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Author for correspondence:

Todd E. Katzner

e-mail: tkatzner@usgs.gov

[†]Present address: US Geological Survey, Forest and Rangeland Ecosystem Science Center, 970 Lusk Street, Boise, ID 83706, USA.

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Use of multiple modes of flight subsidy by a soaring terrestrial bird, the golden eagle *Aquila chrysaetos*, when on migration

Todd E. Katzner^{1,2,†}, Philip J. Turk³, Adam E. Duerr¹, Tricia A. Miller¹, Michael J. Lanzone⁴, Jeff L. Cooper⁵, David Brandes⁶, Junior A. Tremblay⁷ and Jérôme Lemaître⁸

¹Division of Forestry and Natural Resources, West Virginia University, Morgantown, WV 26506, USA

²USDA Forest Service, Northern Research Station, Parsons, WV 26287, USA

³Department of Statistics, Colorado State University, Fort Collins, CO 80523, USA

⁴Cellular Tracking Technologies, LLC, 2405 North Center Avenue, Somerset, PA 15501, USA

⁵Virginia Department of Game and Inland Fisheries, Fredericksburg, VA 22401, USA

⁶Department of Civil and Environmental Engineering, Lafayette College, Easton, PA 18042, USA

⁷Environment Canada, Quebec City, Quebec, Canada G1J 0C3

⁸Ministère des Forêts, de la Faune et des Parcs, Québec, Québec, Canada G1S 4X4

Large birds regularly use updrafts to subsidize flight. Although most research on soaring bird flight has focused on use of thermal updrafts, there is evidence suggesting that many species are likely to use multiple modes of subsidy. We tested the degree to which a large soaring species uses multiple modes of subsidy to provide insights into the decision-making that underlies flight behaviour. We statistically classified more than 22 000 global positioning satellite–global system for mobile communications telemetry points collected at 30-s intervals to identify the type of subsidized flight used by 32 migrating golden eagles during spring in eastern North America. Eagles used subsidized flight on 87% of their journey. They spent $41.9\% \pm 1.5$ ($\bar{x} \pm \text{s.e.m.}$, range: 18–56%) of their subsidized northbound migration using thermal soaring, $45.2\% \pm 2.1$ (12–65%) of time gliding between thermals, and $12.9\% \pm 2.2$ (1–55%) of time using orographic updrafts. Golden eagles responded to the variable local-scale meteorological events they encountered by switching flight behaviour to take advantage of multiple modes of subsidy. Orographic soaring occurred more frequently in morning and evening, earlier in the migration season, and when crosswinds and tail winds were greatest. Switching between flight modes allowed migration for relatively longer periods each day and frequent switching behaviour has implications for a better understanding of avian flight behaviour and of the evolution of use of subsidy in flight.

1. Introduction

Animals fly by generating their own lift (flapping flight or gliding) or by using subsidy to promote forward progress [1,2]. Use of updrafts, vertical movements of air, to subsidize flight is widespread across taxa [3,4], but is especially characteristic of large birds such as vultures, eagles and albatrosses. Because of their body size and the strict power requirements of flapping flight, these species are more constrained by the availability of environmental updraft than are smaller species. However, although vultures, eagles and albatrosses are all soaring birds, they also have different wing morphologies and flight behaviours, and thus may subsidize their soaring flight differently [5].

Updrafts sufficient to subsidize flight are not uniform over land and are determined by meteorological conditions, landform and land cover [6]. Updrafts primarily are generated by energy transfer from surface to air (thermals) or by air currents deflected by physical obstructions—topography, trees or buildings

(so-called orographic updraft). A third form of subsidy occurs in zones of high wind shear or gradients. In such places, so-called dynamic soaring (or gust soaring; [7,8]) is used by birds to gain altitude by flying across a wind-speed gradient. Although gust soaring is thought to be most heavily used by seabirds to subsidize flight over water, it also occurs over land, almost certainly more frequently than is generally recognized [9].

In spite of the diversity of updrafts available, most previous work on the use of subsidy by birds in terrestrial systems has simplified the aerocape by focusing on thermal soaring in flat regions, to the exclusion of other mechanisms (e.g. [10–12]; but see [13] for an exception). However, it is long established that many species use multiple modes of subsidized flight [14]. The exclusive focus on a single uplift mode is useful because it simplifies models, but it comes at a cost. As a consequence of this focus, the reasons why birds might use different types of updrafts and the potential evolutionary implications of switching between these behaviours remain poorly understood [15].

Most previous research has keyed in exclusively on thermal soaring in part because it has been nearly impossible to track specific movements of multiple individual wild animals over extended periods of space and time and in part because it is difficult to use accelerometry alone to distinguish different types of soaring flight [16]. If individuals were tracked in great detail for extended periods, predictions could be tested about different potential models for in-flight decision-making by birds. For example, large birds flying in systems where one type of updraft predominates may exclusively use only one type of subsidy. This flight response is exemplified by long- and narrow-winged seabirds that use dynamic (or gust) soaring almost to the complete exclusion of other modes of subsidized flight [7]. Similarly, other large soaring birds apparently show a preference for different subsidized flight modes—published reports suggest that broader-winged *Gyps* vultures and frigatebirds (family Fregatidae) are near exclusive users of thermal updrafts [17,18].

In reality though, large birds flying in spatially or temporally variable environments are likely to take advantage of multiple modes of subsidy. This strategy might be especially advantageous when used by a highly migratory species that encounters great environmental variability throughout the annual cycle and that would require use of optimal and suboptimal types of updraft to balance time versus energy trade-offs [19]. In such a situation, we would expect soaring birds regularly to switch among different modes of subsidy in a spatially and temporally context-dependent manner closely tied to their availability. In spite of the prevalence of research focused on the use of a single mode of subsidy (thermal updrafts), this type of behaviour seems most logical for large soaring birds in variable environments.

We tested the degree to which a large soaring species, the golden eagle, switches between modes of subsidy. Golden eagles are a useful model for this study because they rely heavily on flight subsidy when migrating across highly variable terrain in eastern North America. Local observation collected since the 1930s at hawk watches across the Appalachian Mountains suggests that these and other late autumn migrating raptors make frequent use of orographic updrafts when migrating [15,20]. However, more recent work posited strong energetic benefit for the use of thermal uplift [19] and a tendency to travel in weather that promotes thermal uplift development [21].

We tracked migratory movements of eagles with telemetry systems designed to collect GPS locations so frequently as to

allow us to interpret flight behaviour. This is the first time that flight modes of large numbers of migratory terrestrial birds have been characterized in precise detail over extremely long distances (small numbers of individuals have been followed with gliders; [1]). Our approach to analyses of these data involved four steps, as follows: (i) we created a statistical framework to distinguish the characteristics of different subsidized flight modes; then (ii) we evaluated the amount of time in which different subsidized flight modes were used on migration (e.g. *how frequently* subsidy is used); then, (iii) we compared the degree to which different subsidized flight modes were used by eagles (e.g. *relative use* of different types of subsidy); and finally (iv) we measured how the use of different subsidized flight modes varied in response to spatial and temporal variation in availability of updrafts (e.g. *why* different modes of subsidy are used). Finally, we interpret these data to provide insights into animal decision-making and to suggest routes for exploration into the evolution of flight behaviour.

2. Methods

We used a multi-step process to statistically classify GPS telemetry data from eagles. Once tracking data were collected, we first manually classified a subset of them into flight modes. Subsequent to that, we decomposed the raw data to develop, for each GPS datum, a set of characteristics associated with position, speed, directionality, etc. We then used a set of parametric generalized linear mixed models to understand characteristics relevant to the manually described flight classes. We removed from consideration characteristics for which *F*-tests were not statistically significant and we input the remaining characteristics into a non-parametric weighted-*k* nearest-neighbour (wkNN) analysis of the classified flight mode. Once a final wkNN model was developed, we used that model to classify the remaining (non-manually classified) flight data. Finally, we used a linear model to understand how modelled flight classes varied with temporal (hour, month) and environmental (solar radiation, winds) parameters. A detailed description of these steps follows.

2.1. Field data collection

Golden eagles were captured [6,19,21,22] during winter and spring of 2008–2011 in the central Appalachians region of eastern North America and outfitted with solar-recharged global positioning satellite–global system for mobile communications (GPS–GSM) telemetry units weighing approximately 80–95 g (less than 3% of body mass; Cellular Tracking Technologies, LLC, Somerset, PA; technical specifications for the telemetry unit are available at www.celltracktech.com). 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 [22]. Between 39.5° and 42.5° north latitude and during daylight hours, the GPS collected data on bird movements at 30–60 s intervals (this is as rapidly as the technology would allow; figure 1). Each GPS fix contained information on latitude, longitude, horizontal dilution of precision, fix quality, course over ground, speed and altitude. All data were archived and sent over the GSM network approximately once per day. When birds were outside of GSM coverage, data were stored until the unit was able to register on and send over a GSM network.

2.2. Management and interpretation of GPS telemetry data

Telemetry data were downloaded from a web server and imported into a geodatabase (ARCGIS 10) and post-processed to remove errors and two-dimensional or low-quality fixes (horizontal dilution

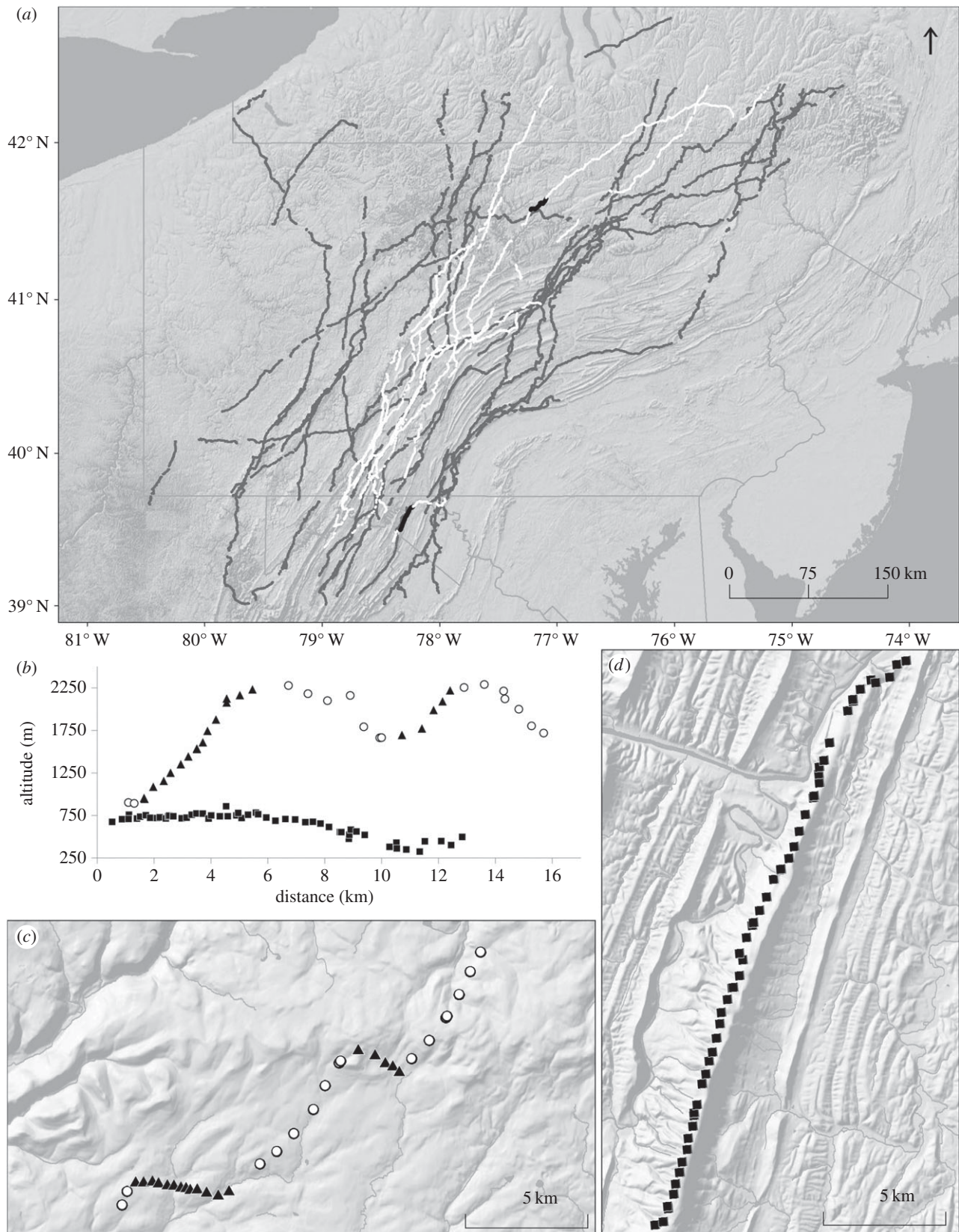


Figure 1. Maps of eagle migration through the central Appalachian region show flight behaviour in the context of topography and flight classification. Part (a) shows tracks of all 32 eagles monitored with 30-s GPS telemetry; tracks in white were those manually classified to flight mode, others were statistically classified to flight mode; track segments in black are shown in detail and against topography in parts (c,d); (b) shows flight altitude profiles of eagles engaged in a thermal soar (filled triangles) and glide (open circles; top profile and part c) and using orographic updrafts (filled squares; bottom profile and part d).

of precision (HDOP) > 10). Flight tracks were then plotted over topographic maps, allowing interpretation of behaviours in the context of variation in topography, landform and land cover (figure 1).

A single expert observer (T.A.M.) manually classified a subset of the eagle flight tracks with a two-step process [19,22]. First, data

points that indicated perching or other non-flying behaviour (i.e. speed less than 3 knots (1.5 m s^{-1}), and altitude above ground level (AGL) < 30 m) were excluded from subsequent analyses, as were GPS data we interpreted as corresponding to non-migratory behaviours (potential other behaviours we did not classify include

Table 1. Data types collected (first three variables) or interpreted (remainder) from high-frequency GPS–GSM telemetry systems on 32 golden eagles migrating through the central Appalachian Mountains. More details on data types are provided in the electronic supplementary material, S1.

variable name	variable description	mathematical expression
bird	bird (random effect)	
day of the year	day of the year, as measured by GPS (fixed effect)	
hour	hour of the day	
cumulative time	accumulated time to point n , 0 = first point in day	$T_{\text{cum}} = T_n - T_0$
northness course	northing component of the course measured by GPS	hN (on $[-1, 1]$)
eastness course	easting component of the course measured by GPS	hE (on $[-1, 1]$)
northness bearing	northness component of the bearing, estimated by the direction between points n and $n - 1$	bN (on $[-1, 1]$)
eastness bearing	eastness component of the bearing, estimated by the direction between points n and $n - 1$	bE (on $[-1, 1]$)
speed between points	distance between points $n - 1$ and n divided by change in time between points	$S_n = ([x_n - x_{n-1}]^2 + [y_n - y_{n-1}]^2)^{1/2} / (T_n - T_{n-1})$
vertical rate	change in GPS-recorded altitude above sea level between point n and $n - 1$ divided by change in time at T_n and T_{n-1}	$VR = (\text{alt}_n - \text{alt}_{n-1}) / (T_n - T_{n-1})$
absolute vertical rate	absolute value of VR	$\text{absVR} = VR $
change in speed	change in speed between points n and $n - 1$	$\Delta S_n = S_n - S_{n-1}$
absolute turning angle	absolute value of the change in bearing at time n	TA (on $[0, 180]$)
projected distance	projected distance travelled between points n and $n - 1$	$P = (T_n - T_{n-1}) \times S_{n-1}$
actual versus projected distance	Euclidean distance travelled between time $n - 1$ and n minus P	$AP = ([x_n - x_{n-1}]^2 + [y_n - y_{n-1}]^2)^{1/2} - P$
avg. change in speed	average change in speed between points n and $n - 1$	$S_{n-\text{avg}} = S_n - S_{n-1}/2$
altitude above ground level (AGL)	altitude above sea level (ASL, from GPS) minus ground elevation	$AGL = ASL - \text{ground elevation}$

hunting and stopovers). Second, all flight points were classified into one of four flight modes. These four flight modes included three components of subsidized flight—use of thermal soaring (T) and gliding (G) and use of orographic updrafts (O)—and one unknown class (U), including all other data (figure 1). Flight classification was based on identification of pattern among data points that is described in greater detail elsewhere [19,22] and that ignores the small proportion of time when these birds probably used flapping flight. As an example, when flight altitude consistently increased without following specific topographical patterns and the bird drifted with the prevailing wind, we identified flight as thermal soaring; gliding is the complement of this behaviour (figure 1*b,c*). When flight altitude stayed relatively constant and birds followed ridge topography, we identified flight as use of orographic updraft (figure 1*b,d*).

We decomposed all flight data points into a series of 17 measured and extrapolated characteristics derived from the post-processed flight data points collected by the GPS–GSM telemetry systems (table 1 and electronic supplementary material, S1). Three of these characteristics were measured directly by the GPS (bird, day of the year, hour of the day). The remaining data required processing to calculate. None, except AGL, required external data to calculate. Detailed descriptions of each of these 17 characteristics are provided in the electronic supplementary material, S1.

2.3. Statistical classification of flight modes

We used the manually classified flight data to train a statistical model to classify flight behaviour with a two-step process. First, we used a parametric generalized linear mixed model (GLMM)

to model subsidized flight classes (v. 9.3 of the SAS System for Unix). The GLMM approach let us evaluate both marginal predictions (those based only on fixed effects, as is typical in linear regression) as well as conditional predictions (those that include random effects as well as the fixed effects). We modelled three subsidized flight classes (G, O, T) and ignored data points classified as unknown (U). We did this because unknown points included occasions when birds were engaged in subsidized flight as well as other types of flight that we could not easily classify (flapping, etc.), and thus their inclusion would have violated statistical assumptions of independent classes and dramatically lessened the performance of the model. A multi-nomial regression model was used with a generalized logit link function with birds classified as random effects and the 16 other standardized predictors noted above (table 1).

Initial collinearity diagnostics of condition indices [23] showed no evidence of multi-collinearity among the predictors used in the fixed design matrix of our GLMM. We then evaluated type III tests of fixed effects for each of the 16 predictors and, in cases where F -tests were not statistically significant ($\alpha = 0.05$), we removed those fixed effects from future consideration. To evaluate potential interactions, we re-fitted the GLMM including the four two-way interaction terms we thought would be most likely to be relevant to the model. Those were between AGL and four parameters that we expected to covary with AGL—northness course, day of the year, hour of the day and speed between points.

Our second step involved using the remaining standardized predictors (those for which F -tests were statistically significant) in a wkNN analysis (R v. 2.15.2, package *knn*; [24,25]) to model

the classified flight mode. The advantage of wkNN is that the classification is obtained via cross-validation, thereby avoiding bias imparted by using the observed data to generate a fitted model and then using the same fitted model to classify the data.

The classified dataset was divided at random into two parts (33%/66%), and we used the larger (training) dataset to cross-validate the observations of the smaller (validation) dataset. Cross-validation used 50 random 33%/66% splits and the mean and standard error of classification accuracy over these splits allowed us to assess overall classification accuracy. Bird and year were not used in the wkNN model as they would have been treated as 'fixed' factors in the multi-nomial GLMM and the inclusion of these factors appeared to degrade model classification accuracy. As a consequence, predictions from this analysis only use fixed effects (i.e. they are marginal predictions). We simulated a range of kernel sizes and values of k and q , over the 50 random splits described above, to optimize classification accuracy.

Third, to measure minimum classification accuracy, we used the optimized wkNN model to obtain predicted flight behaviours for a validation set of unclassified birds. In this case, the manually classified data were the training set and the data in the validation set (a random sample of 200 GPS points) were processed by removal of all 'perching' points, but leaving points that would be classified as T, O, G and U. We then compared the classified validation data points with predicted (modelled) flight classes to assess model classification accuracy. Because the model does not predict unknown flight behaviour (U), this is a minimum accuracy assessment.

Fourth, we used the optimized wkNN model to obtain predicted flight behaviours for all data points. We then used these classified flight data to evaluate the degree to which subsidized flight was used on migration and to understand the variable use of different modes of subsidized flight.

2.4. Characterizing differences among flight modes

To characterize and distinguish between flight modes, we used kernel-weighted within-neighbourhood distances to construct normalized probabilities of flight class selection, one for each of the three flight modes. We then used these three-dimensional vectors of probabilities to construct log-ratio response data for a subsequent linear mixed model analysis. This compositional analysis [26] assumes that a bird is equally likely to engage in any one of the three possible flight classes at any time point. As a consequence, we were able to model the natural logarithm of the probability associated with a flight mode divided by the probability associated with a reference flight class. For each of the resultant three models (one for each pair of flight classes, G versus O, G versus T, O versus T), we analysed those time points where one of the two flight classes used in the log-ratio response was the predicted flight mode from wkNN. The model contained random bird effects and all predictors used in the wkNN classification model (those identified as significant in the initial GLMM). We used 'sandwich' estimation to compute the estimated covariance of the mixed effects parameter estimates. Residual diagnostics were used to verify model assumptions and outlier speed values (more than 50 m s^{-1}) were removed from consideration. Finally, we computed a mixed model r^2 with restricted maximum-likelihood (REML) and Kenward–Roger fixed-effects standard errors to assess variation in response captured by the fixed effects.

2.5. Testing for variation in flight behaviour

To understand how flight behaviour responded to spatial and temporal variation in the availability of updrafts, we evaluated daily and seasonal cycles in the use of subsidized flight. Our models assumed that the proportion of time that a bird spent using orographic updrafts was inversely proportional to the proportion of time that it spent thermalling and gliding (using thermal updraft).

Thus, by modelling the proportion of time spent in orographic updrafts as a response to temporal and environmental parameters, we are able to understand the binary response of eagles to changes in the environment that birds experience. To model these behaviours, we used generalized estimating equations with a binomial response distribution, a logit link function and empirical (sandwich) fixed-effects estimates (PROC GLIMMIX, SAS v. 9.3).

We focused analyses on external parameters predicted to impact flight response of soaring migrants, including two binned temporal parameters (month of year and hour of the day) and three binned environmental parameters (downward solar radiation (in bins of 100 W m^{-2}), east-to-west wind vector (uwnd), and north-to-south wind vector (vwnd; both in bins of 2 m s^{-1})). Weather variables came from the National Centers for Environmental Prediction/National Center for Atmospheric Research Reanalysis II dataset [27]. We used the RNCPE package [28] in R (R Core Team 2012) to interpolate surface-level weather conditions at each eagle location. We used the east-to-west wind vector (uwnd) as a proxy for orographic updraft, because these winds are perpendicular to the general direction of topography and to migration (crosswinds), and the north-to-south wind vector (vwnd) to represent winds travelling approximately parallel to the general direction of migration (positive values = tailwinds and negative values = headwinds). Comparison of these external parameters is useful, because none are included as predictors in either the GLMM or wkNN classification models.

3. Results

3.1. Flight data

We collected 22 252 GPS data points at 30-s intervals from 32 golden eagles ($\bar{x} = 695 \pm 586$ points per bird ($\pm \text{s.d.}$), range = 54–2260 points per bird) migrating through our study area from 15 February to 18 May in the years 2009 and 2012 (details on the number of records per bird and age and sex can be found in electronic supplementary material, S2). Average daily flight speed was $48.1 \pm 1.1 \text{ km h}^{-1}$, and eagles spent from 2 to 14 days within the study area (details on number of days and track length are in the electronic supplementary material, S3).

We manually classified 5733 data points generated from 13 of these eagles into the four classes described in the methods (G, O, T and U). We identified golden eagle use of subsidized flight in 87% of data points. Of the total number of points manually classified, we identified 2114 (36%) in which the eagle used thermals to subsidize flight (T), 2211 (39%) in which the eagle subsidized flight by gliding from a thermal (G) and 683 (12%) in which the eagle used orographic updrafts to subsidize flight (O). We were unable to classify manually the flight behaviour of an additional 725 (13%) data points; these were U. A large subset (86%) of these manually classified data points were complete cases in which all fixed effects could be calculated and used in subsequent GLMM and wkNN analyses (table 2).

3.2. Choosing fixed effects

Of the 16 fixed effects describing flight characteristics, the GLMM suggested that 13 were important in determining model outcomes (table 3). The non-significant parameters ($p > 0.05$) included the eastness component of the course, the projected distance and the average change in speed. Upon model convergence, we obtained bird variance component estimates on the logit scale of 1.026 (s.e. ± 0.291) and

Table 2. Confusion matrix showing classification accuracy for manually classified versus modelled wkNN predictions of flight mode of migratory golden eagles in eastern North America. Manual classification by a single expert observer (T.A.M.). Flight behaviours are gliding (G), use of orographic updraft (O) and use of thermal updraft (T). Unknown points (U; see text) were not modelled and thus not included here.

expert classification	model classification			total
	G	O	T	
G	2088	27	69	2184
O	23	618	31	673
T	91	10	1996	2097
total	2202	655	2096	4954

Table 3. Type III tests for fixed effects from a generalized linear mixed model of flight behaviour of golden eagles on northbound migration, spring 2009–2012. *F*-statistics provide insight into the relative weight of the different parameters in the model. Parameters unimportant to the model are indicated in bold. Degrees of freedom = 24 847.

parameter	<i>F</i> -statistic	<i>p</i> -value
day of the year	3.22	0.040
northness course	21.04	<0.001
eastness course	1.59	0.204
hour	19.73	<0.001
cumulative time	29.50	<0.001
northness bearing	21.35	<0.001
eastness bearing	13.03	<0.001
speed between points	199.62	<0.001
vertical rate	33.46	<0.001
absolute vertical rate	9.28	<0.001
change in speed	60.03	<0.001
absolute turning angle	28.79	<0.001
projected distance	1.41	0.737
actual versus projected distance	58.31	<0.001
avg. change in speed	0.30	0.737
AGL	157.30	<0.001

0.930 (s.e. = 0.419) for orographic/gliding and thermalling/gliding, respectively. A maximum-likelihood-based likelihood ratio test on the variance components (no G-side random effects) was significant (*p*-value < 0.001) based on a simple mixture of central chi-squared distributions.

When we re-fitted the GLMM including the four two-way interaction terms noted in the methods, only the first two interactions (AGL and northness course, and AGL and day of the year) were significant to model outcomes.

3.3. Classification of flight mode

Based on outcomes from the hypothesis tests from the GLMM, three non-significant predictors were not included

in subsequent analyses. The remaining 13 standardized predictors were used in the wkNN classification model. We kept day of the year in the model, in spite of the fact that the *F*-statistic for this test was smaller than most of the others ($F = 3.22$, $p = 0.040$; table 3), because other analyses [21] suggest substantial differences in thermal availability as day of the year varies, as expected owing to increasing solar input as spring progresses.

In our initial pilot evaluation based on random splits of the manually classified dataset, maximum modelled classification accuracy of 0.806 (s.e. = 0.002) was achieved with a triangular kernel, $k = 14$ and $q = 1$. For comparison, when all the cases were used for both the training and the validation set, the classification rate was 0.949 (table 2). We also ran the wkNN model with the two significant interaction terms noted in §3.2. Their inclusion did not improve classification accuracy and thus the more parsimonious model (without interaction) was adopted.

Once the most effective wkNN model was established, we used that final model to classify the remaining 17 320 GPS data points collected from the other 19 eagles (i.e. we statistically classified those data points that had not been previously manually classified). Of the 200 validation data points we randomly sampled, 11 were not manually classifiable to a flight type (recorded as U). The classification accuracy for the remaining 189 data points was 0.714 (95% CI = 0.650, 0.779).

Classified flight data suggested that the 32 observed golden eagles spent from 18% to 56% ($\bar{x} = 41.9\% \pm 1.5$ (±s.e.)) of their northbound migratory transit subsidizing flight through thermal soaring, from 12% to 65% ($\bar{x} = 45.2\% \pm 2.1$) of their northbound migratory transit subsidizing flight by gliding, and from 1% to 55% ($\bar{x} = 12.9\% \pm 2.2$) of their migratory transit subsidizing flight with orographic updraft. These classified data included infrequent flapping flight and other flight behaviours (likely approx. 13% of the total time in flight; see §3.1) that our model was not trained to recognize.

3.4. Distinguishing between flight modes

Our linear mixed model analysis (§2.4) produced three models, one comparing gliding versus thermal soaring (G versus T), one comparing gliding versus orographic soaring (G versus O) and one comparing orographic versus thermal soaring (O versus T). The prevailing message that came from this analysis (described in detail below) is that AGL, flight speed, direction of travel and amount of turning are the key parameters that separate the three flight behaviours from each other.

Thermal soaring and gliding almost always were complements of each other; birds left thermals to enter into a glide and, when a glide was completed, birds often entered another thermal. Thus, when eagles subsidized flight, thermalling and gliding behaviour were more similar to each other than they were to orographic flight. Bird-to-bird variance in the G versus T model was 0.991, (s.e. = 0.281; $P[Z \geq 3.52] < 0.001$), whereas the error variance (σ^2) was 9.280. Thus, roughly 9.7% ($0.991/[9.280 + 0.991]$) of the variation in log-ratios in this compositional analysis was attributable to bird-to-bird differences, and the remainder was due to random variation. The mixed model r^2 statistic for this regression was 0.893 ($p < 0.001$), suggesting that 89% of the variation in the response can be explained by the 13 fixed effects.

The three characteristics that best separated these two flight modes were speed, turn angle and northness of course (G versus T; table 4 and figure 2). Thus, thermal soaring was slower, less linear and tended to be less unidirectional than gliding flight, which was faster, straighter and tended to be northbound. Although this is intuitive, because eagles move in a circular fashion as they rise in a thermal and they move in a more direct fashion while gliding, circling within a thermal is not necessarily evident at the 30-s temporal scale of our GPS measurements. The parameters least useful in distinguishing these flight behaviours (i.e. the parameters most similar among flight types) were AGL, day of the year, hour of the day, cumulative time, difference in speed between points, and eastness of bearing.

Exponentiating the estimated regression coefficient provides a wkNN-driven odds ratio showing the likelihood of a bird engaging in one behaviour over another. In this case, when all other predictors were held constant, the odds of a bird soaring in a thermal instead of gliding decreased by about 36% with every 1 ms^{-1} increase in speed, they increased by about 2% for every 1° increase in absolute turn angle and they decreased by about 83% for every one unit increase in northness of course.

Birds in orographic flight are predicted to behave dramatically differently from those in gliding flight. Bird-to-bird variance in the G versus O model was 3.6038 (s.e. = 0.9930; $P[Z \geq 3.63] < 0.001$), whereas the error variance (σ^2) was 9.494. Thus, roughly 27.5% of the variation in log-ratios in this compositional analysis is attributable to bird-to-bird differences, and the remainder is due to random variation. The mixed model r^2 statistic for this regression (proportion of variation explained by fixed effects) was 0.582 ($p < 0.001$).

Flight subsidized by orographic updrafts is distinctively different from that when gliding between thermals. The parameters that best distinguished between orographic flight and gliding flight were AGL and speed between points (G versus O; table 4 and figure 2). Thus, gliding flight was faster and higher than orographic flight. The parameters least useful in separating these flight modes were the vertical rate, the absolute vertical rate, the eastness bearing and the northness course. When all other predictors were held constant, the odds of a bird engaging in orographic soaring instead of gliding decreased by 6% with every 1 m increase in flight altitude and by 19% with every 1 ms^{-1} increase in speed.

Finally, birds in orographic flight should also appear dramatically different from those soaring in thermals. Bird-to-bird variance in the O versus T model was 4.173 (s.e. = 1.203; $P[Z \geq 3.47] < 0.001$), whereas the error variance (σ^2) was 12.541. Thus, roughly 25.0% of the variation in log-ratios in this compositional analysis was attributable to bird-to-bird differences and the remainder to random variation. The mixed model r^2 statistic for this regression (proportion of variation explained by fixed effects) was 0.659 ($p < 0.001$).

The parameters that were most relevant to distinguishing between orographic flight and thermalling flight were AGL, speed between points and northness of bearing (O versus T; table 4 and figure 2). Thus, orographic flight was lower, faster and more northward than thermal soaring. The parameters least useful in distinguishing between these flight behaviours were the turn angle and the eastness of bearing. When all other predictors were held constant, the odds of a bird using orographic updrafts instead of thermal updrafts decreased by 6% with every 1 m increase in flight altitude,

they increased by 31% with every 1 ms^{-1} increase in speed, and they increased by 343% with every unit increase in northness of bearing.

3.5. Daily and seasonal flight response of eagles

Analysis of statistically classified flight behaviour shows that eagles spent proportionately more time using orographic updrafts early in the morning and late in the day than they did in the middle of the day ($F_{11,22356} = 3.21$, $p < 0.001$; figure 3). At most, 29% of data recorded in any 1 h was indicative of orographic flight and, at times, as little as 3% of data points per hour were categorized as belonging to birds using orographic updraft.

Analysis of seasonal patterns suggested a strong linear response in the proportion of time spent using orographic updrafts over the approximately 85 day migration season ($F_{6,22356} = 5.76$, $p < 0.001$; figure 3). In this case, the mean proportion of time spent in orographic flight during two-week periods ranged from 30% (early in the season) to 3% (late in the season).

3.6. Response of eagles to a varying meteorological environment

Eagles responded strongly to changes in weather by changing the mode of subsidized flight they used. As a rule, when thermal updrafts were available, eagles used them. Thus, when downward solar radiation was low, the probability that eagles used orographic updrafts was higher than when downward solar radiation was greater ($F_{5,22356} = 4.86$, $p < 0.001$; figure 4a). Likewise, when east-to-west winds (uwnd; crosswinds) were high in either direction, golden eagles were more likely to use orographic updrafts than they were when these winds were close to zero ($F_{9,22356} = 6.08$, $p < 0.001$; figure 4b). Finally, golden eagles used progressively less orographic updrafts as the north-to-south wind vector (vwnd) switched from tailwind (positive values) to a headwind (negative values; $F_{7,22356} = 3.98$, $p < 0.001$; figure 4c). In all cases though, the modelled mean proportion of time in orographic flight never rose above 45%.

4. Discussion

Our data demonstrate how a large soaring bird interacts with its aerial environment by using multiple modes of subsidized flight. We also show that many of these behaviours were a direct response to spatial and temporal variation in the availability of thermal and orographic updrafts. The extent of this switching behaviour and the degree to which subsidy underpins the migratory flight of these birds provide unique insights into the circumstances under which an organism may seek to subsidize flight [29]. These patterns consequently provide insights into the possible evolution of use of subsidy in flight.

Subsidy that supports movement is an important organism–environment interaction. Although all fliers are likely to receive some type of subsidy, there has been only limited work on the use of subsidy by insects [3,4,30] or bats [31,32] (this is in part due to the fact that it is challenging to track small fliers who often travel at night when thermals are limited). It is, however, well known that millions of migratory raptors soar past hawk watches each spring and

Table 4. Estimated regression coefficients for 13 predictors from modelled flight classes from 32 golden eagles on northbound migration in the Appalachian Mountains. Estimates are generated for each of three models comparing flight classes (G–T, 0–G, 0–T).

parameter	G versus T (d.f. = 31, 20 530)			G versus 0 (d.f. = 31, 12 740)			0 versus T (d.f. = 31, 11 576)		
	estimate $\pm$ s.e.	T-statistic	p	estimate $\pm$ s.e.	T-statistic	p	estimate $\pm$ s.e.	T-statistic	p
intercept	5.61 $\pm$ 1.13	4.96	<0.001	3.60 $\pm$ 2.65	1.36	0.0183	–2.59 $\pm$ 2.47	–1.05	0.302
day of the year	–0.02 $\pm$ 0.01	–1.63	0.103	–0.11 $\pm$ 0.02	–5.26	<0.001	–0.09 $\pm$ 0.02	–4.37	<0.001
northness course	–1.76 $\pm$ 0.17	–10.13	<0.001	0.16 $\pm$ 0.19	0.84	0.404	1.27 $\pm$ 0.20	6.48	<0.001
hour	0.07 $\pm$ 0.05	1.57	0.116	0.68 $\pm$ 0.12	5.73	<0.001	0.68 $\pm$ 0.12	5.80	<0.001
cumulative time	–0.02 $\pm$ 0.01	–1.32	0.187	–0.14 $\pm$ 0.02	–5.78	<0.001	–0.15 $\pm$ 0.02	–7.24	<0.001
northness bearing	–0.56 $\pm$ 0.21	–2.62	0.009	1.58 $\pm$ 0.33	4.85	<0.001	1.49 $\pm$ 0.14	10.27	<0.001
eastness bearing	–0.19 $\pm$ 0.17	–1.12	0.264	0.50 $\pm$ 0.29	1.76	0.078	0.17 $\pm$ 0.15	1.13	0.259
speed between points	–0.45 $\pm$ 0.02	–20.62	<0.001	–0.22 $\pm$ 0.17	–13.16	<0.001	0.27 $\pm$ 0.02	12.18	<0.001
vertical rate	0.11 $\pm$ 0.02	6.75	<0.001	0.02 $\pm$ 0.02	1.14	0.254	–0.06 $\pm$ 0.01	–4.34	<0.001
absolute vertical rate	0.14 $\pm$ 0.02	6.78	<0.001	0.01 $\pm$ 0.03	0.43	0.670	–0.10 $\pm$ 0.02	–4.02	<0.001
change in speed	0.05 $\pm$ 0.03	1.57	0.117	0.08 $\pm$ 0.02	4.62	<0.001	–0.07 $\pm$ 0.03	–2.68	0.007
absolute turning angle	0.02 $\pm$ 0.001	12.33	<0.001	0.006 $\pm$ 0.003	2.70	0.007	–0.002 $\pm$ 0.002	–1.43	0.152
actual versus projected distance	–0.002 $\pm$ 0.001	–3.09	0.002	–0.001 $\pm$ 0.0003	–3.71	<0.001	0.002 $\pm$ 0.0006	3.23	0.001
altitude above ground level	0.0001 $\pm$ 0.002	0.07	0.946	–0.06 $\pm$ 0.03	–21.35	<0.001	–0.06 $\pm$ 0.003	–17.31	<0.001

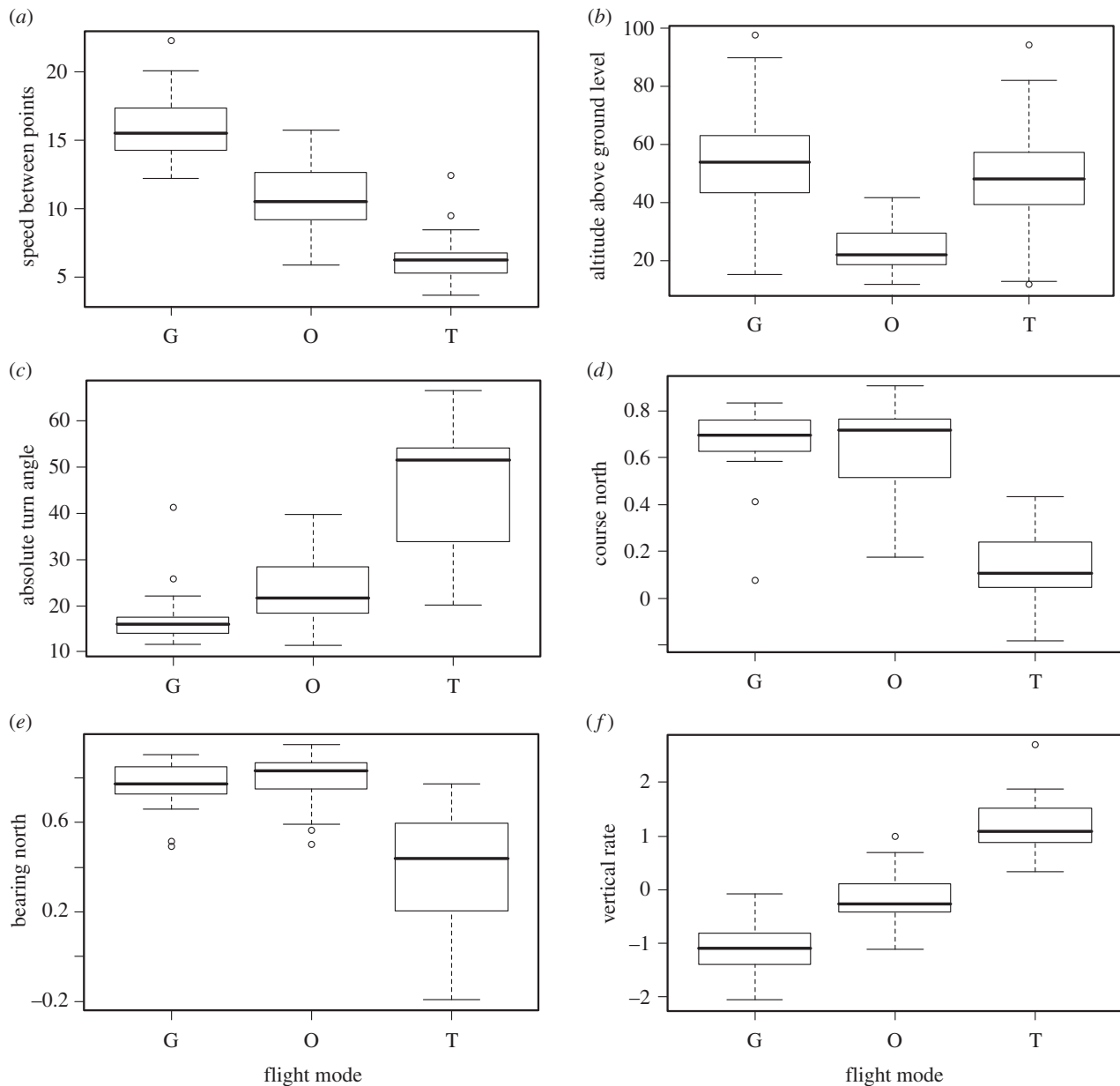


Figure 2. Boxplots showing empirical values (median, quartiles) of a subset of characteristics (predictors) of flight type as characterized by wkNN classification models of golden eagles migrating through the central Appalachian Mountains of eastern North America ($n = 32$). These predictors were those that our wkNN model suggested were especially useful in distinguishing among flight types.

autumn, in air moving fast enough to subsidize flight of objects as large as mechanical gliders. Our data show that, when golden eagles migrate, the vast majority (*how frequently*) of their time is spent subsidizing flight with environmental updrafts (approx. 87% of each bird's time measured in migration). Thus, the use of subsidized flight occurs not just within sight of hawk watches but throughout migration.

The extent of use of updrafts to subsidize flight appears to vary widely among taxa. Extended use of this subsidy is characteristic of golden eagles and many other species of soaring migrant raptors. Nevertheless, this behaviour contrasts directly with the migratory flight of other types of terrestrial fliers that have been followed which, in the few cases evaluated, predominantly use flapping flight and subsidize migration only part of the time (e.g. approx. 50% of bee-eater *Merops apiaster* flight segments are subsidized; [12]). A more analogous situation may be with oceanic fliers, who may forage for days at a time with minimal energy expenditure via dynamic or gust soaring [33,34].

Golden eagles' *relative use* of different types of subsidized updrafts during spring—in a manner dramatically skewed (greater than 8:1) towards thermal uplift—also provides important and concurrent ecological insight. Terrestrial birds occupy and interact with an environment that is simultaneously less dynamic and less predictable than that occupied by oceanic birds. This is because oceanic waves not only move constantly (they are dynamic) but also they are highly dependable, and wind currents and shear are highly predictable relative to each wave. In contrast, updraft over land is less dependable because, although the terrain is static, air movement is driven by highly variable weather patterns moving over complex terrain and producing multiple co-occurring and interacting forms of updraft. These subsidies include dynamic shear, orographic and thermal air flows, lee and mountain waves [35], thermal streets [5] and other micro-scale phenomena that make sustained flight energetically feasible for large-bodied organisms. Modelling flight as either orographic, thermal soaring and gliding, or 'unknown' is an improvement over the majority of previous studies that

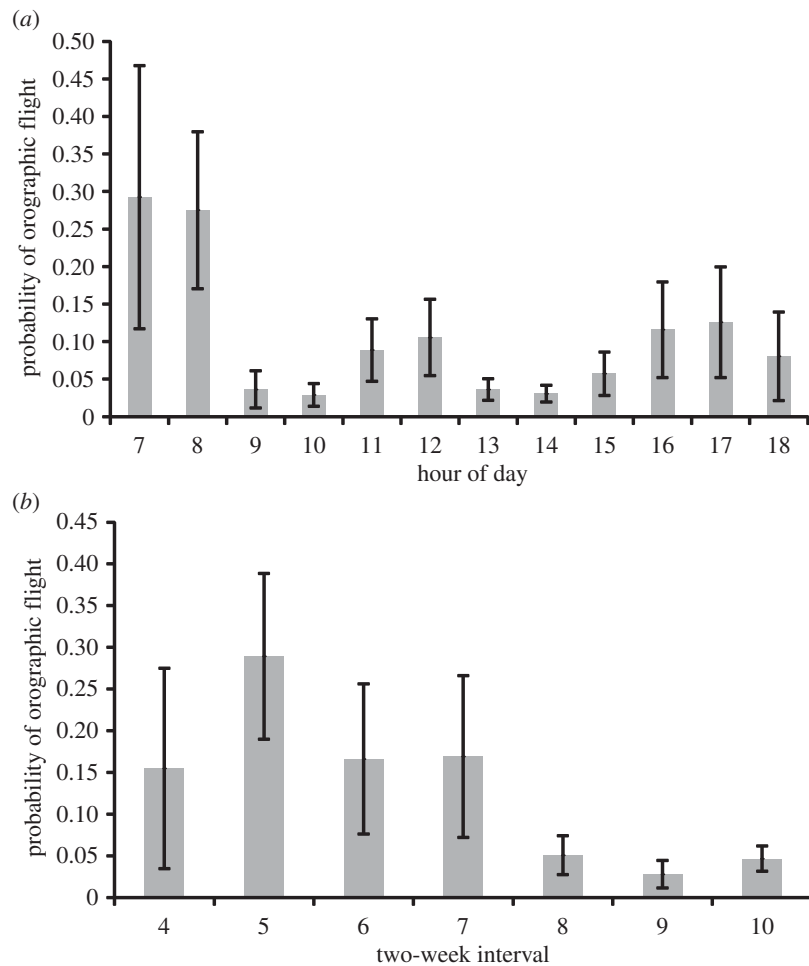


Figure 3. Proportion of time golden eagles ($n = 32$) spent in flight subsidized by orographic updrafts while on migration in eastern North America throughout (a) a daily cycle and (b) a seasonal cycle. The daily cycle of eagle migration in Pennsylvania begins with daylight, roughly 07.00. The seasonal cycle of migration begins on 12 February, at the start of the fourth two-week period of the year, when birds begin to move north from wintering grounds. The migration cycle we recorded in Pennsylvania ends with the tenth two-week period of the year, on 20 May.

focus on a single type of subsidy (but see [13,16] for exceptions). However, by focusing on the two most prevalent types of uplift, we set aside some of the real-world complexity in terrestrial systems that creates many other types of uplift. Nevertheless, our analysis makes clear that flight behaviour of terrestrial soaring migrants is dramatically different from, and is likely to be more complex than, that of oceanic fliers. This complexity is reflected in the fact that golden eagles respond to the variable local-scale meteorological events they encounter by switching flight behaviour to take advantage of at least two, and probably several other, types of subsidy over short temporal intervals.

Use of flight subsidy is driven by interactions not only with weather but also with topography [36]. Thus, hawk counts are conducted at locations where topography diverts and concentrates flight paths of migrating raptors. At the two eastern North American hawk counts that observe the largest numbers of golden eagles in spring (the Allegheny Front and Tussey Mountain), the greatest number of north-bound migrants are counted during the first three weeks of March (www.hawkcount.org). Our data suggest that during this period a relatively greater proportion of the subsidy eagles use is provided by orographic updrafts (figure 3b), which are strictly low altitude and concentrated along ridge-lines. Later in the season when eagles are almost exclusively using thermal soaring, the numbers of birds observed at ridgetop hawk counts drops. This is not surprising, given that

(i) thermal soaring puts the birds at high altitudes, sometimes beyond the maximum distance a hawk counter can see [15,37,38] and (ii) thermal updrafts are more broadly distributed across the landscape than are orographic updrafts and therefore are less likely to concentrate birds at ridgetops. Thus, when thermal updraft dominates, the number of soaring migrants observed at hawk counts is unlikely to be indicative of the actual number of individuals migrating through the region [39].

Organisms vary their interactions with the environment and our results show that use of different types of subsidy is reflected in distinctive behaviours. Characterizing those behaviours is a first critical step to understanding *why* an organism may engage in one type of subsidized flight instead of another. This process then gives us insights into the decision-making underpinning soaring flight. For example, it is reasonable to expect organisms to be able to distinguish between subsidized flight modes and to select those modes that allow progress both more quickly and with less divergence from a straight path. This was reflected in the relative differences in speed among flight modes (speed was important in separating orographic soaring from other golden eagle flight modes) and in directionality of travel (northness of course and bearing separated thermalling from the other flight modes).

Our data show that golden eagles responded directly to environmental variation by changing the mode of subsidized

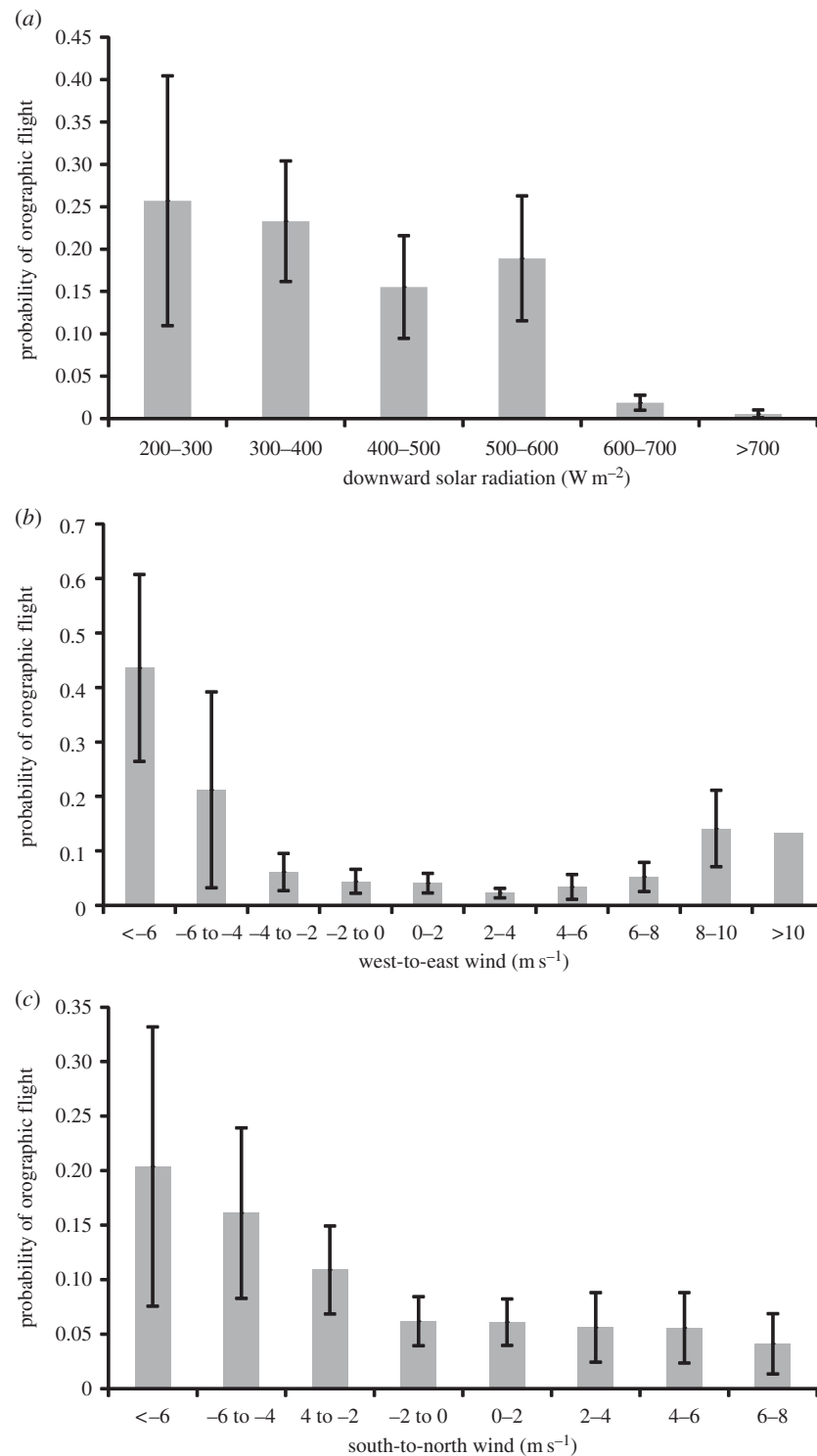


Figure 4. Proportion of time golden eagles ($n = 32$) spent in flight subsidized by orographic updrafts while on migration in eastern North America under conditions of varying (a) downward solar radiation; (b) west-to-east wind (winds perpendicular to topography and the general direction of migration); and (c) south-to-north winds (winds parallel to the general direction of migration).

flight they used. Previous work indicates that eagles demonstrate a flight altitude response to changes in topography [36] and to variation in wind speed [22]. We also know that flight speed of eagles using a thermal-glide strategy is faster than that of eagles using exclusively orographic updraft [19], that eagles preferentially migrate when weather conditions favour availability of that thermal updraft [21], and that adult and pre-adult eagles face different temporal and energetic pressures when migrating [21]. Collectively, these analyses suggest that golden eagles regularly alter their flight behaviour in response to variable aerial environments.

These data also hint at the possibility that high-resolution movement data may shed additional light on the complex flight strategies of species other than eagles.

Implementation of a flight strategy involving regular switching among types of subsidy is a different approach to use of subsidy than that apparently taken by Procelliformes, which are said to exclusively use dynamic soaring [7,8], and *Gyps* vultures and frigatebirds, both said to predominantly use thermal soaring [17,18]. Further evidence for this switching strategy should come from behavioural observations. For example, we would expect a well-fed, but time-limited adult golden eagle

rushing to northern breeding grounds to use energetically inefficient [19] orographic updrafts to subsidize relatively slow and less directional spring migration early in the season when thermals are not available. Likewise, we would expect a time-insensitive pre-adult golden eagle that may be food and energy limited to delay northbound migration until energetically efficient thermal updraft [19] becomes available later in the season, enabling faster, straighter migration. In fact, golden eagles exhibit exactly this behavioural variation.

Understanding migratory flight behaviour also creates opportunities for effective conservation management. For example, collision with industrial wind turbines kills large numbers of soaring birds of prey [40], including golden eagles, and turbines are being rapidly installed in the central Appalachians. In this region, eagles are at greatest risk from turbines when they are using orographic updraft. Flight subsidized by thermal uplift is characterized by greater AGL [39] and thus lower risk. To date, modelling of risk to eagles from turbines in this region has been based simply on flight altitude, where low-altitude flight is classified as risky flight [41]. Because bird behaviour is likely to be directly linked to risk [42,43], a next generation of models could use flight classification algorithms to refine prediction risk by linking risk to specific low-altitude flight behaviours (foraging, use of orographic updraft).

Finally, organisms that rely on environmental subsidy for migration or any other essential behaviour may be especially at risk from the changes in wind patterns brought on by global climate change [34]. Our data demonstrate that golden eagles have the capacity to respond to local-scale variability in availability in updrafts brought on by changes

in weather. It is therefore reasonable to predict that this species should also easily adapt to synoptic-scale variation brought on by climate change. By virtue of their ability to use multiple types of subsidized updrafts, this species, therefore, may experience relatively fewer flight-related energetic or demographic costs from climate change than may other species more tightly tied to specific weather types.

Authors' contributions. T.E.K., P.J.T., D.B., T.A.M., A.E.D., M.J.L., J.A.T. and J.L.C. designed the study and organized analyses, M.J.L., T.A.M., T.E.K., J.L.C., J.L. and J.A.T. trapped and telemetered eagles, P.J.T. performed the initial GLMM, wkNN and compositional analyses, A.E.D. performed the GEEs to test for flight response. T.E.K., T.A.M. and A.E.D. wrote the manuscript, all authors revised the manuscript.

Competing interests. At the time of this research, T.E.K. and M.J.L. were owners of Cellular Tracking Technologies that manufacture GPS–GSM transmitters used in this project.

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