Bird orientation: compensation for wind drift in migrating raptors is age dependent

Kasper Thorup[1]*, Thomas Alerstam[2], Mikael Hake[3] and Nils Kjellén[2]

[1]*Zoological Museum, University of Copenhagen, DK-2100 Copenhagen, Denmark*
[2]*Department of Animal Ecology, Lund University, Ecology Building, SE-22362 Lund, Sweden*
[3]*Grimsö Wildlife Research Station, Swedish University of Agricultural Sciences, SE-73091 Riddarhyttan, Sweden*
Author for correspondence (kthorup@zmuc.ku.dk).

Despite the potentially strong effect of wind on bird orientation, our understanding of how wind drift affects migrating birds is still very limited. Using data from satellite-based radio telemetry, we analysed the effect of changing winds on the variation of the track direction of individual birds. We studied adults and juveniles of two raptor species, osprey *Pandion haliaetus* and honey buzzard *Pernis apivorus*, on autumn migration between North Europe and Africa, and demonstrate an important difference between the age categories of both species in the extent of wind drift. For juveniles, side- and following-wind components affected the rates of movement perpendicular to and along the mean direction, respectively, to a similar degree, suggesting full wind drift. By contrast, for adults the rate of crosswind displacement was significantly smaller than the effect of wind on forward movement, showing much reduced wind drift (29%). This indicates that adults have acquired a more sophisticated orientation system, permitting detection of and compensation for wind drift, than juveniles. These drift effects are likely to reduce the ability of juveniles to locate species-specific wintering areas in case of rapid climatic wind change.

Keywords: bird orientation; wind drift; satellite tracking; raptor migration

1. INTRODUCTION

The track direction and ground speed of a flying bird is the sum of the wind vector and the bird's own flight vector (heading direction and airspeed) relative to the surrounding air. Because wind speeds and birds' airspeeds are often of a similar magnitude, wind is of paramount importance for the orientation and travel economy of migrating birds. Revealing the effect of wind on flight directions of birds will help to understand the birds' orientation system and their capability of exploiting winds in an optimal way. Furthermore, birds' vulnerability to misorientation because of wind drift is important for migration-dependent mortality and for the evolution of migration patterns in regions of different wind regimes and of different climatic wind change.

The fundamental question about drift or compensation has been evaluated for migrating birds by numerous radar and field studies over several decades, resulting in a highly complex and partly contradictory picture. Patterns of drift, partial drift, compensation or even overcompensation have been reported (Alerstam 1990; Richardson 1991; Alerstam & Hedenström 1998). Theoretical evaluations have demonstrated that both drift and compensation may be optimal for minimizing flight time and energy consumption, depending on wind pattern and variability, and distance to the goal (Alerstam 1979; Alerstam & Hedenström 1998). A serious problem with many radar studies is the difficulty of separating true wind drift from pseudo-drift, which is the correlation between wind and average direction of a migratory movement that may also arise when the birds compensate completely for wind drift, as a consequence of differential departures of migrants with different preferred track directions under different wind directions (Evans 1966; Nisbet & Drury 1967; Alerstam 1978). Spurious patterns of drift or compensation may also arise for other stochastic and trigonometric reasons in analyses of migratory cohorts with an angular scatter in preferred directions between individuals and flocks (Green & Alerstam 2002).

We analyse the effect of changing winds on the variation of the track direction of individual birds, recorded by satellite tracking throughout their autumn migration. By using the course variation of individual birds relative to the observed mean directions we avoid the complications of pseudodrift and other spurious patterns.

2. MATERIAL AND METHODS

(a) *Satellite tracking data*

Adults and juveniles (yearlings) of osprey (11 adults, 2 juveniles) and honey buzzard (6 adults, 3 juveniles) were tracked by satellite-based radio telemetry in the Argos system (figure 1) (Hake *et al.* 2001, 2003; Kjellén *et al.* 2001; Thorup *et al.* 2003). In both species, the juveniles migrate independently from the adults, and ospreys, in particular, normally travel solitarily (Hake *et al.* 2001). We used segments between positions separated by at least 1 day in time and 100 km in distance, resulting in a total of 297 segments (319 position readings). For most individuals, positions were separated by at least 3 days in time, and segment length was usually 300–800 km (see above references regarding accuracy etc.). A few segments directed along the coastline of West Africa (reflecting birds travelling along the coast) were excluded. Segments were separated by at least one stationary nocturnal resting period giving ample time for new orientation decisions. Hence, we have generally regarded these segments as independent observations concerning the birds' response to wind in our statistical analyses. The components of perpendicular and forward rates of movement (km day^{-1}) in relation to the overall mean direction of each species and age group (adult ospreys, juvenile ospreys, adult honey buzzards and juvenile honey buzzards, respectively) were calculated as dependent variables for our analyses.

A significant effect of variation between individuals on perpendicular rate of movement was found for the full dataset using an overall mean direction for calculation of perpendicular rate of movement ($p < 0.005$). The track of one adult osprey (due to its aberrant migratory route to southeast Africa) and the tracks of the honey buzzards south of 30° N (due to their change of direction) were eliminated, producing a total of 232 segments from the tracks of 21 individual birds. When using mean directions for each species and age group as reference directions for calculating perpendicular and forward movements from this restricted dataset, there was no additional statistically significant between-individuals variation (between all individuals: $p = 0.85$, between juveniles: $p = 0.46$ or between adults: $p = 0.87$). However, we also calculated components of perpendicular and forward rates of movement in relation to individual mean directions. We used the group-based rather than individual reference directions to minimize a possible bias towards compensation, but main results remained the same irrespective of which alternative was used.

Proc. R. Soc. Lond. B (Suppl.) **270**, S8–S11 (2003)
DOI 10.1098/rsbl.2003.0014

S8

(b) *Statistical analysis*

Statistical inference was based on general linear models (GLM) fitted using the GLM procedure in SYSTAT (SYSTAT 1998) using both forward and backward stepwise elimination of insignificant parameters ($p < 0.05$). Using GLMs for analysis allows the inclusion of both categorical and numerical independent variables (Littell *et al.* 1991) and is equivalent to ANCOVA. Parameter estimates are obtained in SAS (SAS 1999) using the models identified with SYSTAT. In addition to wind, geographical coordinates, magnetic declination, Julian date and interactions were used as independent variables for analysis (electronic Appendices A and B, available on The Royal Society's Publications Web site, include further details of the GLM analysis).

(c) *Wind data*

For each segment, perpendicular and tail-wind components were calculated in relation to mean segment direction from wind vectors at the mid-point of the segment. Wind data were NCEP Reanalysis data provided by the NOAA-CIRES Climate Diagnostics Center, Boulder, CO, USA, from their Web site at http://www.cdc.noaa.gov/. Wind-vector data consisted of uwind (E–W wind) and vwind (N–S wind) components at barometric pressure levels of 1000 hPa (corresponding to low-altitude winds) and 925 hPa (corresponding to winds *ca.* 750 m above sea level) at 12Z and interpolated from data given for a 2.5° latitude/longitude grid. Winds at these altitudes are of primary relevance since raptors normally travel by thermal soaring migration in the altitude stratum 0–1500 m (Kerlinger 1989).

3. RESULTS

The perpendicular as well as forward rate of movement of satellite-tracked ospreys and honey buzzards are strongly correlated with the corresponding wind vector component, as seen from figure 2. Fitting of GLMs with wind and other independent variables, in addition to species and age categories (see electronic Appendix B), demonstrates that the relationship between perpendicular rate of movement and wind differs markedly between adults and juveniles ($p = 0.001$) as seen in figure 2a, whereas there are no additional influences due to other variables ($p > 0.05$ for other variables and interactions). At an individual level, juveniles generally have a steeper regression coefficient between perpendicular rate of movement and wind ($p = 0.04$, two-sample t-test, means ± 1 s.e. of 6.35 ± 1.35, $n = 16$, and 12.75 ± 2.75, $n = 5$, for adults and juveniles, respectively). The relationship between forward rate of movement and wind is the same irrespective of age ($p > 0.05$) and other variables, although the overall forward migration speed differs between age/species and regions as already demonstrated in earlier studies (Hake *et al.* 2001, 2003; Kjellén *et al.* 2001).

The intercept in figure 2b gives a mean forward rate of movement in zero winds at 180 km day^{-1}, which corresponds to an effective daily travelling time of *ca.* 5 h using thermal soaring flight (preferred by both species) with a typical resulting cross-country airspeed of 10 m s^{-1} (Kjellén *et al.* 2001). The potential effect of a 1 m s^{-1} tail- or head-wind during 5 h is 18 km, which is close to the slope values for the wind effect in figure 2b (16.8 for adults and 16.5 for juveniles). This schematic reasoning, although affected by several potential biases, suggests that the birds are fully affected by the following-wind component as expected. In comparison, the slope for the relationship between perpendicular movement and the corresponding wind component (figure 2a) is distinctly smaller for adults (4.9), while for the juveniles (13.9) it approaches the slope expected for a full wind effect. Thus, we conclude that juveniles are subjected to virtually full drift by crosswinds, whereas adults compensate, to a large degree, leaving only a limited wind-drift effect (4.9/16.8 = 29%).

The effect of using the restricted dataset with group means compared with the full set with an overall mean was investigated by fitting GLMs with all factors, including wind, to both datasets. The same result, a marked age dependence in the effect of perpendicular but not of forward winds, emerges from both analyses. The restricted model has a higher explained variation in perpendicular movement ($R^2 = 0.167$) than the corresponding model on the full dataset ($R^2 = 0.128$), showing that the additional directional variation between groups and individuals in the full dataset are not due to wind. For forward movement, less difference is found between the explained variation in restricted ($R^2 = 0.170$) and full ($R^2 = 0.188$) datasets.

Only small differences are found using wind data from high (925 hPa) or low (1000 hPa) altitude. GLMs fitted using wind data from high and low altitude contain the same parameters (perpendicular) or differ by one parameter (forward). A slightly lower explained variation is found with wind data from high than from low altitude (perpendicular movement: $R^2 = 0.141$ and $R^2 = 0.167$, respectively; forward movement: $R^2 = 0.284$ and $R^2 = 0.290$, respectively, for GLM with the same parameters).

There are no indications (no significant wind × latitude interaction; see electronic Appendix B) that wind drift is more pronounced at a greater distance from the final destination with compensation gradually increasing with decreasing distance from the destination, as would be expected to be optimal under certain conditions (Alerstam 1979; Alerstam & Hedenström 1998).

4. DISCUSSION

Our results, demonstrating partial compensation for wind drift by adults, are consistent with indicated elements of both compensation and drift according to field and radar studies of raptors using thermal soaring migration (Trowbridge 1902; Kerlinger 1989; Spaar & Bruderer 1997). That adult birds are still exposed to limited drift is also consistent with partial drift effects recorded for other types of migrants, e.g. geese, on spring migration (Green 2001). The susceptibility of juvenile birds migrating solitarily to extensive wind drift probably not only applies to the thermal soaring migrants in this study but also to nocturnal passerine migrants, as indicated by strong drift effects for this category during autumn migration (Liechti 1993; Zehnder *et al.* 2001).

The detection of a strong age-dependent effect of wind drift is, to our knowledge, new and, if valid more generally among migrating birds, may help to explain the variable extent of drift that has been reported from numerous studies. One may speculate that juveniles migrating in mixed flocks with adults benefit from the compensatory ability of the adults. The reason for the age-dependent difference in compensatory ability may be related to the possible availability of acquired map information, allowing experienced adults to detect and correct for lateral displacement, whereas juveniles on their first migratory journey may be more restricted to simple vector orientation, as indicated by classical displacement experiments with migratory sparrowhawks, starlings and chaffinches (Drost 1938; Perdeck 1958; Berthold 2001). In addition, the adaptive value of crosswind compensation may be smaller for juveniles that, unlike adults, have no specific individual prior winter site as their destination. Alternatively, compensa-
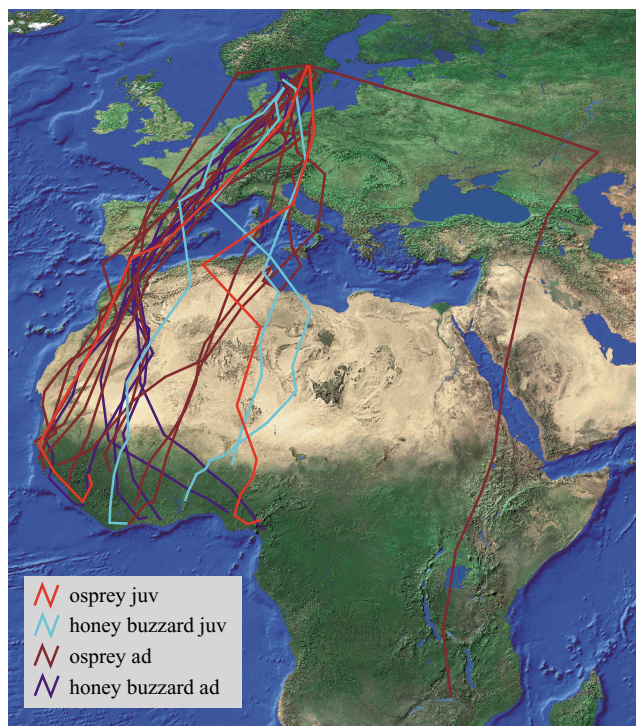
Figure 1. Tracks of ospreys and honey buzzards followed by satellite-based radio telemetry (Hake *et al.* 2001, 2003; Kjellén *et al.* 2001). Abbreviations: juv, juvenile; ad, adult.

tory behaviour during flight, for example, involving determination of the resulting track direction relative to the landscape below (Alerstam & Pettersson 1976), may be such a complex faculty as to require long-term learning, not least for thermal soaring migrants that constantly switch between phases of circling and gliding flight (Kerlinger 1989).

Extensive wind drift in juveniles will contribute to the maintenance of genetic variation in the inherited migratory orientation programme (because changing winds will favour different inherited directions in different years) essential for the evolution of new migratory routes, and may have important consequences in relation to rapid climatic wind change.

Alerstam, T. 1978 A graphical illustration of pseudodrift. *Oikos* **30**, 409–412.

Alerstam, T. 1979 Wind as selective agent in bird migration. *Ornis Scand.* **10**, 76–93.

Alerstam, T. 1990 *Bird migration*. Cambridge University Press.

Alerstam, T. & Hedenström, A. 1998 The development of bird migration theory. *J. Avian Biol.* **29**, 343–369.

Alerstam, T. & Pettersson, S.-G. 1976 Do birds use waves for orientation when migrating across the sea? *Nature* **259**, 205–207.

Berthold, P. 2001 *Bird migration. A general survey*, 2nd edn. Oxford University Press.

Drost, R. 1938 Über den Einfluss von Verfrachtung zur Herbstzugzeit auf den Sperber *Accipiter nisus*. *Proc. Int. Orn. Congr.* **9**, 502–509.

Evans, P. R. 1966 Migration and orientation of passerine night migrants in northeast England. *J. Zool. Lond.* **150**, 319–369.
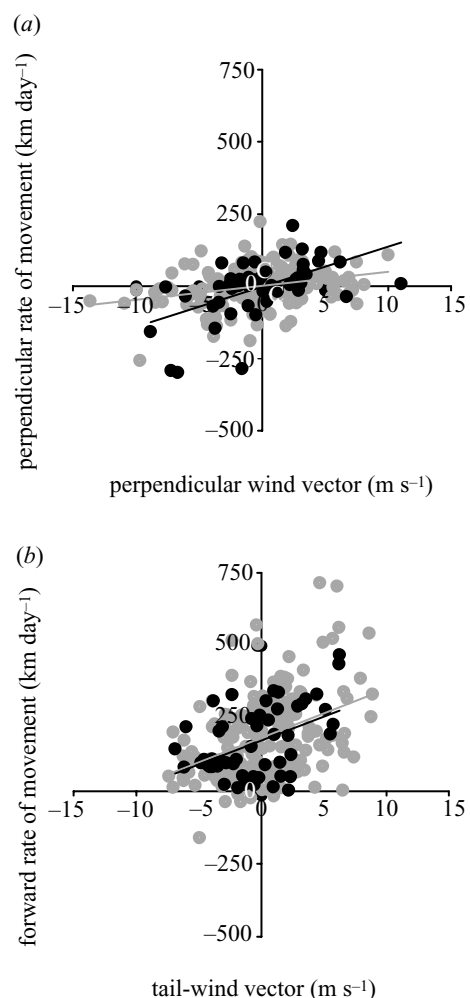
Figure 2. The effect of wind on rate of movement (*a*) perpendicular to and (*b*) along the migration direction. The respective components of wind and movement vectors are calculated in relation to mean segment directions for each species and age group. Based on data for 53 segments of juveniles (black circles; osprey 15 segments, two individuals; honey buzzards 38 segments, three individuals) and 179 segments of adults (grey circles; osprey 126 segments, ten individuals; honey buzzards 53 segments, six individuals). There are no significant differences between the two species in the relationships between movement and wind, and the combined data for both species are given in the figures.
(*a*) Juveniles, $y = 13.9x - 2.0$; adults, $y = 4.9x + 1.4$.
(*b*) Juveniles, $y = 16.5x + 174.1$; adults, $y = 16.8x + 183.0$.

Green, M. 2001 Is wind drift in migrating barnacle and brent geese, *Branta leucopsis* and *Branta bernicla*, adaptive or non-adaptive? *Behav. Ecol. Sociobiol.* **50**, 45–54.

Green, M. & Alerstam, T. 2002 The problem of estimating wind drift in migrating birds. *J. Theor. Biol.* **218**, 485–496.

Hake, M., Kjellén, N. & Alerstam, T. 2001 Satellite tracking of Swedish ospreys *Pandion haliaetus*, autumn migration routes and orientation. *J. Avian Biol.* **32**, 47–56.

Hake, M., Kjellén, N. & Alerstam, T. 2003 Age-dependent migration strategy in honey buzzards *Pernis apivorus* tracked by satellite. *Oikos*. (In the press.)

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

Kjellén, N., Hake, M. & Alerstam, T. 2001 Timing and speed of migration in male, female and juvenile ospreys *Pandion haliaetus* between Sweden and Africa as revealed by field observation, radar and satellite tracking. *J. Avian Biol.* **32**, 57–67.

Liechti, F. 1993 Nächtlicher Vogelzug im Herbst über Süddeutschland, Winddrift und Kompensation. *J. Ornithol.* **134**, 373–404.

Littell, R. C., Freund, R. J. & Spector, P. C. 1991 *SAS system for linear models*, 3rd edn. Cary, NC: SAS Institute Inc.

Nisbet, I. C. T. & Drury, W. H. 1967 Orientation of spring migrants studied by radar. *Bird-Banding* **38**, 173–186.

Perdeck, A. C. 1958 Two types of orientation in migrating starlings *Sturnus vulgaris* and chaffinches *Fringilla coelebs* as revealed by displacement experiments. *Ardea* **46**, 1–37.

Richardson, W. J. 1991 Wind and orientation of migrating birds: A review. In *Orientation in birds* (ed. P. Berthold), pp. 226–249. Basel: Birkhäuser.

SAS 1999 *SAS version 8.02*. Cary, NC: SAS Institute Inc.

Spaar, R. & Bruderer, B. 1997 Optimal flight behaviour of soaring migrants, a case study of migrating steppe buzzards, *Buteo buteo vulpinus*. *Behav. Ecol.* **8**, 288–297.

SYSTAT 1998 S*YSTAT version 8.0*. Chicago, IL: SPSS Inc.

Thorup, K., Alerstam, T., Hake, M. & Kjellén, N. 2003 Can vector summation describe the orientation system of juvenile ospreys and honey buzzards? *Oikos*. (In the press.)

Trowbridge, C. C. 1902 The relation of wind to bird migration. *Am. Nat.* **36**, 735–753.

Zehnder, S., Åkesson, S., Liechti, F. & Bruderer, B. 2001 Nocturnal autumn migration at Falsterbo, South Sweden. *J. Avian Biol.* **32**, 239–248.

Visit http://www.pubs.royalsoc.ac.uk to see electronic appendices to this paper.