biology letters

Animal behaviour

Lekking birds in a tropical forest forego sex for migration

W. Alice Boyle[1,4,*], Christopher G. Guglielmo[1], Keith A. Hobson[2,3] and D. Ryan Norris[4]

[1]Department of Biology, Advanced Facility for Avian Research, University of Western Ontario, London, Ontario, Canada N6A 5B7
[2]Environment Canada, 11 Innovation Boulevard, Saskatoon, Saskatchewan, Canada S7N 3H5
[3]Department of Biology, University of Saskatchewan, Saskatoon, Saskatchewan, Canada S7N 5E2
[4]Department 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.

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 initiate 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, and clipped the distal 1.5 mm 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 ($r^2 = 0.48$, $F_{1,8} = 7.3$, $p = 0.027$), 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 δD 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‰ ($\pm 4.9‰$) 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: $F_{3,156} = 5.3$, $p = 0.002$; 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).

In 2009, status was related to migratory tendency, with betas being less migratory than alphas or lower ranking males (status × year: $F_{3,107} = 2.8$, $p = 0.041$). 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
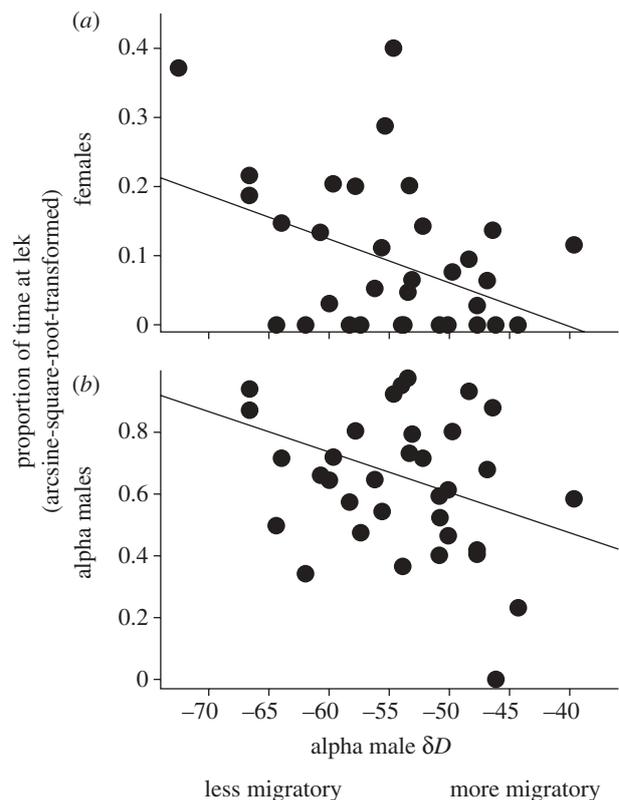

Figure 1. Relationship between δD values in claws of alpha males and the proportion of time that (a) females visited and (b) alphas attended their leks.
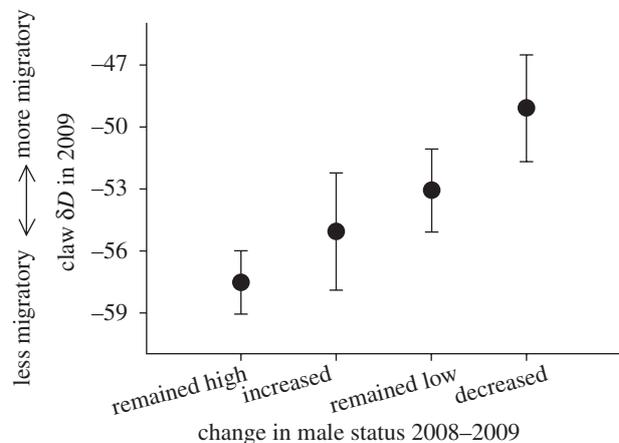

Figure 2. Change in male status between the 2008 and 2009 breeding seasons relative to δD values in their claws (indicating migratory tendency) in the intervening non-breeding season. Error bars represent ± 1 s.e.m.

status. Males with the most migratory δD values decreased in status upon returning to breed the subsequent year, whereas males with the most resident δD values retained their high status from one year to the next (figure 2; $F_{3,34} = 2.9$, $p = 0.048$).

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 aerobatic 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 decisions are flexible from year to year, and show how isotopes can be combined with mating information to understand evolutionary trade-offs. Because climate is a key factor influencing trade-offs, anthropogenic climate changes will alter the relative pay-offs of different migratory decisions, possibly resulting in the loss of this behavioural phenomenon [22].

1 Dingle, H. 1996 *Migration: the biology of life on the move.* New York, NY: Oxford University Press.

2 Fretwell, S. D. 1980 Evolution of migration in relation to factors regulating bird numbers. In *Migrant birds in the Neotropics* (eds A. Keast & E. S. Morton), pp. 517–527. Washington, DC: Smithsonian Institution Press.

3 Griswold, C. K., Taylor, C. M. & Norris, D. R. 2010 The evolution of migration in a seasonal environment. *Proc. R. Soc. B* **277**, 2711–2720. (doi:10.1098/rspb.2010.0550)

4 Lundberg, P. 1988 The evolution of partial migration in birds. *Trends Ecol. Evol.* **3**, 172–175. (doi:10.1016/0169-5347(88)90035-3)

5 Fryxell, J. M. & Sinclair, A. R. E. 1988 Causes and consequences of migration by large herbivores. *Trends Ecol. Evol.* **3**, 237–241. (doi:10.1016/0169-5347(88)90166-8)

6 Rosselli, L. 1994 The annual cycle of the white-ruffed manakin, *Corapipo leucorrhoa*, a tropical frugivorous altitudinal migrant, and its food plants. *Bird Conserv. Int.* **4**, 143–160. (doi:10.1017/S0959270900002732)

7 Boyle, W. A. 2008 Can variation in risk of nest predation explain altitudinal migration in tropical birds? *Oecologia* **155**, 397–403. (doi:10.1007/s00442-007-0897-6)

8 Boyle, W. A. 2008 Partial migration in birds: tests of three hypotheses in a tropical lekking frugivore. *J. Anim. Ecol.* **77**, 1122–1128. (doi:10.1111/j.1365-2656.2008.01451.x)

9 Boyle, W. A. 2010 Does food abundance explain altitudinal migration in a tropical frugivorous bird? *Can. J. Zool.* **88**, 204–213. (doi:10.1139/Z09-133)

10 Boyle, W. A., Norris, D. R. & Guglielmo, C. G. 2010 Storms drive altitudinal migration in a tropical bird. *Proc. R. Soc. B* **277**, 2511–2519. (doi:10.1098/rspb.2010.0344)

11 Lachniet, M. S. & Patterson, W. P. 2002 Stable isotope values of Costa Rican surface waters. *J. Hydrol.* **260**, 135–150. (doi:10.1016/S0022-1694(01)00603-5)

12 Hobson, K. A. 2005 Stable isotopes and the determination of avian migratory connectivity and seasonal interactions. *Auk* **122**, 1037–1048. (doi:10.1642/0004-8038(2005)122[1037:SIATDO]2.0.CO;2)

13 Mazerolle, D. F. & Hobson, K. A. 2005 Estimating origins of short-distance migrant songbirds in North America: contrasting inferences from hydrogen isotope measurements of feathers, claws, and blood. *Condor* **107**, 280–288. (doi:10.1650/7681)

14 Rosselli, L., Vasquez, P. & Ayub, I. 2002 The courtship displays and social system of the white-ruffed manakin in Costa Rica. *Wilson Bull.* **114**, 165–178. (doi:10.1676/0043-5643(2002)114[0165:TCDASS]2.0.CO;2)

15 McDonald, D. B. 2007 Predicting fate from early connectivity in a social network. *Proc. Natl Acad. Sci. USA* **104**, 10 910–10 914. (doi:10.1073/pnas.0701159104)

16 Hobson, K. A., Wassenaar, L. I., Milá, B., Lovette, I., Dingle, C. & Smith, T. B. 2003 Stable isotopes as indicators of altitudinal distributions and movements in an Ecuadorean hummingbird community. *Oecologia* **136**, 302–308. (doi:10:1007/s00442-003-1271-y)

17 IAEA 2006 Isotope hydology information system. The global network of isotopes in precipitation ISOHIS database. See http://www.iaea.org/water.

18 Kokko, H., Lindström, J., Alatalo, R. V. & Rintamäki, P. T. 1998 Queuing for territory positions in the lekking black grouse (*Tetrao tetrix*). *Behav. Ecol.* **9**, 376–383. (doi:10.1093/beheco/9.4.376)

19 Ketterson, E. D. & Nolan, V. 1983 The evolution of differential bird migration. *Curr. Ornithol.* **1**, 357–402.

20 Hebblewhite, M. & Merrill, E. H. 2009 Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. *Ecology* **90**, 3445–3454. (doi:10.1890/08-2090.1)

21 Brodersen, J., Nilsson, P. A., Hansson, L. A., Skov, C. & Brönmark, C. 2008 Condition-dependent individual decision-making determines cyprinid partial migration. *Ecology* **89**, 1195–1200. (doi:10.1890/07-1318.1)

22 Brower, L. P. & Malcolm, S. B. 1991 Animal migrations: endangered phenomena. *Am. Zool.* **31**, 265–276.