biology
letters
Animal behaviour

Biol. Lett. (2012) **8**, 710–713
doi:10.1098/rsbl.2012.0359

Flight responses by a migratory soaring raptor to changing meteorological conditions

Michael J. Lanzone[1,*], Tricia A. Miller[2,7], Philip Turk[2], David Brandes[3], Casey Halverson[1], Charles Maisonneuve[4], Junior Tremblay[4], Jeff Cooper[5], Kieran O'Malley[6], Robert P. Brooks[7] and Todd Katzner[1,2,8]

[1]*Cellular Tracking Technologies, LLC, Somerset, PA, USA*
[2]*West Virginia University, Morgantown, WV, USA*
[3]*Lafayette College, Easton, PA, USA*
[4]*Ministère des Ressources naturelles et de la Faune, Québec, Quebec, Canada*
[5]*Virginia Department of Game and Inland Fisheries, Richmond, VA, USA*
[6]*West Virginia Division of Natural Resources, Romney, WV, USA*
[7]*Riparia—The Pennsylvania State University, University Park, PA, USA*
[8]*Timber and Watershed Laboratory, USDA Forest Service, Parsons, WV, USA*
**Author for correspondence* (*mlanzone@gmail.com*).

Soaring birds that undertake long-distance migration should develop strategies to minimize the energetic costs of endurance flight. This is relevant because condition upon completion of migration has direct consequences for fecundity, fitness and thus, demography. Therefore, strong evolutionary pressures are expected for energy minimization tactics linked to weather and topography. Importantly, the minute-by-minute mechanisms birds use to subsidize migration in variable weather are largely unknown, in large part because of the technological limitations in studying detailed long-distance bird flight. Here, we show golden eagle (*Aquila chrysaetos*) migratory response to changing meteorological conditions as monitored by high-resolution telemetry. In contrast to expectations, responses to meteorological variability were stereotyped across the 10 individuals studied. Eagles reacted to increased wind speed by using more orographic lift and less thermal lift. Concomitantly, as use of thermals decreased, variation in flight speed and altitude also decreased. These results demonstrate how soaring migrant birds can minimize energetic expenditures, they show the context for avian decisions and choices of specific instantaneous flight mechanisms and they have important implications for design of bird-friendly wind energy.

Keywords: movement ecology; flight behaviour; migration; flight response; high-resolution GPS–GSM telemetry

1. INTRODUCTION

Characterizing flight behaviour is essential to understanding the evolution of flight strategies. This is especially relevant for large-bodied birds that undertake long-distance migration and that are closest to the maximum possible size for flighted species. Exploration of the link between demography and movement strategies is fundamental to the rapidly emerging field of movement ecology [1]. Because survival can depend on flight strategy, strong selective pressures are expected for energy minimization tactics in response to weather and topography. However, the minute-by-minute flight mechanisms birds use in response to changing environments are largely unknown. This is because study of flight strategies of birds requires precise spatial data collected at extremely high temporal frequencies [2–4]. Until recently, research in this area was constrained by limitations of data from short-duration tracking [4–6], infrequent GPS satellite telemetry [7] or GPS data loggers requiring manual download [3,8–10]. Because large, wary and sparsely distributed birds of prey are difficult to recapture for data logger retrieval and impractical to track over long distances with gliders, there have historically been no tools useful to study the in-flight micro-scale decisions birds make over long distances.

We used global positioning system–global system for mobile communications (GPS–GSM) telemetry units we designed to collect and send high-resolution locational data on migrating birds. The data collected have high-applied conservation and biological value because of the rapid growth of wind energy along migration routes and the known rarity and susceptibility of this species to collision with industrial wind turbines [11]. They also demonstrate the utility of integrating new data-collection techniques with standard environmental datasets.

We evaluated golden eagle (*Aquila chrysaetos*) flight response to changing meteorological conditions during migration. Our work focuses on variation in flight mode, characterized by flight altitude and changes in flight altitude in response to changes in wind speed (WS) and on characterization of previously undescribed aspects of flight behaviour, especially speed in specific behaviours and flight modes. Other studies predict individually distinct responses to variable environments [2]; our study is the first to quantitatively evaluate this prediction. These results also demonstrate how soaring migrant birds minimize energetic expenditures and show the context for avian decisions and choices of specific minute-by-minute flight mechanisms.

2. MATERIAL AND METHODS

We tracked spring migration of golden eagles through a topographically diverse region of the central Appalachian Mountains of North America. Ten eagles were trapped with cannon nets in winters 2008–2009 and 2009–2010, and outfitted with CTT-1100 solar-recharged GPS–GSM telemetry units weighing approximately 95 g (Cellular Tracking Technologies, LLC). Eagles weighed 3370–5120 g, and transmitter weight was between 1.9 and 2.8 per cent of body weight. Tested GPS horizontal precision was less than or equal to 2.5 m, and vertical precision was less than or equal to 22.5 m (M. Lauzone & T. Miller 2011, unpublished data). Locational data were collected at 30–60 s intervals for birds moving between 39.5° and 42.5° north latitude. When the bird was not moving or was outside of the high-resolution area, data were collected at 15 min intervals. Units were automatically shut off between nautical sunset and sunrise. Specific information collected included latitude, longitude, horizontal dilution of precision, fix quality, course over ground, speed and altitude. When birds were out of the GSM coverage area, data were stored and transmitted when GSM service was encountered. All data were transferred over GSM networks to a server, downloaded and imported into a geodatabase for analysis.

We described flight-behaviour patterns by the speed of movement, the depth of vertical airspace used (height band, HB) and

Received 16 April 2012
Accepted 26 April 2012

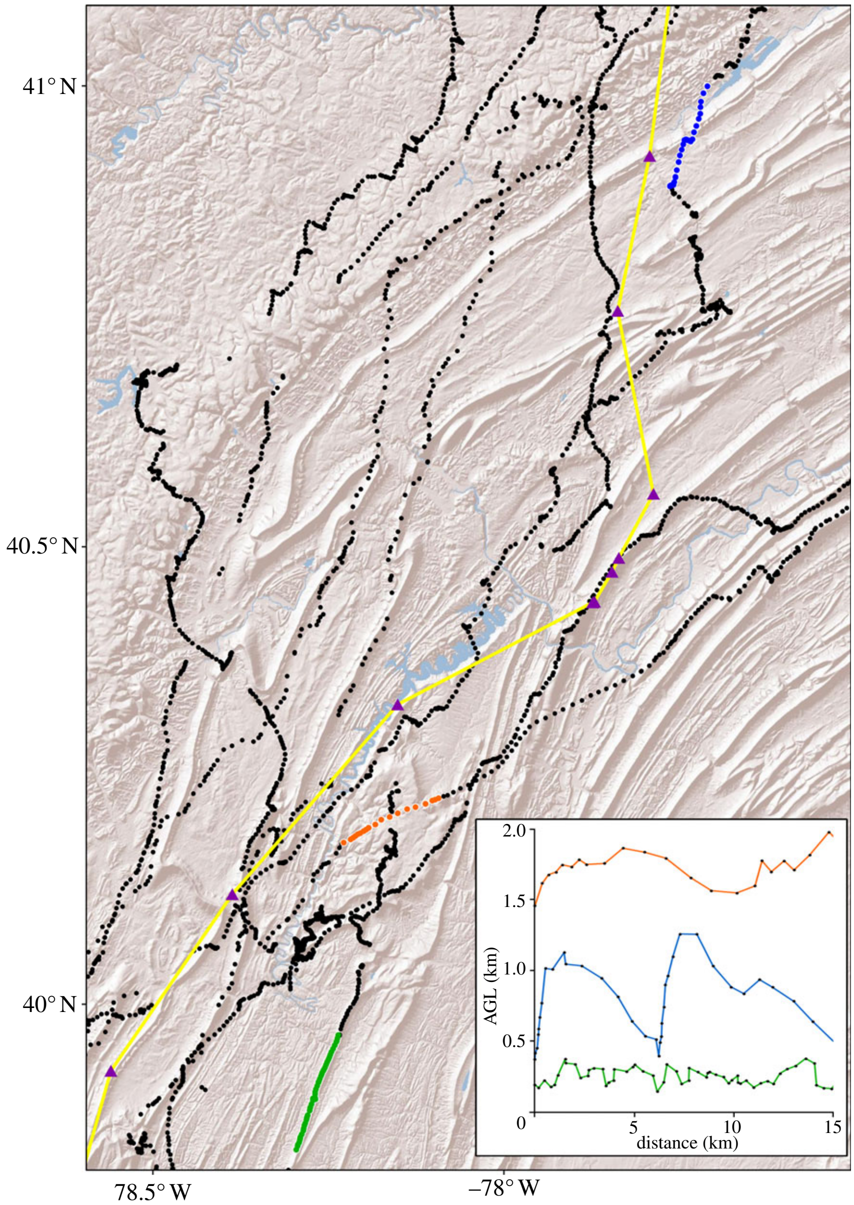

Figure 1. Northbound high-resolution telemetry data from golden eagles migrating through the Appalachian Mountains, PA, USA in 2009–2010. Tracking data are from 30 to 60 s GSM–GPS telemetry (circles) and, for comparison, from a single GPS-Argos backpack unit collecting hourly data (triangles connected with lines) on a shaded relief map [18]. Coloured segments depicted 15 km sections showing flight behaviours of three eagles. These correspond to the vertical profiles in inset. Shown here, from bottom to top, are an eagle using orographic lift (line 1; HB = 204 m, WS = 12.75 $\mathrm{m\ s^{-1}}$), an eagle using thermals (line 2; HB = 832 m, WS = 3.97 $\mathrm{m\ s^{-1}}$) and an eagle using a thermal street [14] (line 3; HB = 504 m, WS = 5.14 $\mathrm{m\ s^{-1}}$).

altitude above-ground level (AGL). HB was defined as the difference between the maximum and the minimum altitude over 6 h, 2.5 × 2.5° NCEP weather blocks [12]. Large HBs are indicative of thermal soaring, whereas narrow HBs suggest low-altitude slope soaring or high-altitude use of thermal streets or lee waves [13–15]. WS was measured in $\mathrm{m\ s^{-1}}$ at 925 mb (approx. 600 m a.s.l.). We calculated altitude AGL at each data point by overlaying GPS data on a 10 m elevation dataset [16] and subtracting recorded flight altitude above sea level from baseline ground elevation. Sink and climb rates were calculated based on the altitudinal and time differences between sequential data points less than 60 s apart.

We evaluated the effects of WS on 10 eagles' HB and AGL averaged over 6 h weather blocks using linear mixed models (PROC MIXED; SAS [17]). Golden eagles were treated as random effects and nested within a fixed year effect. Other explanatory variables included day of year, total number of observations during the 6 h period of interest and interaction terms for WS × day and WS × year. We used residual diagnostics to evaluate the degree to which model assumptions were met. Finally, we manually classified flight behaviour of five eagles and we report trends in their mean climb rate and mean flight speeds when in thermals and when using orographic lift. Because of concerns over statistical assumptions regarding normality, we used a non-parametric Wilcoxon signed-rank test to analyse these data. Because prospective investigation suggested that, given our sample size, the minimum possible significance level this test could report was 0.0625, we used $\alpha = 0.1$.

3. RESULTS

Between 06–30 March 2009 and 09 March–30 April 2010 all birds crossed the 333 km high-resolution area in 5.2 ± 0.96 (±s.e.) days. For the birds whose units functioned continuously during this period ($n = 3$), this involved 740.4 ± 137.4 minutes of flight. During this period, we collected 1178 ± 180 GPS data points per bird ($n = 10$ eagles; range: 513–2458). Of these, 905 ± 140 (78 ± 4%) were collected while in-flight (range: 337–1840; figure 1). This translated to

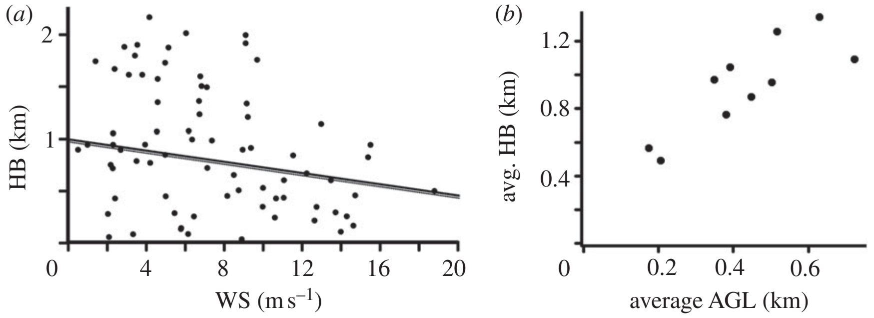

Figure 2. Response in eagle flight behaviour, measured as height band (max–min flight altitude; HB) to variation in (*a*) wind speed (WS); and (*b*) average above-ground altitude (AGL) of 10 golden eagles migrating through the central Appalachians in 2009–2010. Eagles responded to increases in WS by decreasing altitudinal variation in flight. Likewise, as AGL increased, HB also increased. WS was determined from NCEP weather blocks [12]. Regression lines are from 2009 data (solid) and 2010 data (dotted).

50.82 ± 5.53 in-flight GPS data points per hour per bird, far in excess of that provided by satellite-based telemetry systems (figure 1).

Our models show that in greater winds, eagles used thermals less frequently (HB decreased; $F_{1,68} = 5.04$; $p = 0.03$; figure 2*a*) and flew at lower altitudes ($F_{1,68} = 5.19$; $p = 0.03$). For each 1 m s^{-1} increase in WS, HB decreased by 26.95 m (95% CI = −50.92, −2.99 and AGL decreased by 20.39 m 95% CI = −38.24, −2.53). Neither AGL nor HB was impacted by day of the year (AGL: $F_{1,68} = 0.19$; $p = 0.67$; HB: $F_{1,68} = 1.18$; $p = 0.28$) or year (AGL: $F_{1,68} = 1.06$; $p = 0.31$; HB: $F_{1,68} = 0.04$; $p = 0.84$), and there was no evidence for an interaction between WS and year (HB: $F_{1,66} = 0.16$; $p = 0.69$; AGL: $F_{1,66} = 0.18$; $p = 0.68$) or day (HB: $F_{1,66} = 0.25$; $p = 0.62$; AGL: $F_{1,66} = 0.13$; $p = 0.72$). An overall model comparison test suggested interaction terms were not required (HB: $F_{2,66} = 0.49$; $p = 0.61$; AGL: $F_{2,66} = 0.38$; $p = 0.69$). HB and AGL were positively and linearly correlated ($r = 0.83$; $t_8 = 4.19$, $p = 0.003$; figure 2*b*); this is expected of birds that use orographic lift and thermals, but inconsistent with birds that use thermal streets [14] or lee waves [15] for flight. A likelihood ratio test on the restricted maximum-likelihood estimate of the variance components indicated that bird-to-bird variation in both responses was not significantly different from zero (HB: estimated $\sigma^2_{\text{bird}} = 0$; AGL estimated $\sigma^2_{\text{bird}} = 6891$; $p = 0.5$). Comparison of Akaike's Information Criterion values did not suggest temporal correlation in the errors and thus we assumed an independently and identically distributed model for the error covariance. Other covariance structures (spatial linear, spatial exponential, spatial power, spatial spherical and spatial Gaussian) were considered and eliminated.

The high-resolution data provided previously unknown detail about a suite of flight characteristics and behavioural patterns (figure 1). Average in-flight AGL of five migrating golden eagles measured at 30–60 s intervals was 965 ± 54 m (mean range 200–2568 m). Sink rate (1.49 ± 0.14 m s^{-1}) of flying eagles was generally greater than their climb rate (1.35 ± 0.15 m s^{-1}). For birds using orographic lift (figure 1*a*, line 1), mean sink and climb rates were similar (0.94 ± 0.11 versus 1.04 ± .06 m s^{-1}; $V = 11$, $p = 0.44$), but mean ground speed during sink was different from during a climb (12.57 ± 1.08 versus 11.28 ± 0.78 m s^{-1}; $V = 0$, $p = 0.0625$). Likewise, for birds using thermal lift (figure 1*a*, line 2), mean climb and sink rates were also similar (1.76 ± 0.19 versus 1.91 ± 0.13 m s^{-1}; $V = 4$, $p = 0.44$), but mean ground speeds were dramatically faster when descending than when ascending (17.56 ± 1.35 versus 10.17 ± 0.74 m s^{-1}; $V = 0$, $p = 0.0625$).

4. DISCUSSION

Telemetered eagles exhibited stereotyped flight behaviour in response to variable weather conditions. All 10 birds tracked with high-frequency GSP–GSM telemetry responded to increases in WS by changing from thermalling to orographic flight, all the while using available lift to subsidize the energetic costs of migration. In addition, all 10 birds both moved and responded to changes in wind availability in similar manners. The high-resolution data presented address a variety of previously unanswerable fine scale biological, behavioural and ecological questions. For example, we provide, for the first time, detailed measurements of flight speed of actively migrating individual birds engaged in different types of behavioural patterns, validating both observational data and radar studies [19–21]. At the scale of this analysis, we observed no temporal trends in flight patterns. This contrasts with anecdotal observation of changes in flight behaviour with seasonality and suggests novel avenues for future investigation.

With increasing demand for wind energy, volant wildlife require innovative conservation strategies based on understanding the behavioural patterns that put them at risk. The high-resolution data we collected showed that as WS increase, eagles fly lower and used less vertical air space, implying the use of orographic lift and increased risk from industrial scale wind energy development on ridges. Additionally, because golden eagles flight behaviour is so stereotyped, interactions of topography and weather conditions can identify times and locations for orographic lift by all eagles, leading to improved population-level risk analysis. This should lead to development of multiple eagle-safe avenues for prevention of collision, through improved siting of new facilities or operational mitigation at existing ones.

Funding was received from PASWG (grants nos. T-12, T47-R-1) USDoE (grant no. DE-EE0003538) and author's organizations.

1 Nathan, R. 2008 An emerging movement ecology paradigm. *Proc. Natl Acad. Sci. USA* **105**, 19 050–19 051. (doi:10.1073/pnas.0808918105)

2 Kerlinger, P. 1989 *Flight strategies of migrating hawks.* Chicago, IL: University of Chicago Press.

3 Nagy, M., Akos, Z., Biro, D. & Vicsek, T. 2010 Hierarchical group dynamics in pigeon flocks. *Nature* **464**, 890–893. (doi:10.1038/nature08891)

4 Pennycuick, C. J. 1972 Soaring behaviour and performance of some east African birds, observed from a motor-glider. *Ibis* **114**, 178–218. (doi:10.1111/j.1474-919X.1972.tb02603.x)

5 Ákos, Z., Nagy, M. & Vicsek, T. 2008 Comparing bird and human soaring strategies. *Proc. Natl Acad. Sci. USA* **105**, 4139–4143. (doi:10.1073/pnas.0707711105)

6 Leshem, Y. & Yom-Tov, Y. 1996 The use of thermals by soaring migrants. *Ibis* **138**, 667–674. (doi:10.1111/j.1474-919x.1996.tb04539.x.)

7 Mandel, J. T., Bildstein, K. L., Bohrer, G. & Winkler, D. W. 2008 Movement ecology of migration in turkey vultures. *Proc. Natl Acad. Sci. USA* **105**, 19 102–19 107. (doi:10.1073/pnas.0801789105)

8 Dell'Ariccia, G., Dell'Omo, G., Wolfer, D. P. & H.-P., Lipp, 2008 Flock flying improves pigeons' homing: GPS track analysis of individual flyers versus small groups. *Anim. Behav.* **76**, 1165–1172. (doi:10.1016/j.anbehav.2008.05.022)

9 Biro, D., Freeman, R., Meade, J., Roberts, S. & Guilford, T. 2007 Pigeons combine compass and landmark guidance in familiar route navigation. *Proc. Natl Acad. Sci. USA* **104**, 7471–7476. (doi:10.1073/pnas.0701575104)

10 Sapir, N., Wikelski, M., McCue, M. D., Pinshow, B. & Nathan, R. 2010 Flight modes in migrating European bee-eaters: heart rate may indicate low metabolic rate during soaring and gliding. *PLoS ONE* **5**, e13956. (doi:10.1371/journal.pone.0013956)

11 Bell, D. A. & Smallwood, K. S. 2010 Birds of prey remain at risk. *Science* **330**, 913. (doi:10.1126/science.330.6006.913-a)

12 Kalnay, E. *et al.* 1996 The NCEP/NCAR 40-year reanalysis project. *Bull. Am. Meteor. Soc.* **77**, 437–471. (doi:10.1175/1520-0477(1996)077<0437:TNYRP>2.0.CO;2)

13 Reichmann, H. 1978 *Cross-country soaring* (*Streckensegelflug*), 1st edn. Santa Monica, CA: Thomas Publications.

14 Pennycuick, C. J. 1998 Field observations of thermals and thermal streets, and the theory of cross-country soaring flight. *J. Avian Biol.* **29**, 33–43. (doi:10.2307/3677338)

15 Durran, D. R. 2003 Lee waves and mountain waves. In *Encyclopedia of atmospheric sciences* (eds J. R. Holton, J. Pyle & J. A. Curry), pp. 1161–1169. Amsterdam, The Netherlands: Elsevier Science Ltd.

16 U.S. Geologic Survey. *National elevation dataset*. Sioux Falls, SD: Earth Science Information Center.

17 SAS. Cary, NC: SAS Institute Inc.

18 World Shaded Relief 2009. See http://services.arcgisonline.com/arcgis/services (accessed 10 October 2011).

19 Kerlinger, P. & Moore, F. R. 1989 Atmospheric structure and avian migration. In *Current ornithology*, vol. 6 (ed. D. M. Power), pp. 109–141. New York, NY: Plenum Press.

20 Bruderer, B. 1997 The study of bird migration by radar. *Naturwissenschaften* **84**, 45–54. (doi:10.1007/s001140050348)

21 Spaar, R. & Bruderer, B. 1997 Optimal flight behavior of soaring migrants: a case study of migrating steppe buzzards, *Buteo buteo vulpinus*. *Behav. Ecol* **8**, 288–297. (doi:10.1093/beheco/8.3.288)