BEHAVIORAL ECOLOGY - ORIGINAL PAPER

Can variation in risk of nest predation explain altitudinal migration in tropical birds?

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Abstract Migration is among the best studied of animal behaviors, yet few empirical studies have tested hypotheses explaining the ultimate causes of these cyclical annual movements. Fretwell's (1980) hypothesis predicts that if nest predation explains why many tropical birds migrate uphill to breed, then predation risk must be negatively associated with elevation. Data from 385 artificial nests spanning 2,740 m of elevation on the Atlantic slope of Costa Rica show an overall decline in predation with increasing elevation. However, nest predation risk was highest at intermediate elevations (500–650 m), not at lowest elevations. The proportion of nests depredated by different types of predators differed among elevations. These results imply that over half of the altitudinal migrant bird species in this region migrate to safer breeding areas than their non-breeding areas, suggesting that variation in nest predation risk could be an important benefit of uphill migrations of many species.

Keywords Costa Rica · Elevational gradients · Evolution of migration · Tropical rainforest

Communicated by Scott Robinson.

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Introduction

Animals from all major vertebrate and many invertebrate lineages engage in cyclical annual migrations, which are the subject of an extensive literature (Alerstam 1990; Dingle 1996). An overwhelming majority of the research on migration has sought to elucidate spatial patterns of migration and identify the proximate cues responsible for the initiation of annual migratory movements (Berthold 2001; Gauthreaux 1996; Keast 1995). In contrast, mechanistic hypotheses explaining why this behavior evolved have rarely been tested. Consequently, we still lack an understanding of the underlying ecological reasons why some species migrate, while others remain at a single site year-round.

Bird migration is commonly explained as a response to temporal and spatial variation in food resources (Alerstam and Enckell 1979; Alerstam et al. 2003; Chesser and Levey 1998; Morton 1977). However, alternative explanations rely on variation in physiologically optimal climate (Ramos-Olmos 1983) or in quality of breeding sites. In particular, differences in the relative risk of nest predation among regions may be a factor promoting the evolution of migration (Fretwell 1980; Greenberg 1980). Fretwell (1980) proposed that birds migrate away from their non-breeding areas to minimize risks of nest predation. Fretwell (1980) invoked density-dependence to explain variation in nest predation risk among sites, although differences in predator species composition or predator densities (independent of nesting bird densities) could also produce gradients in nest predation risk. Despite the fact that predation risk influences many aspects of avian life history strategies (e.g., Conway and Martin 2000; Ghalambor and Martin 2001; Martin et al. 2000), few studies have examined how nest predation risk might influence migratory behavior.

Bird migration occurs over many spatial scales. Short-distance altitudinal migrations are common, especially in tropical regions. Altitudinal migration involves annual movements of all or part of a population between non-breeding and breeding elevations. Breeding sites are usually at higher elevations than non-breeding sites despite considerable variation in the elevations spanned by each species (Burgess and Mlingwa 2000; Johnson and Maclean 1994; Loiselle and Blake 1991). On the Atlantic slope of Costa Rica, approximately 30% of breeding bird species migrate altitudinally (Stiles 1983), and over 85% of these altitudinal migrant species migrate uphill to breed.

As with latitudinal migration, spatial and temporal variation in food is generally invoked to explain altitudinal migration (Chaves-Campos et al. 2003; Loiselle and Blake 1991; Solórzano et al. 2000). Yet the evidence for variation in food availability explaining altitudinal migration is inconclusive. Results of several studies reveal inconsistencies between predicted and observed correlations between food resources and bird movements (Boyle 2006; Chaves-Campos 2004; Loiselle and Blake 1991; Rosselli 1994). Spatial variation in predation risk is one of the primary alternative explanations proposed for altitudinal migration (Loiselle and Blake 1991). Although nest predation risk could explain only the uphill portion of the migratory cycle, tropical birds likely experience different habitat requirements and nutritional needs during breeding and non-breeding seasons. Thus, different processes may well explain uphill and downhill portions of the migratory cycle.

If variation in predation risk explains uphill altitudinal migration, then the risk of predation should decrease with increasing elevation. Support for this prediction would not eliminate alternative hypotheses, but failure to find such a pattern could lead to rejection of the predation hypothesis. Data to support this prediction come from Skutch (1985) who reported a linear decline in the incidence of nest predation with increasing elevation in Central America (Fig. 1). Because Skutch's (1985) lowest elevation site (Barro Colorado Island, 88 m) is a man-made island in the Panama Canal with potentially elevated predation rates relative to mainland sites (Sieving 1992), I corroborated lowland values with data from nearby mainland sites reported in Robinson et al. (2000; Fig. 1, triangles). Several problems with these data make conclusions tenuous however. Skutch (1985) calculated the proportion of successful nests based on an average of only 1.7 nests per species and 67 nests per site. Using different species to compare relative nest predation risk across elevational gradients is problematic because species vary widely in risk of nest predation due to differences in nesting substrate and parental behavior (Conway and Martin 2000; Martin 1993). Moreover, Skutch's (1985) sites, located from Panama to Guatemala, were not adjacent and they varied dramatically in degree of disturbance,

Fig. 1 Relationship between elevation and nest predation at seven Neotropical sites redrawn from Skutch (1985; *filled circle*) and Robinson et al. (2000; *inverted shaded triangle*). Points in the figure represent mean proportion of depredated nests at the median elevation from the range at each site. Sites, elevational ranges, and sample sizes (n_{nests}/$n_{species}$) used to calculate means are as follows: Limbo, Panama in 1996 (*LP '96*), 35–85 m, (242/51); Limbo, Panama in 1997 (*LP '97*), 35–85 m, (454/55); Barro Colorado Island, Panama (*BCI*), 25–125 m, (62/38); Motagua Valley, Guatemala (*MV*), 60–240 m, (68/41); El General, Costa Rica (*EG*), 610–700 m, (85/61); Montaña Azul, Costa Rica (*MA*), 1,525–1,830 m, (80/47); Los Cartagos, Costa Rica (*LC*), 1,980–2,285 m, (41/27); Sierra de Tecapán, Guatemala (*SDT*), 2,440–3,050 m, (67/28). Note that the data from mainland Panama (LP '96 and LP '97) come from four sites (Robinson et al. 2000). However the data are plotted at the median elevation of the Limbo site where 72% of the nests were found. The *regression line* depicts the linear relationship between elevation and nest predation (proportion of failed nests = 0.67–0.000078 elevation, $t = -2.9$, $P = 0.029$, $R^2 = 0.575$)

ranging from old-growth forest (Montaña Azul, 1,687 m) to banana plantations (Motagua Valley, 150 m) and cattle pastures (Los Cartagos, 2,132 m). Because of these problems, comparisons in nest predation risk along a single contiguous elevational gradient are needed to more adequately test the nest predation hypothesis.

Skutch (1985) proposed a mechanism for the elevational decline in nest predation, noting that snakes seem to be more abundant at low than high elevations. Thus far, little evidence supports a linear decrease in snake abundance with increasing elevation. Indeed in Costa Rica, the diversity of snakes does not decline until above 800 m and the abundance of all leaf-litter-dwelling herpetofauna may peak at even higher elevations (Scott 1976). Likewise, in other tropical and subtropical regions, the relationship between elevation and both snake diversity (Fu et al. 2007) and reptile abundance (Hofer et al. 1999) is non-linear. Because some altitudinal migrants leave lowland forests to breed in premontane forests where snakes (including bird-eating *Pseustes* and *Spilotes*) appear to be just as common as in nearby lowland sites (T. Leenders, personal communication; personal observation) it is unlikely that differences in snake abundance can fully explain Skutch's (1985)

pattern. Furthermore, snakes are not the only predators of eggs and nestlings; both mammals and birds are important predators of Neotropical bird nests (Robinson and Robinson 2001). Thus, the relationship between elevation and the abundance of potential avian nest predators is far from clear.

Here I test a critical prediction of the nest predation hypothesis by conducting an experiment using artificial nests to understand how predation risk varies along an elevational gradient within the humid tropics. Moore and Robinson (2004) critiqued the use of artificial nests based on evidence that artificial nests often fail to reveal the same patterns of relative predation risk among sites as real nests (e.g., Burke et al. 2004). Artificial nests differ from natural nests in important ways, including lacking parents who provide additional camouflage and may defend nests from predators (Major and Kendal 1996). Additionally, artificial nest studies estimate the relative risk of egg predation between sites; the actual risk of nest predation extends beyond the egg stage through hatching and fledging. Thus, the inferences drawn from studies using artificial nests are clearly limited. However, artificial and real nests may provide different kinds of information about how predation risk varies across biological gradients. Studies of real nests estimate predation risk after local adaptation to the biological landscape has already occurred. In contrast, predation on artificial nests may better estimate the relative risk among sites for a naïve species whose nest placement, design, and parental behavior has not already been shaped by local selective pressures. Thus, I used artificial nests to estimate the relative risk of different elevations for incipient migratory populations.

This study addresses the following specific questions:

1. What is the pattern of predation on artificial nests along an elevational gradient in Costa Rica?
2. Is that pattern consistent with the hypothesis that birds migrate uphill to reduce their risk of nest predation?
3. Are elevational patterns of nest predation related to elevational changes in the types of nest predators?

Materials and methods

I worked on the Atlantic slope of Costa Rica on a continuous, elevational gradient of tropical forest. Protected forest extends from 30 m above sea level at La Selva Biological Station to 2,906 m in Braulio Carrillo National Park (BCNP) and adjacent private reserves of Rara Avis and Selva Tica (see Appendix, Electronic Supplementary Material). At 9°30′N, seasonal fluctuations in temperature and day length are small. Rainfall peaks geographically in premontane forest between 600 and 800 m, and peaks

seasonally from May to August, and again from November to December. Mean annual rainfall is very high, ranging from 3,000 to 4,000 mm/year at both highest and lowest elevations to >8,000 mm/year at 700 m. Seasonal patterns of rainfall and temperature are similar over the entire elevational gradient (Gómez and Herrera 1986).

I placed nests over the widest elevational range possible, from the base of the mountains to within 130 m of the peak of Barva volcano in BCNP. All sites were located in "old-growth" forest (based on regional satellite imagery and not known to have been selectively logged). I placed 385 nests at eight sites (Appendix): two locations at La Selva (40 and 120 m elevation; lowland forest), Quebrada Gonzalez, Selva Tica, and Rara Avis (500, 650, and 820 m, respectively; premontane forest), and Puesto Zurquí, Chateau Barva, and Puesto Barva (1,650, 2,050, and 2,780 m, respectively; montane cloud forest). I placed 50 nests at each site except at 2,050 m, where I placed 35 nests. I placed all 385 nests over 8 consecutive days, and monitored nests over the subsequent 2 weeks, returning to each site in the same sequence as nests were originally placed. The experiment ran from 3 to 24 May 2004. Over 80% of the birds in this region breed during May (Stiles and Skutch 1989).

At each site, I placed nests along two 250-m transect lines separated by ≥100 m. I chose the location of these lines based on digital elevation models to maintain relatively uniform elevations along each transect line. All transects were >0.5 km from roads and >20 m from trails. I placed nests >5 m alternately left and right from transect lines at 10-m intervals in the nearest understory tree judged capable of supporting a small nest.

I used artificial nests constructed from small baskets of bark strips covered with moss to mimic nests of understory open-cup nesting passerines breeding in the region (e.g., *Tanagara icterocephala*, *Chlorothraupis carmioli*, *Myadestes melanops*). I attached nests to trees 1–2 m above the ground using black wire, then adorned nests with small epiphytes, leaf skeletons, twigs, and rootlets collected from the vicinity of the nest site. I attempted to locate and camouflage nests to closely resemble real nests, based on photos, descriptions, and personal observations of nests in tropical wet forest. In each nest, I placed one infertile canary egg and one plasticine (modeling clay) egg. Both eggs were of the same size and color and were similar in size to eggs of the species listed above (~20 mm long and ~15 mm diameter). I used canary eggs rather than the larger quail eggs often used in artificial nest studies because smaller eggs may attract a more realistic range of nest predators (Rangen et al. 2000). Baiting nests with both real and plasticine eggs is a useful approach: the real egg may attract olfactory hunting predators because their odors more closely resemble wild bird eggs than do artificial eggs (Pärt

and Wretenberg [2002]), and the plasticine egg often retains the tooth, bill, or claw marks of the nest predator.

I checked nests after 1 week (day 6, 7 or 8) and again after 2 weeks (day 13, 14, or 15). I considered nests to have been depredated if either or both eggs were damaged or missing. When an egg was missing, I searched the ground for fragments of eggshell or plasticine in a radius of ~3 m around the nest. I removed any depredated nests after the first check, and removed all nests after the second check. I inspected plasticine eggs for signs of bill or tooth marks to determine the type of predator responsible for attacking the nest. Biologists at La Selva Biological Station and the University of Arizona confirmed the identification of mammalian and reptile marks.

I used logistic regression to model the relationship between nest success and elevation, treating elevation as a continuous variable. To test whether this relationship was better described by a polynomial model than a linear model, I used a likelihood ratio test to assess the variation explained by the quadratic term (elevation^2). To account for slight differences among sites in the number of days between nest checks, I calculated daily Mayfield survival probability for each site (Johnson [1979]). I constructed linear and polynomial regression models using $1 -$ daily survival probability (daily predation probability) as the response variable and elevation as the explanatory variable. To compare the relationship between elevation and the proportion of nests depredated in this study with the relationship depicted in Fig. [1], I used daily survival probabilities to standardize the proportion of nests depredated to 14 days. This was the median number of days my nests were exposed and falls within the range of incubation durations for understory passerines in the region. I then combined the standardized proportions with the proportions reported by Skutch ([1985]) and calculated from Robinson et al. ([2000]) in a single ANOVA model. I tested whether the slope of the relationship between predation and elevation differed between datasets by including an elevation × dataset interaction term in the model. I used a likelihood ratio test to determine if predator type differed with elevation, grouping predators into taxonomic categories (birds, mammals, snakes, and ants) which correspond to the sensory modality used in locating prey.

Artificial nests underestimate the relative importance of snakes as nest predators (Marini and Melo [1998]; Thompson and Burhans [2004]; Weatherhead and Bloun-Demers [2004]) because snakes seem to rarely attack artificial nests, and also because they swallow prey whole, leaving no trace of their attack. If nests at lower elevations are subject to higher risk of snake predation, then the number of canary eggs that disappear from nests should decrease with increasing elevation. I evaluated this prediction by comparing the proportions of nests at each elevation from which

the canary egg disappeared and around which I found no eggshell fragments.

Results

Overall, predation risk declined with increasing elevation (Fig. [2]). I found strong evidence for a linear relationship between the likelihood of nest predation and elevation (likelihood ratio test, $\chi^2 = 9.8$, $P = 0.002$) that closely resembles the relationship presented by Skutch ([1985]). The slope of the linear fit of the proportion of nests depredated at each elevation (-0.057 per 1,000 m, SE = 0.018) did not differ statistically from the slope of the linear fit of the Skutch–Robinson data (-0.078 per 1,000 m, SE = 0.027; $t = 0.6$, $P = 0.920$). Although the highest daily probability of predation was at 500 m rather than at the two lowland sites (Fig. [2]), the relationship between the likelihood of nest predation and elevation was not well described by a curvilinear fit (likelihood ratio test, $\chi^2 = 1.1$, $P = 0.534$). Both linear ($F_{1,6} = 4.8$, $P = 0.070$, $R^2 = 0.446$) and polynomial ($F_{2,5} = 4.5$, $P = 0.075$, $R^2 = 0.645$) regression models provided comparable fits to the daily predation probability data. However, I found little evidence that the polynomial model improved the fit to these data over the linear model ($t = -1.7$, $P = 0.155$).

Only 9% of nests were not attacked during the 2-week experiment. Nest predators marked plasticine eggs in 81% of depredated nests (Table [1]). In 14% of nests the canary egg was damaged or removed while the plasticine egg

Fig. 2 Relationship between elevation and daily probability of nest predation for 375 nests placed at eight sites ranging in elevation from 40 to 2,780 m on the Atlantic slope of Costa Rica. Daily probability of nest predation is calculated as $1 -$ daily survival probability. *Error bars* represent the SE of the maximum likelihood estimator (Hensler and Nichols [1981]; Johnson [1979]). The *right-hand y-axis* represents the proportion of nests depredated standardized to 14 days at each site using daily survival probability to enable direct comparison with Fig. [1]. The *regression line* depicts the linear relationship between elevation and nest predation (daily probability of predation = 0.20–0.000031 elevation, $t = -2.2$, $P = 0.070$, $R^2 = 0.446$). See Table [1] for summary of nest fates

Table 1 Summary of nest fates along an elevational gradient in Costa Rica. I considered a nest to have been depredated if either one or both eggs were damaged or removed. Results are based on 375 nests; nine nests were lost due to flooding and one nest was accidentally destroyed

Nest fate	Number of nests	Percentage of all nests
Neither egg attacked	35	9.3
Plasticine egg removed	15	4.0
Only canary egg attacked	51	13.6
Avian marks on plasticine egg	115	30.7
Mammalian marks on plasticine egg	71	18.9
Snake marks on plasticine egg	5	1.3
Ant marks on plasticine egg	5	1.3
Unknown marks on plasticine egg	78	20.8

remained intact. The plasticine egg disappeared entirely from 4% of the nests. Birds left more marks in plasticine eggs than did any other predator group. Of the nests to which a predator could be assigned ($n = 196$), birds attacked 59%, mammals attacked 36%, and snakes and bullet ants combined attacked 5% of the nests. Mammalian tooth marks included dentition patterns of both marsupials and rodents. The relative incidence of attack by predator groups differed among elevations for nests to which I could assign a predator type ($\chi^2 = 59.8$, $P < 0.0001$). Bird attacks were most common at 650 m, whereas mammal attacks were most common at 1,650 m (Fig. 3). Canary egg disappearance did not decrease with elevation (linear regression, $t = 0.8$, $P = 0.445$, $R^2 = 0.100$). The highest incidence of canary egg disappearance was at 1,650 m. I found no relationship between elevation and incidence of unknown marks (linear regression, $t = -0.4$, $P = 0.681$, $R^2 = 0.030$).

Fig. 3 Relationship between elevation and proportion of nests depredated by birds (*shaded circle*) and mammals (*inverted filled triangle*). Proportions are based on the total number of nests placed at each elevation that were not destroyed by flooding or humans; $n = 50$ nests per elevation except at 40 m ($n = 41$), 2,050 m ($n = 35$), and 2,780 m ($n = 49$)

Discussion

The results of this study generally support the prediction that nest predation risk declines with elevation consistent with the hypothesis that altitudinal migration has evolved in response to elevational differences in nest predation risk. Many migrant species (57% of those breeding in the region) move uphill from riskier non-breeding elevations to breed in safer higher-elevation forests. However, the highest risk of nest predation in this region seems to be at 500 and 650 m in premontane forests, not in lowland forests. Consequently, species that migrate from forests below 300 m to breed in premontane forests actually migrate up to the riskiest elevations on the entire gradient. Roughly 26% of Costa Rican altitudinal migrant species exhibit such migration patterns, breeding wholly or partly between 400 and 800 m, and spending their non-breeding season wholly or partly below 300 m (Loiselle and Blake 1991; Stiles and Skutch 1989). Interestingly, these elevations also appear to be those with the highest densities of understory birds (Blake and Loiselle 2000; unpublished data), potentially indicating density-dependent predation risk in this region. The relative risk of nest predation among elevations is thus consistent with the migration patterns of much, but not all, of the migrant avifauna. While the pattern of canary egg disappearance was not consistent with a linear decline in snake predation with elevation, snakes do not attack artificial nests as frequently as they do real nests (Thompson and Burhans 2004). Until we better understand how predation by snakes varies altitudinally, the extent to which alternate factors must be invoked to explain uphill movements of lower-elevation migrant birds is not clear.

Differences in the predominance of bird and mammalian predation among elevations imply that selective pressures imposed by visual versus olfactory predators probably change along this elevational gradient. These results predict that at lower elevations where visual predators (birds) depredate more nests, there should be stronger selection for nest crypsis and inconspicuous parental behavior. At higher elevations where olfactory nest predators (mammals) predominate, there should be stronger selection for nest placement in sites inaccessible to non-volant vertebrates.

This study represents a significant advance in our understanding of spatial variation in nest predation risk in Neotropical forests. Despite the limitations of artificial nest studies, data from artificial nests are better than no data (Faaborg 2004), especially in landscape-scale studies where multiple species are involved and the use of real nests is impractical (Villard and Pärt 2004). Additionally, by using realistic nest construction, placement, and appropriately sized real eggs, these results may better approximate patterns of predation on real nests than do many nest experiments (Davison and Bollinger 2000). Finally, experiments

using artificial nests may be more appropriate for understanding why traits such as bird migration evolved. Nesting behavior of birds at different elevations has presumably been subject to strong selection imposed by the nest predators at those elevations. In the absence of experiments, we can only guess at how nests of those species might fare at higher or lower elevations.

To further our understanding of spatial variation in nest predation risk will require replication on other elevational gradients. Unfortunately, few forested elevational gradients remain in the Neotropics that would permit replication at such a large elevational scale. Second, we should corroborate these patterns of relative predation risk using real bird nests. The desirability of controlling for nest characteristics suggests that smaller-scale elevational comparisons within species may be the best approach.

The results of this study suggest that Fretwell's (1980) hypothesis could contribute to explaining why birds migrate uphill if density-dependence plays a role in creating the gradient of predation risk observed. These data from a contiguous forested elevational gradient are also generally consistent with the pattern described by Skutch (1985) from widely separated Central American sites. However, the relationship between predation risk and elevation may not be strictly linear. To better understand the factors promoting the evolution of altitudinal migration, future studies should acknowledge that a single factor may not explain the patterns of all migrant species, and that species-specific tests of multiple hypotheses will be required to better understand migratory behavior.

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