Lekking birds in a tropical forest forego sex for migration

W. Alice Boyle1,4*, Christopher G. Guglielmo1, Keith A. Hobson2,3 and D. Ryan Norris2

1Department of Biology, Advanced Facility for Avian Research, University of Western Ontario, London, Ontario, Canada N6A 5B7
2Environment Canada, 11 Innovation Boulevard, Saskatoon, Saskatchewan, Canada S7N 5E2
3Department of Biology, University of Saskatchewan, Saskatoon, Saskatchewan, Canada S7N 5E2
4Department of Integrative Biology, University of Guelph, Guelph, Ontario, Canada N1G 2W1
*Author for correspondence (aboyle7@uwo.ca).

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 activate breeding at 100–200 h of weather conditions, males increased the intensity of displays with

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attentiveness (time within 15 m of log; females spent visiting leks also increased with male
females more frequently (F 4.9; p = 0.012). Alphas with more resident
than 2009 samples (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 δD 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 δD 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

\( F_{1,58} = 19.5, p < 0.0001 \). 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 (\( r^2 = 0.48, F_{1,8} = 7.3, p = 0.027 \)), and male display rates (log landings: \( r^2 = 0.84, F_{1,8} = 43.8, p = 0.0002 \); aerial dives: \( r^2 = 0.56, F_{1,8} = 10.3, p = 0.012 \); butterfly flights: \( r^2 = 0.74, F_{1,8} = 23.2, p = 0.001 \)).

We estimated migratory tendency of 216 individual-year combinations including 90 adult males (25 in both years) using 6D measurements from claws [16]. δD 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].

δD 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 δD data in 2009 also corroborated capture data, indicating that adult males were the sex most likely to migrate [8, 10] (whole model: \( F_{5,156} = 5.3, p = 0.002 \); sex × year: \( F_{1,156} = 3.5, p = 0.062 \)).

Alpha males with more resident δD 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 δD 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 δD values in video data closely paralleled the observation data (electronic supplementary material, figure S4).
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 $\delta D$ 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 $\delta D$ values indicative of residency. If retaining alpha as 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 (lek breeding system), that individual selection (weather-related fasting ability) and sexual selection (Coratipio leucorhoa, a tropical frugivorous altitudinal migrant, and its food plants.

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