the elevation gradient.

Statistical analyses

We used a 2-way ANOVA to test the prediction of the Nest Predation Risk Hypothesis that females experiencing increased predation risk would lay a smaller clutch than control females (Table 1, Prediction *a*) and the prediction of the Food Limitation Hypothesis that females with access to additional food would lay a larger clutch than control females (Table 1, Prediction *c*). Clutch size was

the dependent variable, the 2 experimental treatments (increased predation risk and food supplementation) were fixed factors, and elevation and year were covariates. We also included the interaction between the 2 experimental treatments (food and predation) in the model. We did not use a Poisson regression because, as is typical of avian clutch size data (Ridout and Besbeas 2004; Kery and Royle 2016), our data were highly under-dispersed and an ANOVA model proved to be a more appropriate model. Indeed, a post-hoc AIC comparison of the fit of an ANOVA versus Poisson regression model indicated that the ANOVA model was a better fit ($AIC_{(ANOVA)} = -63$, $AIC_{(Poisson)} = 299$).

We used a logistic regression and AICc for model selection to test the prediction of the Nest Predation Hypothesis that nest predation rates at artificial nests are positively correlated with elevation (Table 1, Prediction *b*). We compared 14 candidate models for which nest outcome was the binary dependent variable and we considered 6 potential explanatory variables: elevation, the date the artificial nest was deployed (“Initiation Date”), the quadratic terms for elevation and date deployed, the interaction between elevation and date deployed, and the number of exposure days. We assumed that predation rates of artificial nests would reflect the relative risk of nest predation experienced by red-faced warblers across the elevational gradient. For all analyses employing a model selection approach, we considered any model with a $\Delta AICc \leq 2$ to be a competing model. When the presence of multiple competing models inhibited our interpretation of results, we used the Multi-model Inference (MuMIn) package in R to model-average across all candidate models (Lukacs et al. 2010) in order to account for model uncertainty. Model details and AIC ranks, as well as model averaging results, are reported in Supplementary Materials.

We used an AICc model selection approach through RMark (Laake 2013) to test the prediction of the Nest Predation Hypothesis that nest predation rates at real red-faced warbler nests were positively correlated with elevation. The 23 candidate models included nest fate as the response and elevation, elevation², nest initiation date, year, and nest age as potential explanatory variables.

We used a negative binomial regression to test the predictions of the Food Limitation Hypothesis that elevation is negatively correlated with food abundance during the: 1) peak egg-laying period, and 2) peak nestling period in our study area, thereby accounting for variation in larva phenology (Table 1, Prediction *d*). We included the number of *Lepidoptera* larva counted per point as the response variable and elevation and elevation² of each survey point as explanatory variables.

To test the prediction of the Female Quality Hypothesis that female condition was negatively correlated with elevation (to explain why clutch size is negatively correlated with elevation; Table 1, Prediction *e*), we used a general linear model and AICc for model selection, with female body condition as the response variable and elevation, elevation², capture date, and the number of days past nest initiation that the bird was captured as potential explanatory variables. We included the number of days between when the female had initiated her nest and when we measured body mass in our model because body condition may change as the breeding season progresses and capture dates varied among females. We compared 11 candidate models.

We used a general linear model and AICc for model selection to examine the relationship between nestling growth rates and elevation to test the prediction of the Female Quality Hypothesis (Table 1, Prediction *f*) as well as to distinguish among the 3

mechanisms by which nest predation may constrain clutch size (Table 2, Prediction *b*). The composite index of nestling growth rate was the dependent variable, and elevation, elevation², nest initiation date, brood size, and year were potential explanatory variables. We compared 11 candidate models.

RESULTS

Nest predation risk hypothesis

We found support for both of the predictions of the Nest Predation Risk Hypothesis. Females that experienced an experimentally increased perception of nest predation risk laid a smaller average clutch than control females ($F_{[1,78]} = 4.00$, $P = 0.049$, $CI = -0.09, -0.02$; Figure 2), as predicted by the Nest Predation Risk Hypothesis (Table 1, Prediction *a*). We did not detect a significant interaction between predation risk and food abundance treatments ($F_{[1,78]} = 0.10$, $P = 0.754$).

Moreover, the probability of predation of artificial nests was highest (0.7) at the highest elevations (Figure 3), supporting the second prediction of the Nest Predation Risk Hypothesis—that we should expect the highest predation rates at high elevation, where clutch size is the smallest, if nest predation constrains clutch size in this system (Table 1, Prediction *b*). The top model to explain variation in artificial nest predation rates included an interaction between initiation date and elevation, as well as the linear and quadratic terms for elevation ($wAICc = 0.25$; Figure 3a). The linear and quadratic terms for elevation were also in the 4 other competing models: 1) elevation, elevation², initiation date, and initiation date² ($\Delta AICc = 0.04$); 2) elevation, elevation², and initiation date ($\Delta AICc = 0.39$); 3) elevation, elevation², initiation date, initiation date², elevation \times initiation, and number of exposure days ($\Delta AICc = 1.11$); and 4) elevation and elevation² ($\Delta AICc = 1.39$). Hence, the relationship between elevation and the probability of artificial nest predation was nonlinear, but artificial nests had the highest probability of predation at high elevations. Elevation and elevation² were more important than date or number of exposure days in explaining variation in fate of artificial nests after model averaging (relative variable importance = 0.98, 0.97, 0.87, 0.15, respectively). Moreover, the 95% confidence intervals for elevation and elevation² did not include zero in any of these models, although the 95% confidence intervals for all model terms containing initiation date did include zero in every instance.

Our results supported the prediction of the Nestling Begging and Parental Activity Mechanisms (but not the Bet-hedging Mechanism) of the Nest Predation Risk Hypothesis—nest predation rates of real red-faced warbler nests did not increase with elevation (Figure 3b; Table 2, Prediction *a*) opposite to the pattern for artificial nests (Figure 3a). The top model to explain variation in nest fate included only elevation ($wAICc = 0.12$), but there were 12 competing models including the intercept-only model ($\Delta AICc = 1.16$, $wAICc = 0.07$). Although the elevation-only model had slightly more weight than the null model, that model suggested a weak *negative* relationship between risk of nest predation and elevation and the 95% confidence interval for elevation in this model included zero.

Food limitation hypothesis

We did not find support for any of the predictions of the Food Limitation Hypothesis. Females that received supplemental food did not lay a larger clutch than control females (Table 1, Prediction *c*; $F_{[1,78]} = 0.28$, $P = 0.600$, Figure 2). Additionally, we found that

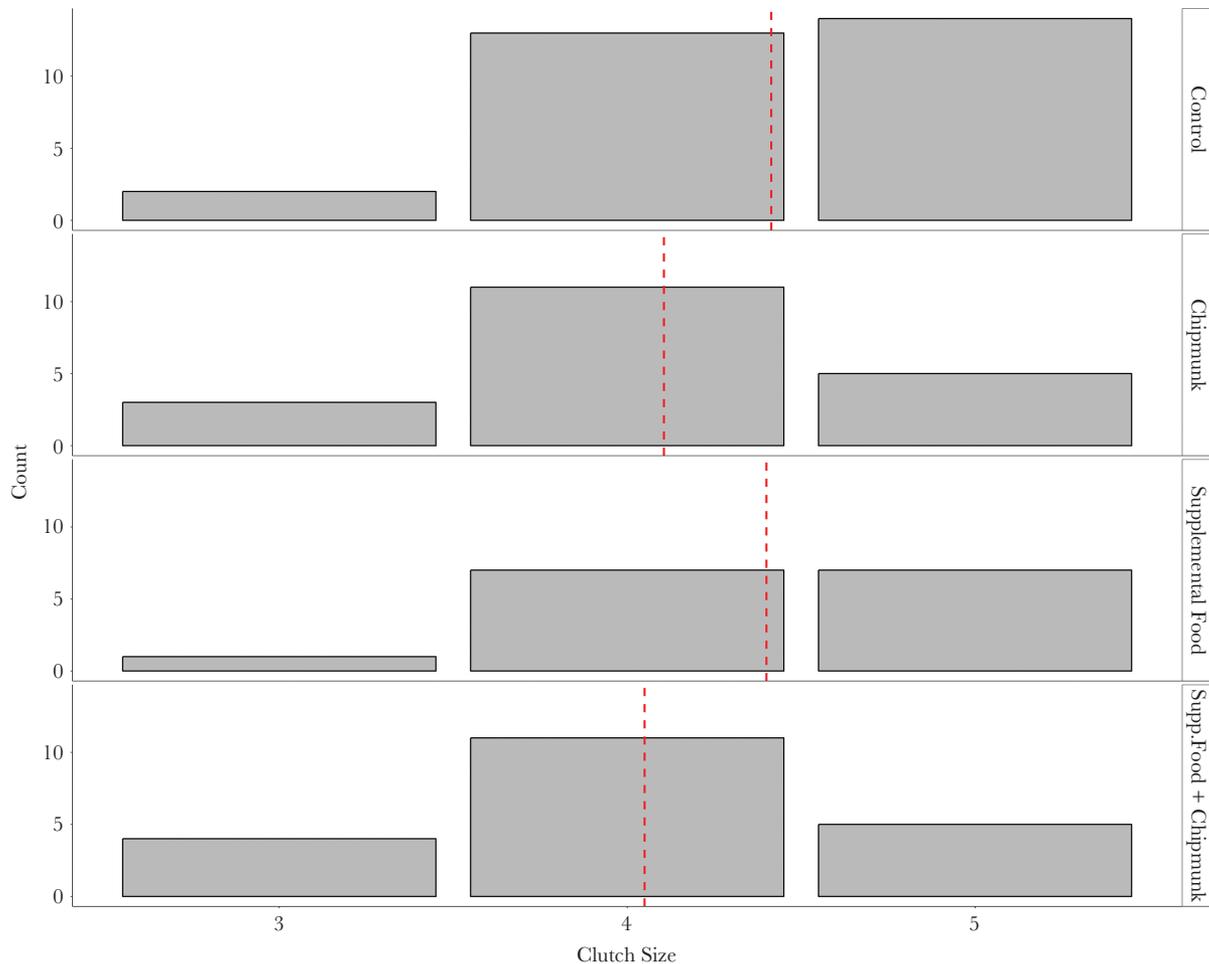


Figure 2

Female red-faced warblers that experienced an experimentally increased perception of nest predation laid a smaller clutch than controls. Clutch size did not differ between female red-faced warblers that received supplemental food and control females. Histograms depict the distribution of clutch sizes by treatment group. Dashed lines indicate the mean clutch size of each treatment group.

food supplementation did not affect nest predation rates compared to control nests ($\chi^2 = 0.77$, $P = 0.381$). Moreover, *Lepidoptera* larva were more abundant (not less abundant) at higher elevations than lower elevations during both the window of peak egg-laying (6400% higher; $\chi^2 = 48.17$, $P < 0.001$, $CI_{\text{elevation}} = 0.025\text{--}0.010$; Figure 3c) and during the peak nestling period (900% higher; $\chi^2 = 20.60$, $P < 0.001$, $CI_{\text{elevation}} = 0.002\text{--}0.005$; Figure 3d). Thus, food abundance during the peak egg-laying and peak nestling periods increased (rather than decreased) with elevation in direct contrast with the prediction of the Food Limitation Hypothesis (Figure 3c,d; Table 1, Prediction d) and the pattern was similar in both years of the study.

Female quality hypothesis

We found no support for the prediction of the Female Quality Hypothesis that female body condition declines with increasing elevation: our results suggest that female body condition does not vary along the elevational gradient (Table 1, Prediction e). As expected, female body condition declined as capture date (relative to nest initiation) increased and the top model to explain variation in body condition included time since nest initiation at capture and elevation ($wAICc = 0.29$, $R^2_{\text{adj}} = 0.19$). The competing models included 1) only time since nest initiation at capture ($\Delta AICc = 1.17$,

$wAICc = 0.16$, $R^2_{\text{adj}} = 0.12$) and 2) elevation and capture date ($\Delta AICc = 1.89$, $wAICc = 0.11$, $R^2_{\text{adj}} = 0.14$). Female body condition was 145% higher during the middle of the incubation stage than the middle of the nestling stage (Figure 4a). The small elevation effect was attributed to 2 influential outliers (1 at high elevation and 1 at low elevation; Figure 4b); female condition was predicted solely by time since nest initiation when those observations were removed. Indeed, the 95% confidence intervals for elevation in the competing models all included zero whereas the 95% confidence intervals for the other variables included in the top models did not include zero.

We measured nestling growth rates to test the Female Quality Hypothesis as well as to distinguish among 3 potential mechanisms of the Nest Predation Risk Hypothesis at 42 nests. Our results did not support the Female Quality Hypothesis, but did support 2 of the 3 mechanisms of the Nest Predation Risk Hypothesis. Nestling growth rates increased with increasing elevation (nestlings at the highest elevation grew 234% faster than those at the lowest elevation). Variation in nestling growth rates were best explained by a model that contained elevation and year ($wAICc = 0.32$, $R^2_{\text{adj}} = 0.40$, $CI_{\text{elevation}} = 0.001\text{--}0.003$, $CI_{\text{year}} = -0.61\text{--}0.08$); the 2 competing models contained 1) only elevation ($\Delta AICc = 0.15$, $wAICc = 0.29$, $R^2_{\text{adj}} = 0.38$), and 2) elevation and elevation² ($\Delta AICc = 0.81$, $wAICc = 0.21$, $R^2_{\text{adj}} = 0.39$).

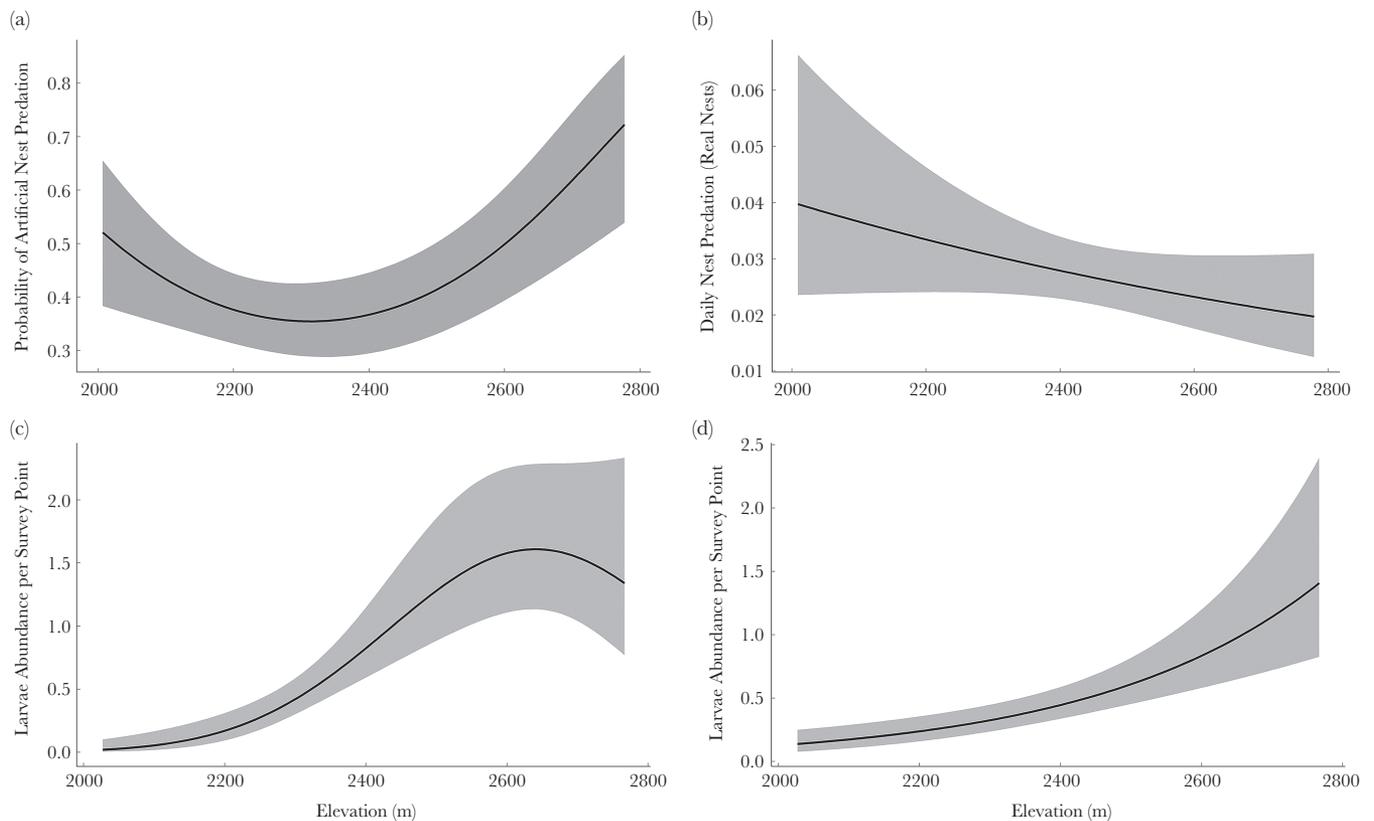


Figure 3

Probability of predation for artificial nests deployed across an 800-m elevation gradient in red-faced warbler breeding habitat was highest at the upper portions of the species' breeding elevations (a). Probability of predation at real red-faced warbler nests decreased with increasing elevation. The top model to explain variation in fate of real nests included only elevation, but the model only had 10% of the cumulative weight, there were 12 competing models including the null (intercept-only) model, and the 95% confidence interval included zero (b). Abundance of *Lepidoptera* larva increased across the elevation gradient during the peak red-faced warbler egg-laying period (c), and during the peak nestling period (d). The solid line is the inferred relationship from the model, and the shaded area is the 95% confidence interval.

DISCUSSION

The relative importance of food, predation risk, and intrinsic quality as constraints on reproductive output have long been debated as to their roles as mechanisms driving life-history tradeoffs. Elevational gradients provide a unique opportunity to experimentally test commonly invoked hypotheses to distinguish between those mechanisms. To our knowledge, this is the first empirical study to test multiple mechanistic hypotheses to explain the negative relationship between avian clutch size and breeding elevation, a pattern observed both within and across species in many regions of the world (Badyaev and Ghilambor 2001; Boyce et al. 2015; Boyle et al. 2015; Dillon and Conway 2015). Moreover, it is among the only field studies to simultaneously test 3 common hypotheses that have been proposed to explain variation in clutch size more generally.

Food limitation was once considered the primary cause of clutch size variation in most taxa (Lack 1947; Ricklefs 1980; Martin 1987). However, variation in food abundance clearly did not explain the elevational gradient in clutch size in our system. Female red-faced warblers did not increase clutch size in response to food supplementation (Figure 2). More importantly, food abundance during both peak egg-laying and peak nestling periods was substantially greater at high elevations where clutch size was smaller. Likewise, many (but not all) previous studies have found that experimentally

increased food availability did not cause birds to lay larger clutches, rather the added energy was converted to earlier lay dates or earlier onset of incubation (Arnold 1992; Nilsson and Svensson 1993). Our results refute the hypothesis that elevational variation in food abundance on the breeding grounds is responsible for the elevational gradient in clutch size of red-faced warblers.

Red-faced warblers are migratory and food abundance on their wintering or migration stopover grounds may cause variation in individual condition that constrains investment in reproduction by birds in poor condition (i.e., red-faced warblers may be capital breeders to some extent; Jonsson 1997). However, we detected no relationship between elevation and female body condition. Thus, the observed elevational gradient in clutch size in our system does not appear to be constrained, intrinsically or extrinsically, by the number of eggs females have the energy to lay or by the number of nestlings that adult females are able to feed. Indeed, the much faster growth rate of high elevation nestlings suggests that parents breeding at the highest elevation sites are able to provide abundant food per nestling (and hence could provision more nestlings).

Our results instead lend support to the Nest Predation Risk Hypothesis, suggesting that clutch size of red-faced warblers is smaller at higher elevation due to a higher risk of nest predation. Indeed, predation can exert strong selection on the evolution of life-history strategies (Martin 1995, 2015; Ibanez-Alamo 2015). And some of the differences in clutch size across the elevational

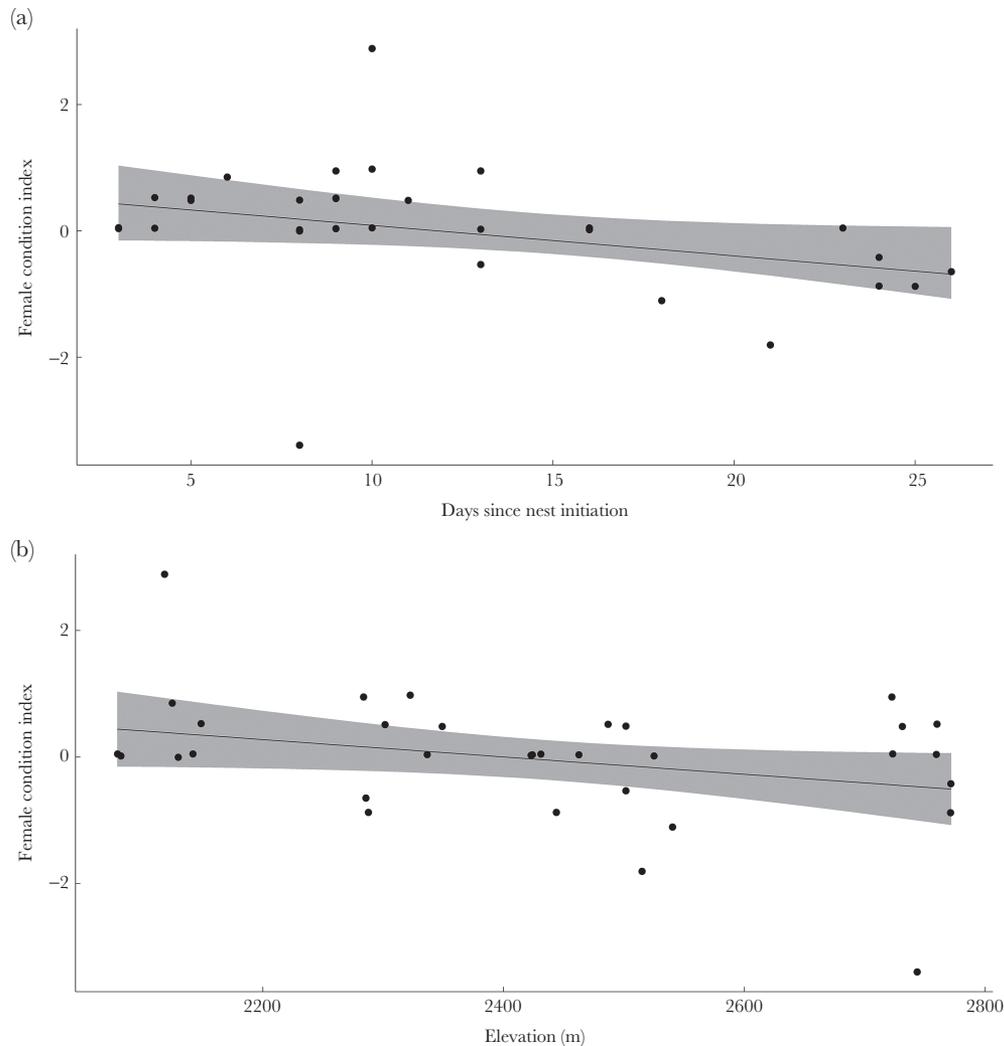


Figure 4

Body condition of female red-faced warblers decreased throughout the nesting cycle, after controlling for elevation (a). We found no compelling evidence that body condition of female red-faced warblers varied with elevation, after controlling for the nest stage when the bird was captured (b). Solid lines are predicted values for each group, shaded areas are 95% confidence intervals, and points are raw data.

gradient appear to reflect a facultative response to risk of nest predation. Female red-faced warblers that experienced an experimentally increased perception of nest predation risk laid fewer eggs than control females, providing a clear experimental demonstration of their proximate sensitivity to, and their plasticity in response to, variation in nest predation risk (also see Fontaine and Martin 2006; Zanette et al. 2011).

Observed elevational patterns of clutch size in red-faced warblers were also predicted by the increase in depredation rates of artificial nests at higher elevations. Indeed, high elevation breeders laid the smallest clutch despite having the highest food abundance and low elevation breeders laid the largest clutch despite having the lowest food abundance, suggesting that nest predation risk has an overriding influence on clutch size in this system. Thus, both experimental and correlative data provide complementary and consistent support for nest predation risk as an important driver of elevational patterns of clutch size variation in our system.

A particularly interesting result of our study was the observation that nest predation increased with elevation in artificial nests (Figure 3a) but not in real nests (Figure 3b). Nest predation can

constrain avian clutch size via several mechanisms (Lima 2009). The Nestling Begging and Parental Activity Mechanisms predict no relationship between elevation and nest predation rates at real nests, because these mechanisms imply that birds have compensated appropriately for high ambient predation risk at high elevation, thereby reducing their risk of nest predation (Fontaine et al. 2007). Furthermore, the Nestling Begging Mechanism predicts a positive relationship between nestling growth rates and breeding elevation (a prediction that our data support). Indeed, louder and more frequent begging comes at the cost of increased nest predation risk (McDonald et al. 2009). However, our ability to distinguish between the potential mechanisms by which nest predation might drive elevational variation in clutch size is limited because it was not the primary focus of the current study. Further research should measure nestling begging directly in order to further distinguish between these and other mechanisms of the Nest Predation Hypothesis.

Clutch size is just one aspect of a bird's entire life-history strategy and the optimal life-history strategy may vary along the elevational gradient (Bears et al. 2009). Our results indicate that clutch size is

negatively correlated with elevation and nestling growth rates are positively correlated with elevation. In other words, it seems that selection favors a strategy of producing fewer offspring of higher quality at higher elevation and a strategy of producing more offspring of lower quality at lower elevation. Indeed, this elevational gradient in life-history strategies may explain interspecific variation in avian clutch size across elevations (Badyaev and Ghalambor 2001) and latitudes (Martin 2015). The optimal strategy along the upper two-thirds of red-faced warblers' elevational breeding range appears to be primarily constrained by variation in nest predation rates, but low elevation breeders may also need to account for the low food abundance at those elevations and the effect that has on their ability to renest following failure. A reduction in food abundance available to black-throated blue warblers (*Setophaga caerulescens*) did not cause a reduction in clutch size but did result in fewer nesting attempts (Rodenhous and Holmes 1992). Further studies should investigate the relationship between phenological changes in food abundance and the number of nesting attempts at different breeding elevations in red-faced warblers and other birds.

The influences of offspring mortality, resource limitation, and female quality have long been considered among the primary constraints on offspring number. Food resource limitation has historically been assumed responsible for the evolution of clutch size in birds (Lack 1947) as well as other taxa (Mountford 1968; Millar 1973). Yet our results suggest that variation in nest predation risk, not food abundance, best explains variation in clutch size of red-faced warblers. Indeed, offspring mortality appears to explain more variation in life-history strategies than previously thought (Reznick and Endler 1982; Martin 1995; Ibanez-Alamo 2015). Some processes, such as parasites or disease (Martin et al. 2001; Neuhaus 2003) were beyond the scope of the current study, and further research should consider these potential constraints on offspring number across elevational gradients.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Dillon and Conway (2017).

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