PREDICTED AND OBSERVED MIGRATION SPEED IN LESSER SPOTTED EAGLE *AQUILA POMARINA*

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Satellite telemetry has recently been used to track the migration of eight Lesser Spotted Eagles *Aquila pomarina* and one Spotted Eagle *A. clanga* (Meyburg *et al.* 1993, 1995a & b). I used aerodynamic theory to predict the overall migration speed in these eagles using either thermal soaring or flapping flight. Using flapping flight the predicted migration speed is maximum 95 km day^{-1} and in thermal soaring the predicted speed varies largely depending on the assumptions on energy deposition rate and climb rate in thermals. The observed mean migration speed was 139 km day^{-1} for the Lesser Spotted Eagle and 150 km day^{-1} for the Spotted Eagle. These speeds are significantly higher than had the birds migrated by flapping flight, and so soaring flight must be involved to a large extent. There were some indications that the prediction in best agreement with the observations will be found for an energy accumulation rate $P_{dep} = 1 \times BMR$ and a climb rate V_c = 1- 1.5 m s^{-1}. However, at present these conclusions are provisional and the predictions may be fraud with uncertainties. I discuss which factors have a major influence on the migration speed and they include fuel accumulation rate in the field, climb rate in thermals, limitations on thermal time and energy cost of gliding flight. Future studies of migration speed using satellite telemetry should focus on these factors.

Key words: *Aquila clanga* - soaring migration - satellite tracking - aerodynamics

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INTRODUCTION

Satellite telemetry has recently become a useful tool in the study of bird migration (e.g. Nowak & Berthold 1991). Its main advantage is the frequent locations obtained from single individuals, which may give detailed information on migratory routes, orientation, stopover time and flight speed. Until recently most studies using satellite telemetry have involved a limited number of individuals and the main focus has been the migration route. However, Gudmundsson *et al.*'s (1995) study of Brent Goose *Branta bernicla hrota* spring migration across the Greenland inland ice is an exception in this respect by reporting data on climb rate

and orientation. Recently, Meyburg and co-workers (Meyburg *et al.* 1993, 1995a & b) have published successful satellite radio trackings of eight Lesser Spotted Eagles *Aquila pomarina* on autumn migration, two on spring migration and one Spotted Eagle *A. clanga* on spring migration, respectively. The spring migrating Lesser Spotted Eagles were the same individuals tracked on autumn migration on their return migration to Europe.

The Lesser Spotted Eagles (four adults, four juveniles) were equipped with satellite transmitters in the breeding area in northern Germany (five individuals), Lithuania (one) and Slovakia (two). They were then tracked during their au-

tumn migration to SSE through Europe to Asia Minor (eight individuals), to the African wintering grounds, mainly SE. Africa (five) and back to Europe the next spring migration (two). See Meyburg et al. 1993, 1995a & b. The Spotted Eagle was caught on 24 October 1993 near Mecca in Saudi Arabia (Meyburg et al. 1995b). It then moved further south and spent a little more than two months in Yemen, before moving northwards in the beginning of February.

In addition to the migration route these studies also reported data on migration speed and body mass for the eagles involved (Meyburg et al. 1993, 1995a & b). Although the data set is limited to a few individuals this provides a unique opportunity to compare the migration performance observed with that predicted by aerodynamic theory (e.g. Pennycuick 1975, Alerstam 1991, Hedenström 1993).

In this paper I present predictions on migration speed during thermal soaring and flapping flight migration for birds of the dimensions of the Spotted and Lesser Spotted Eagles, and compare them with the data reported by Meyburg et al. (1993, 1995a & b). The aim of this paper is not to critically test the theory, but rather to show how the overall migration speed can be calculated and discuss which factors are likely to have a major influence on the migration speed in large birds mainly using thermal soaring.

METHODS

Flight mechanical predictions

Overall migration speed in birds is the average speed when taking into account the flight speed between start and destination, as well as the time spent to accumulate the energy required to fuel the flight (Alerstam & Lindström 1990). Hence, strictly speaking the migration starts when the bird initiates fuel accumulation before the first migratory flight. In cross-country thermal soaring the flight speed is determined by the gliding flight performance and the rate of climb in thermals (e.g. Pennycuick 1972, 1975 & 1989). The gliding

flight performance is determined by the glide super-polar (Tucker 1987, Pennycuick 1989), which in turn is determined by morphological properties of the bird (i.e. body mass, wing span, wing area, body frontal area) and air density. Accordingly, for a specific bird the main factor determining the cross-country soaring speed is the climb rate in thermals, which depends on the turning radius (wing area) of the bird and the actual vertical speed of the rising air. The cross-country speed must not be confused with the overall migration speed (cf. Meyburg et al. 1993). The latter is generally significantly slower since it allows also for time needed to refuel. Because climb rate in thermals is an important factor determining cross-country speed, this will vary between northern latitudes with low or moderate rates of climb and more southerly latitudes providing stronger and more abundant thermals (cf. Bruderer et al. 1994).

Overall speed of migration for a bird using thermal soaring flight can be calculated according to the formula:

$$V_{migr} = V_{cc} \times P_{dep}/(P_{flight} + P_{dep}) \qquad (1)$$

where V_{cc} is the cross country speed, P_{dep} is the energy accumulation rate at stopovers and P_{flight} is the metabolic cost of gliding flight (Hedenström 1993). The maximum resulting cross country speed in thermal soaring and gliding flight is given by

$$V_{cc} = V \times V_c/(V_c - V_z) \qquad (2)$$

where V is the optimal gliding speed as calculated from the superpolar and rate of climb, V_z is sink speed (negative downwards) at the optimal glide speed and V_c is climb rate in thermals (e.g. Pennycuick 1972 & 1989). Useful convective thermals are normally available only during daytime (Kerlinger & Moore 1989), and so migratory flights by using thermal soaring are restricted to the hours when thermals develop. This will influence the resulting cross-country speed, which then can be written as

$$V_{dash} = qV_{cc} \qquad (3)$$

where q is the proportion of the day with thermal activity (Hedenström 1993). Also the resulting energy expenditure, to be used in equation (1), will be modified as

$$P_{dash} = qP_{flight} + (1-q) \times P_{rest} \qquad (4)$$

where P_{rest} is the rate of energy expenditure during resting. A typical value for the duration of the availability of useful thermals is about eight hours (Kerlinger 1989), which yields $q = 1/3$. As a value for the resting metabolism, I assumed that P_{rest} is $1.5 \times$ the basal metabolic rate (*BMR*).

Power requirement for a large bird in gliding flight is likely to be about $3 \times BMR$ (Adams *et al.* 1986, Hedenström 1993). A realistic guess at the maximum possible rate of energy accumulation in free-living birds is about $1.5 \times BMR$ (A. Hedenström & T. Alerstam pers. comm.). However, this probable maximum rate can only be achieved under ideal conditions with abundant food easily accessible and thermoneutral conditions. In most natural situations the true rate of energy accumulation is likely to be less, maybe $0.5-1 \times BMR$.

For calculations of aerodynamic performance I have used adapted versions of the programs in Pennycuick (1989) with default values of all the parameters. Hence, the estimated *BMR* was obtained by using the allometric relationship for non-passerines according to Lasiewski & Dawson (1967). For the Spotted Eagle (body mass 1.9 kg, Meyburg *et al.* 1995a) *BMR* was 6.03 W and for the Lesser Spotted Eagle (average body mass 1.5 kg, range 1.4-1.8 kg, Meyburg *et al.* 1993 & 1995b) the mean of *BMR* was 5.08 W. However, for the aerodynamic calculations P_{flight}, P_{dep}, and P_{rest} were converted into 'mechanical' power assuming an efficiency of 0.23 (Pennycuick 1989).

Wing span, which is also needed for the aerodynamic calculations, was 1.7 m for the Spotted Eagle and varied between 1.5-1.6 m for the Lesser Spotted Eagles (B-U. Meyburg pers. comm.). Wing area was estimated on the basis of body mass according to the allometric relationship in Rayner (1988).

The climb rate in thermals is difficult to estimate without any measurements available for Spotted Eagles. However, Bruderer *et al.* (1994) reported a value of 1.67 m s^{-1} for Honey Buzzards *Pernis apivorus* in Israel, while Steppe Eagles *Aquila nipalensis* had an average climb rate of 1.9 m s^{-1} (Spaar & Bruderer 1997). Thermal conditions are probably very good in Israel and I have therefore assumed a value of 1.5 m s^{-1} to represent the average climb rate during the migration, but I also explore how lower and higher climb rates affect the predictions.

RESULTS

Predicted migration speed

On the basis of the assumptions given above the predicted soaring migration speeds for the Lesser Spotted Eagle, with average body mass and wing span of 1.5 m, are shown in Table 1, for a range of energy accumulation rates and climb rates in thermals. With no restrictions on thermal availability the predicted migration speed varies between 60 km day^{-1} (low energy accumulation rate ($P_{dep} = 0.5 \times BMR$), low climb rate in thermals ($V_c = 0.5$ m s^{-1}) up to 341 km day^{-1} (high energy accumulation rate ($P_{dep} = 1.5 \times BMR$), high climb rate in thermals ($V_c = 3$ m s^{-1}]). With restricted thermal availability (8 h day^{-1}, $q = 1/3$) the predicted migration speeds vary from 28 km day^{-1} up to 146 km day^{-1} (Table 1B). Obviously, the assumptions of climb rate, energy deposition rate and thermal availability have a great impact on the predictions. For the larger Spotted Eagle the predicted soaring migration speeds are slightly larger than for the Lesser Spotted Eagle, e.g. with $V_c = 1.5$ m s^{-1}, $P_{dep} = 1.5 \times BMR$ and $q = 1/3$ (restricted thermal availability) the predicted speed is 152 km day^{-1}.

Figure 1 shows how the calculation of the overall migration speed (equation (1)) can be graphically illustrated for the Lesser Spotted Eagle. The solution, V_{migr}, can be found by drawing a straight line from the extended ordinate, representing energy accumulation rate at stopovers, to a point on the horizontal 'power curve', repre-

Table 1. Predicted overall migration speed (km day^{-1}) for a bird with the dimensions of a Lesser Spotted Eagle (body mass 1.5 kg, wing span 1.5 m) in relation to energy accumulation rate (P_{dep}) and rate of climb in thermals (V_c). Panel (A) soaring migration without restriction on thermal availability, (B) soaring migration with thermals available during 8 h day^{-1} ($q = 1/3$) and (C) flapping flight migration.

$P_{dep} =$	$0.5 \times BMR$	$1.0 \times BMR$	$1.5 \times BMR$
(A) Soaring migration			
$V_c = 0.5$ m s^{-1}	60	105	140
$V_c = 1.5$ m s^{-1}	108	189	251
$V_c = 3.0$ m s^{-1}	146	256	341
(B) Soaring migration, $q = 1/3$			
$V_c = 0.5$ m s^{-1}	28	47	60
$V_c = 1.5$ m s^{-1}	50	84	108
$V_c = 3.0$ m s^{-1}	68	114	146
(C) Flapping flight			
$V_c = 0.5$ m s^{-1}	33	65	95

senting the cost of gliding flight and increasing cross-country speed with increasing climb rate in thermals (see Hedenström 1993). The point where this line intersects the abscissa gives the overall migration speed (Fig. 1; $V_{migr} = 2.91$ m s^{-1} (251 km day^{-1}) with an associated cross-country speed of 8.7 m s^{-1}).

If we assume that the eagles were migrating by flapping flight rather than gliding and soaring flight the cost of flight is increased (cf. Pennycuick 1989). The predicted overall migration speeds for the Lesser Spotted Eagle using flapping flight are shown in Table 1C. In flapping flight the predicted migration speed ranges from 33 km day^{-1} associated with a low energy accumulation rate up to 95 km day^{-1} for a high energy accumulation rate. The predicted values when using flapping flight are identical for the Spotted Eagle to those for the lesser species. Now, I turn to the data on observed migration speeds as reported by Meyburg et al. (1993, 1995a & b).

Observed migration speed

The observed overall mean speed of autumn migration was 133 km day^{-1} (SD = 42.7, $n = 8$) for the Lesser Spotted Eagle. For juveniles it was 118 km day^{-1} (SD = 49.6, $n = 4$) and for adults it was 148 km day^{-1} (SD = 34.8, $n = 4$), but the difference was not statistically significant ($t_6 = 0.98$, $P > 0.05$). However, one juvenile achieved a speed of only 59 km day^{-1} over 45 days, and so there might be a tendency for inexperienced birds to migrate at slower speeds than adults. Spring migration speeds were 161 km day^{-1} and 123 km day^{-1} (mean 142 km day^{-1}), respectively, which were similar to the autumn migration speeds. Combining all ten migration speed observations yields a mean of 135 km day^{-1} (SD = 38.9, $n = 10$). During a few days when crossing Iraq and Iran the tracked Spotted Eagle achieved a speed of 280 km day^{-1}, but the long-term average speed from the Arabian peninsula to its presumed breeding area NW. of Omsk (56°14'N, 71°24'E), Russia, was 150 km day^{-1} during approximately one month of migration (Meyburg et al. 1995a).

The 95% confidence limit of migration speed for the Lesser Spotted Eagle (107-163 km day^{-1}) excludes the predicted maximum speed of powered flight migration (95 km day^{-1}). However, there are some combinations of assumptions which yield predicted values of the migration speed within the 95%-confidence limit of the observed migration speed for both restricted and unrestricted availability of thermals (Table 1). The observed migration speed in the Spotted Eagle was very close to the prediction for soaring migration of 152 km day^{-1} as shown above for restricted soaring, but much higher than the predicted maximum migration speed using flapping flight (95 km day^{-1}). Hence, most likely the eagles cannot have migrated by powered flight only since this would have resulted in an even slower speed than observed, but they must have been using thermal soaring to a significant extent.

DISCUSSION

When evaluating a theoretical prediction against observational data it is important to investigate how sensitive the model is to variation in the parameters and variables used to generate the predicted values. In the present case of migration speed there are a number of such uncertainties that may affect the predictions. I will therefore explore how some of these factors will revise the predicted migration speeds and which factors are likely to have the greatest influence on the predictions. The factors discussed below may of course vary one at a time or in concert.

First, the predictions of soaring migration speed is based on an aerodynamic model of gliding flight (e.g. Tucker 1987, Pennycuick 1989), and possible errors in this theory will of course affect the efficacy of the predictions. The aerodynamic theory used for flapping flight is perhaps more controversial than for gliding flight (see Ellington 1991), even if the most careful and detailed wind-tunnel study so far gave a very encouraging agreement between theory and measurements (Rothe *et al.* 1987). However, for the present purposes it is sufficient to accept the uncontroversial notion that flapping flight is faster and more costly than gliding flight. In the case of gliding flight, wind-tunnel studies have given satisfactory agreement between theory and measured flight performance (e.g. Tucker 1987, Tucker & Heine 1990). Although it is beyond the scope of this paper to evaluate the aerodynamic theory as such, I am convinced that future revisions of it will not alter the main conclusions in this paper.

Secondly, variation in the morphological parameters used is one possible source of error. By way of example, if the wing span in the Lesser Spotted Eagle is 1.6 m instead of 1.5 m, as was used when calculating the values of Table 1, the predicted migration speed increases from 251 km day^{-1} to 254 km day^{-1} (unrestricted soaring, body mass 1.5 kg, $P_{dep} = 1.5 \times BMR$, $V_c = 1.5$ m s^{-1}). Similarly, when varying the body mass from the minimum (1.4 kg) to the maximum (1.8 kg) of the tracked eagles yields calculated migration speeds
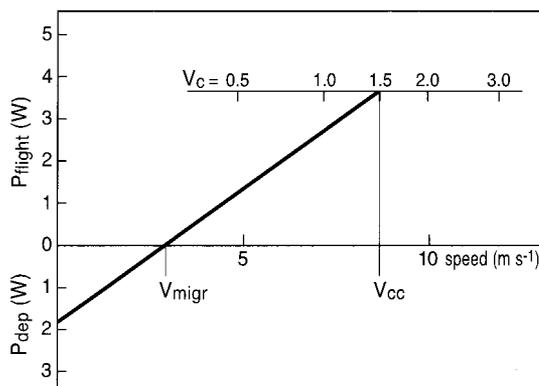
Fig. 1. Graphical solution of overall migration speed in a Lesser Spotted Eagle *Aquila pomarina* migrating by cross-country thermal soaring. The ordinate shows power consumption in flight (P_{flight}, Watt), which is constant in gliding flight, and the abscissa represents speed. The horizontal line shows the cross-country speed (V_{cc}) at different rates of climbs in thermals (V_c) ranging from 0.5-3 m s^{-1}. Energy accumulation rate (P_{dep}, Watt) is represented by the downwards extended ordinate. The overall migration speed (V_{migr}, equation (1)) is obtained where the line from the relevant point on the extended ordinate (representing rate of energy accumulation) to the relevant point on the horizontal line (representing the cross-country speed) intersects with the abscissa. In the illustrated example $P_{flight} = 3 \times BMR$, $V_c = 1.5$ m s^{-1} with an associated cross country speed $V_{cc} = 8.7$ m s^{-1}, resulting in an overall migration speed $V_{migr} = 2.91$ m s^{-1} (251 km day^{-1}). Gliding flight performance was calculated according to Pennycuick (1989) with body mass 1.5 kg, wing span 1.5 m, wing area 0.22 m^2 and air density 1.23 kg m^{-3}.

of 250 km day^{-1} and 254 km day^{-1}, respectively (unrestricted soaring, wing span 1.5 m, $P_{dep} = 1.5 \times BMR$, $V_c = 1.5$ m s^{-1}). By simultaneously changing body mass and wing span from minimum (body mass 1.4 kg, wing span 1.5 m) to maximum (body mass 1.8 kg, wing span 1.6 m) values gives predicted speeds of 250 km day^{-1} and 257 km day^{-1}, respectively. Hence, variation in these morphological parameters only has a minute effect on the predicted overall migration speed as compared with variation in energy accumulation rate and rate of climb in thermals (cf. Table 1).

Thirdly, the assumed metabolic cost of gliding flight ($P_{flight} = 3 \times BMR$) may be too low (cf. Hedenström 1993). With $P_{flight} = 4 \times BMR$ instead and everything else equal (unrestricted soaring, body mass 1.5 kg, wing span 1.5 m, $P_{dep} = 1.5 \times BMR$, $V_c = 1.5$ m s^{-1}) we get a predicted overall migration speed for the Lesser Spotted Eagle of 206 km day^{-1} as compared to 251 km day^{-1}. This reduction of the overall migration speed can be illustrated graphically by studying Fig. 1. Increasing the cost of flight (i.e. shifting the horizontal 'power curve' in Fig. 1 upwards) will move the intersection of the abscissa (representing overall migration speed) by the line between the point on the extended ordinate, representing energy accumulation rate, to the relevant point on the 'power bar' from right to left, i.e. a reduction of the overall migration speed. More studies of flight metabolism in gliding flight of a greater variety of species are certainly needed.

In order to corroborate the theoretical prediction it remains to get authentic estimates on the rate of energy accumulation and rate of climb in thermals. It is evident from Table 1 that various combinations of the assumed values of these variables yield predictions close to the observed migration speeds. For example, high fuel deposition rate and low climb rate in thermals as well as low fuel deposition rate associated with high climb rate both give predictions within the range of observed migration speeds in the case of unrestricted soaring migration. When there is a limitation in the daily time when thermals are available and soaring flight is possible, the overall migration speed becomes reduced (Table 1B). With the assumed reduction of available thermals to 8 h day^{-1}, it is evident that only combinations of intermediate and high fuel deposition rates and climb rates in thermals give predicted values of migration speed within the range of the observations. But which prediction is the correct one? At present we simply have to admit that there are not good enough information available on rates of energy accumulation at stopovers for raptors. However, the satellite tracking of a Lesser Spotted Eagle on autumn migration through Europe allows

an independent provisional estimate of P_{dep} (cf. Meyburg et al. 1993). One eagle showed an average overall migration speed of 150 km day^{-1} during almost 9 days (V_{migr} in equation 1). Luckily, positions were obtained during a single day's flight of this bird during 5 h 20 min over a distance of 140 km. This provides an estimate of the cross-country speed as $V_{cc} = 7.29$ m s^{-1}. By rearranging equation (1), we can use these values and estimate the energy accumulation rate as $P_{dep} = 1.22$ W, which is near $1 \times BMR$ (mechanical equivalents). Another individual on spring migration (adult #22691, Meyburg et al. 1995b) had a migration speed of 161 km day^{-1} during 55 days and an associated cross-country speed $V_{cc} = 8.33$ m s^{-1}, which yield an estimated energy accumulation rate $P_{dep} = 1.06$ W (= $0.9 \times BMR$). Hence, these estimates indicate that P_{dep} may be up to 40% lower than the assumed maximum value. If these values are close to the true situation the correct prediction would be found in the middle column of Table 1, representing $P_{dep} = 1 \times BMR$.

Finally, when it comes to the climb rate when soaring in thermals there are some data available from tracking radar studies of large raptors. In Israel, Steppe Eagles showed a mean climb rate of 1.9 m s^{-1} (Spaar & Bruderer in press), which indicates favourable thermal conditions there. However, in other regions of the migration, such as north and central Europe, thermal convection is less favourable (cf. Schmid et al. 1986, Bruderer et al. 1994). Again, the data on the cross country speed for the juvenile Lesser Spotted Eagle during one day indicates a mean climb rate in thermals of 1.02 m s^{-1} during that flight, while an adult bird (#22691) had an estimated climb of 1.35 m s^{-1}. These estimates were obtained by using equation (2). If these climb rates and the energy deposition rate of about $1 \times BMR$ are representative the prediction in best agreement with the observed migration speed would be found with unrestricted soaring (Table 1A).

In conclusion I have used aerodynamic theory to predict the overall migration speed for thermal soaring Spotted Eagles. A few satellite radio trackings of migrating eagles are available (Mey-

burg *et al.* 1993, 1995a & b), allowing a preliminary comparison with the prediction. It should be clear that the overall migration speed depends on a multitude of aerodynamic, physiological and external factors. I have discussed which factors may influence the overall migration speed and thereby indicated which information is useful when evaluating migration speed in birds. Future studies involving satellite telemetry will prove most valuable for an improved understanding of migration ecology. So far published information involves rather few individuals, but I hope that more systematic studies will be undertaken where satellite tracking will be combined with studies on energy accumulation at stopovers and measurements of flight performance . Although the transmitters are expensive the data obtained are very useful, and show how satellite telemetry is quite a cost-efficient method to study bird migration.

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REFERENCES

Adams N.J., C.R. Brown & K.A. Nagy 1986. Energy expenditure of free-ranging Wandering Albatrosses *Diomedea exulans*. Physiol. Zool. 59: 583-591.

Alerstam T. 1991. Bird flight and optimal migration. Trends Ecol. Evol. 6: 210-215.

Alerstam T. & Å. Lindström 1990. Optimal bird migration: the relative importance of time, energy, and safety. In: E. Gwinner (ed.) Bird migration: physiology and ecophysiology: 331-351. Springer-Verlag, Berlin.

Bruderer B., S. Blitzblau & D. Peter 1994. Migration and flight behaviour of Honey Buzzards *Pernis apivorus* in southern Israel observed by radar. Ardea 82: 111-122.

Ellington C.P. 1991. Limitations on animal flight performance. J. exp. Biol. 160: 71-91.

Gudmundsson G.A., S. Benvenuti, T. Alerstam, F. Papi, K. Lilliendahl & S. Åkesson 1995. Examining the limits of flight and orientation performance: satellite tracking of Brent Geese migrating across the Greenland ice-cap. Proc. R. Soc. Lond. B 261: 73-79.

Hedenström A. 1993. Migration by soaring or flapping flight in birds: the relative importance of energy cost and speed. Phil. Trans. R. Soc. Lond. B 342: 353-361.

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

Kerlinger P. & F.R. Moore 1989. Atmospheric structure and avian migration. Curr. Ornithol. 6: 109-142.

Lasiewski R.C. & W.R. Dawson 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. Condor 69: 13-23.

Meyburg B-U., W. Scheller & C. Meyburg 1993. Satelliten-Telemetrie bei einem juvenilen Schreiadler (*Aquila pomarina*) auf dem Herbstzug. J. Orn. 134: 173-179.

Meyburg B-U., X. Eichaker, C. Meyburg & P. Paillat 1995a. Migrations of an adult Spotted Eagle tracked by satellite. Brit. Birds 88: 357-361.

Meyburg B-U., W. Scheller & C. Meyburg 1995b. Zug und Überwinterung des Schreiadlers *Aquila pomarina*: Satellitentelemetrische Untersuchungen. J. Orn. 136: 401-422.

Nowak E. & P. Berthold 1991. Satellite tracking: a new method in orientation research. In: P. Berthold (ed.) Orientation in birds: 307-321. Birhäuser, Basel.

Pennycuick C.J. 1972. Soaring behaviour and performance of some East African birds, observed from a motor-glider. Ibis 114: 178-218.

Pennycuick C.J. 1975. Mechanics of flight. In: D.S. Farner & J.R. King (eds) Avian biology, 5: 1-75. Academic Press, New York.

Pennycuick C.J. 1989. Bird flight performance: a practical calculation manual. Oxford University Press, Oxford.

Rayner J.M.V. 1988. Form and function in avian flight. Curr. Ornithol. 5: 1-66.

Rothe H-J., W. Biesel, W. Nachtigall 1987. Pigeon flight in a wind tunnel II. Gas exchange and power requirements. J. Comp. Physiol. B 157: 99-109.

Schmid H., T. Steuri & B. Bruderer 1986. Zugverhalten von Mäusebussard *Buteo buteo* und Sperber *Accipiter nisus* im Alpenraum. Ornithol. Beobachter 83: 111-134.

Spaar R. & B. Bruderer 1997 . Soaring migration of Steppe Eagles *Aquila nipalensis* in southern Israel: flight behaviour under various wind and thermal conditions. J. Avian Biol.(in press).

Tucker V.A. 1987. Gliding birds: the effect of variable
    wing span. J. exp. Biol. 133: 33-58.
Tucker V.A. & C. Heine 1990. Aerodynamics of glid-
    ing flight in a Harris' Hawk, *Parabuteo unicinctus*.
    J. exp. Biol. 149: 469-489.

SAMENVATTING

In dit artikel worden enkele met behulp van satelliet-
telemetrie verkregen gegevens over de snelheid waar-
mee acht Schreeuwarenden *Aquila pomarina* en één
Bastaardarend *A. clanga* zich verplaatsten gedurende
de voor- en najaarstrek, vergeleken met voorspellingen
op basis van aerodynamische theorie. De theorie voor-
spelt dat de vogels 95 km per dag kunnen afleggen als
ze geen gebruik maken van thermiek. Als ze wel ge-
bruik maken van thermiek, door steeds tot grote hoogte
te klimmen en vervolgens al zwevend verder te trek-
ken, zouden ze veel langere afstanden per dag kunnen
afleggen. Deze afstand kan wel 341 km per dag bedra-
gen, maar een precieze voorspelling is moeilijk te ma-
ken. Onbekende factoren zoals de snelheid waarmee
hoogte kan worden gewonnen en de tijd per dag waarin
kan worden gebruik gemaakt van thermiek hebben
grote invloed. De satelliet gegevens lieten zien dat de
Schreeuwarenden gemiddeld 139 km per dag aflegden
en de Bastaardarend 150 km. Op grond hiervan wordt
geconcludeerd dat de vogels de thermiek hebben ge-
bruikt. Wel wordt een slag om de arm gehouden, omdat
de theoretische voorspellingen gepaard gingen met een
grote onzekerheid. Zo heeft bijvoorbeeld de snelheid
waarmee energievoorraden kunnen worden opgebouwd
in het veld grote invloed op de voorspellingen, zowel
wanneer wèl als geen wordt gebruik gemaakt van ther-
miek. Er wordt aanbevolen om in toekomstig onder-
zoek naar de trek van vogels met behulp van satelliet-
telemetrie, ook metingen te verrichten aan deze onze-
kere factoren.   (JvdM)