Lekking birds in a tropical forest forego sex for migration

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Facultative, partially migratory animals provide a contemporary window into the evolution of migration, offering rare opportunities to examine the life-history trade-offs associated with migration. For the first time, to our knowledge, we describe the nature of these trade-offs, using a lek-breeding tropical bird, the white-ruffed manakin (Corapipo altera). Previous evidence indicated that weather drives post-breeding migration to lower elevations bringing condition-related benefits. Using elevation-sensitive stable isotope measurements and more than 1200 h of behavioural observations, we show that male manakins which migrate incur costs of diminished social status and matings with females the following breeding season. Because migratory tendency depends on inter-annual variation in weather, physical costs of displays and breeding prospects the following year, migratory decisions are subject to both natural and sexual selection, with the outcome of such decisions linked to changing climatic regimes.

Keywords: carry-over effects; evolution of migration; life-history trade-offs

1. INTRODUCTION

Migration is among the most fascinating of animal behaviours and occurs in a wide variety of taxa worldwide [1]. For migration to evolve under natural selection, the fitness benefits of migrating must outweigh the costs of migrating and benefits of residency [2,3]. In facultative partial migrants, individuals make migratory decisions each year based on the pay-offs of alternative strategies, which in turn depend upon both extrinsic and intrinsic factors [4,5]. Documenting the nature of those pay-offs is both extremely challenging and crucial to understanding the evolution of migration in wild populations.

Using measurements of naturally occurring stable isotopes to track movements, and behavioural observations to estimate mating success, we examined the costs of migration in white-ruffed manakins (Corapipo altera) in northeast Costa Rica. This frugivorous species breeds in montane forests and some, but not all, individuals migrate to lower elevations after breeding [6] (electronic supplementary material). After eliminating alternative hypotheses regarding the causes of altitudinal migration in this community and population [7–9], we showed that residents incur physiological costs of high-elevation storms that limit foraging opportunities, compromising condition [10]. Here, we test the hypothesis that partial migration results from these costs being countered by reproductive benefits of residency, with migratory decisions dependent upon mating prospects the following year (electronic supplementary material, figure S1).

2. MATERIAL AND METHODS

We studied white-ruffed manakins in northeast Costa Rica (10° 17.3' N, 84° 03.1' W, approx. 600–850 m). Caribbean-slope populations actuate breeding in March, and individuals migrate as early as July or as late as December, remaining at lower elevations until February (based on capture data, electronic supplementary material) [6,9]. We captured manakins in mist-nets, aged, sexed and colour-banded individuals, clipped the primaries from the central claw on each foot, measuring claws after clipping and upon recapture to estimate growth rates. We analysed ratios of the stable hydrogen isotope D relative to H (expressed as δD) in claws. δD varies with altitude (and precipitation amount) in terrestrial food webs of Central America [11,12]. Thus, δD values represent an index of ‘migratoriness’, because isotope ratios integrate spatial information over temporal scales that depend upon claw growth rates [13]. Both temporal and spatial components of this index are biologically important because the length of time males are absent from leks probably affects both condition-related benefits and future reproductive costs of migration. Isotope assays were conducted on surface-sterilized 350 μg claw samples at Environment Canada’s Stable Isotope Hydrology and Ecology Research Laboratory (electronic supplementary material).

During breeding, male manakins engage in elaborate displays in dispersed leks to attract females [14]. Display sites are mossy fallen logs, each controlled by one dominant alpha male, who displays singly or in conjunction with hierarchies of subordinate males. Displays include slow, ‘butterfly’ flights, log landings with raised ruff and high-speed aerial dives accompanied by mechanical wing sounds (electronic supplementary material, video S1). Alphas make distinct vocalizations, spend more time at leks, perch closer, and land on logs more frequently than subordinate males. Manakins are long-lived for their size, with ‘alpha’ status typically taking years to achieve [15].

Observers recorded the identity and behaviours of white-ruffed manakins at leks from camouflaged blinds. We assigned status based on each male’s highest status each year. Although 22 leks were active and 25 males were sampled in both years, we used lek-year and male-year combinations as independent data points. This approach is justified because: (i) the identity of the alpha controlling leks frequently changed between years (10 of 22 leks, 45%), (ii) the migratory tendency of individuals depends on age and condition [8], and (iii) male activity and presumed attractiveness of leks varied substantially among years.

We analysed datasets using a general linear model framework, considering models including year, and interactions between year and main effects. When year and interactions did not improve model fit (extra sum of squares F-tests), we analysed only main effects. We arcsine-square-root-transformed proportions, and examined residual plots for homogeneity of variance and outliers.

3. RESULTS

We compiled 946 h of direct observation of 117 colour-marked individuals at 42 leks, and recorded 316 h of video. During 185 female visits to leks during observations, males increased the intensity of displays with 11 of these (6%) culminating in copulations (electronic supplementary material, video S2). Female visits approximate mating success; the time that females spent at leks was 4.4 times greater where we observed copulations than at leks where we observed no copulations.

(F_{1,58} = 19.5, p < 0.0001). The proportion of time females spent visiting leks also increased with male attentiveness (time within 15 m of log: F_{1,58} = 22.8, p < 0.0001), advertisement trills per hour (F_{1,58} = 6.7, p = 0.012) and N subordinate males (F_{1,58} = 22.8, p < 0.0001). Videos confirmed that observers did not affect female visitation or male behaviour. The observation and video datasets were extremely similar in the proportion of time females spent at leks (r^2 = 0.48, F_{1,58} = 7.3, p = 0.027), and male display rates (log landings: r^2 = 0.84, F_{1,58} = 43.8, p = 0.0002; aerial dives: r^2 = 0.56, F_{1,58} = 10.3, p = 0.012; butterfly flights: r^2 = 0.74, F_{1,58} = 23.2, p = 0.001).

We estimated migratory tendency of 216 individual-year combinations including 90 adult males (25 in both years) using 6D measurements from claws [16]. 6D measurements in precipitation predicted an 11.7‰ difference between breeding and non-breeding elevations [17] (electronic supplementary material, figure S2). Supporting this, white-ruffed manakin claws collected at breeding sites were 16.0‰ (+4.9‰) more depleted in D than those collected at low elevations in November–December 2008 (electronic supplementary material, figure S3a; t_{16} = 3.2, p = 0.005), mirroring differences in claws of other non-migratory frugivorous species sampled at both elevations (electronic supplementary material, figure S3b,c). White-ruffed manakin claws grew 0.030 mm d^{-1} (+0.007), indicating that turnover of claw tissue takes approximately four months. Thus, samples collected early in March reflect the elevation of individuals during November–February when the greatest number of migrants are at low elevations [9].

6D values in 2008 samples averaged 4.8‰ higher than 2009 samples (t_{214} = 4.1, p < 0.0001), indicating that more individuals migrated prior to 2008 than 2009. This result is consistent with capture data showing that migratory tendency is related to storm severity [10], as rainfall was 44 per cent higher prior to the 2008 than the 2009 breeding season. Claw 6D data in 2009 also corroborated capture data, indicating that adult males were the sex most likely to migrate [8,10] (whole model: F_{3,156} = 5.3, p = 0.002; sex × year: F_{1,156} = 3.5, p = 0.062).

Alpha males with more resident 6D values attracted females more frequently (F_{1,34} = 4.9, p = 0.035) and for longer durations (figure 1a; F_{1,35} = 7.1, p = 0.012). Alphas with more resident 6D values also tended to spend more time at their lek (figure 1b; F_{1,35} = 3.5, p = 0.068), vocalize more (trills per hour: F_{1,35} = 3.0, p = 0.094) and have larger subordinate male groups (F_{1,35} = 2.4, p = 0.130). The slope and intercept of the relationship between the proportion of time females spent at leks and male 6D values in video data closely paralleled the observation data (electronic supplementary material, figure S4).

In 2009, status was related to migratory tendency, with betas being less migratory than alphas or lower ranking males (status × year: F_{1,107} = 2.8, p = 0.041). Changes in male status between 2008 and 2009 were related to migratory tendency during the intervening non-breeding season. Out of 38 males, 17 retained a high status (alpha or beta) from 2008 to 2009, 10 remained low, six increased and five decreased in status. Males with the most migratory 6D values decreased in status upon returning to breed the subsequent year, whereas males with the most resident 6D values retained their high status from one year to the next (figure 2; F_{1,34} = 2.9, p = 0.048).

4. DISCUSSION

Our results are consistent with the hypothesis that the survival costs of residency trade off with benefits in mating success. Furthermore, we reveal a novel link between sexual selection and migratory behaviour. In
formerly high-status males whose status decreased between years, strenuous aerobic displays may compromise condition, reducing their ability to withstand climatic stressors the following non-breeding season with carry-over effects into the next breeding season. Decreases of up to 20 per cent (mean 10%) in adult male body mass during breeding confirm that displays can be costly. Thus, residency in males may be an honest signal to females of quality.

Differences between years in δD values are consistent with the costs of residency being weather-related [10]. In 2008, when the preceding season was rainier, more individuals abandoned breeding areas, regardless of social status. Interestingly, in 2009, more betas than alphas had δD values indicative of residency. If retaining alpha status is easier than displacing an incumbent alpha as a rising beta [18], betas would have greater pay-offs of residency than would all other males. All current and previous evidence indicates that migratory decisions in this species represent a finely-tuned assessment of the survival and reproductive pay-offs of alternative migratory strategies, pay-offs that vary with social status, environment and condition. A goal of future work will be to quantify migration-related survival benefits by incorporating isotopes into mark-recapture models.

Studies of many migrant taxa have proposed similar life-history trade-offs associated with migratory decisions [19–21]. However, our work provides, to our knowledge, the first empirical link between migration and factors that can affect both survival and reproduction in the same wild vetebrate population. We show that migratory decisions are subject to both natural selection (weather-related fasting ability) and sexual selection (lek breeding system), that individual selection (weather-related fasting ability) and sexual selection (lek breeding system), that individual

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