

## **Daily Travel Schedules of Adult Eurasian Hobbies *Falco subbuteo* — Variability in Flight Hours and Migration Speed Along the Route**

Authors: Strandberg, Roine, Klaassen, Raymond H.G., Olofsson, Patrik, and Alerstam, Thomas

Source: *Ardea*, 97(3) : 287-295

Published By: Netherlands Ornithologists' Union

URL: <https://doi.org/10.5253/078.097.0304>

---

BioOne Complete ([complete.BioOne.org](https://complete.bioone.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](https://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

# Daily travel schedules of adult Eurasian Hobbies *Falco subbuteo* – variability in flight hours and migration speed along the route

Roine Strandberg<sup>1,\*</sup>, Raymond H.G. Klaassen<sup>1</sup>, Patrik Olofsson<sup>2</sup> & Thomas Alerstam<sup>1</sup>



Strandberg R., Klaassen R.H.G., Olofsson P. & Alerstam T. 2009. Daily travel schedules of adult Eurasian Hobbies *Falco subbuteo* – variability in flight hours and migration speed along the route. *Ardea* 97(3): 287–295.

We analysed satellite tracking data to reveal the daily travel schedules of Hobbies *Falco subbuteo* migrating between northern Europe and southern Africa. By comparing movements during short-time intervals of 1–8 h at different times of the day between the three different regions Europe, Sahara Desert and tropical Africa, we found significant higher hourly speeds in the Sahara compared to the other two regions. The migration started early in the morning and continued throughout the day, resulting in daily travel time exceeding that of typical thermal soaring migrants. Due to fast hourly speeds in combination with the long travel days during Sahara crossings, the Hobbies exceeded daily travel distances recorded for soaring migrants. In Europe and tropical Africa, the speed was highly variable during the day, and lower flight speeds, especially during afternoons, suggest a fly-and-forage strategy. Our predictions about regular occurrence of nocturnal flight especially across geographical barriers as the desert were not fulfilled. In the Sahara, the Hobbies restricted their movement to diurnal migration. Nevertheless, 10% of the flight segments in tropical Africa were partly or completely during night hours and Hobbies often started their daily flight before or at sunrise. We attribute the special characteristics of the daily travel schedules of Hobbies primarily to their use of a fly-and-forage strategy, possibly in combination with preparedness for exploiting thermals during the daily thermal time window. Further studies are needed to understand why Hobbies do not increase daily travelling hours to include regular nocturnal flight in the Sahara Desert. We suggest that the daily travel schedules of the Hobby, which were distinctly different from those of other diurnal migrants like large raptors (which mainly exploit thermal soaring migration) or pipits, wagtails, finches and pigeons (which mainly travel during the morning hours) may be typical for bird species that primarily use a fly-and-forage migration strategy.

Key words: migration, satellite tracking, Eurasian Hobby, daily travel schedules, fly-and-forage strategy

<sup>1</sup>Department of Animal Ecology, Lund University, Ecology Building, SE-223 62 Lund, Sweden; <sup>2</sup>Furubodavägen 73, SE-29692 Yngsjö, Sweden;

\*corresponding author (Roine.Strandberg@zooekol.lu.se)

## INTRODUCTION

Many bird species migrate during the night, while others travel mainly during daytime and still others are more flexible and perform both nocturnal and diurnal flights. The reasons for these differences in daily travel schedules are not fully understood, but several different factors that make either nocturnal or diurnal migration

favourable have been suggested (reviewed by Kerlinger & Moore 1989).

A fundamental advantage of nocturnal migration is that the migratory flights do not occupy potential foraging and refuelling time during the day (for diurnal foragers), which will, other things being equal, make the resulting total speed of migration, including both flight transport and fuel accumulation, faster for

nocturnal compared to diurnal migration (Alerstam 2009). Furthermore, the atmospheric structure is generally more suitable for migratory flights during the night than during daytime. This gives nocturnal migrants the benefits of reduced evaporative water loss, reduced exposure to turbulence and lower and less variable wind speeds (Kerlinger & Moore 1989). In addition, predation risk may be lower during nocturnal flights (Walter 1979).

There are two main factors that favour diurnal migration: exploitation of thermal air in soaring flight and the use of a fly-and-forage strategy (Alerstam 2009). Many birds like raptors, storks, pelicans and cranes reduce their energy costs of transport by thermal soaring migration, which takes place during daytime when thermal air develops over land (Kerlinger & Moore 1989, Kerlinger 1989). Birds that fly extensively during their foraging, e.g. when hunting on the wing for insect or bird prey, or making search flights to locate food on the ground or in water, may combine foraging with covering migration distance. The food intake will help to offset the net energy expenditure during travelling. Such a fly-and-forage migration strategy may be very favourable with respect to both energy and time minimization and may therefore be an important explanation for diurnal migration habits among many bird species such as many seabirds, harriers, sparrowhawks, falcons, terns, gulls, swifts, swallows and martins (e.g. Rudebeck 1950–51, Dorst 1962, Strandberg & Alerstam 2007).

Satellite tracking provides important possibilities to analyse the daily migration schedule of individual birds and its variability in different regions along the entire migration route. Such tracking results have confirmed that large raptors like Osprey *Pandion haliaetus* (Kjellén *et al.* 1997, 2001) and Honey Buzzard *Pernis apivorus* (Hake *et al.* 2003) migrate primarily between 8:00 am and 5:00 pm local time, which is typical for birds depending strongly on thermal soaring migration (Kerlinger 1989). Ospreys show a large degree of flexibility in flight time within the main daily thermal time window, depending on if they travel over habitats/landscapes that permit them to combine their thermal soaring flight with a fly-and-forage strategy or not (Klaassen *et al.* 2008).

Satellite tracking has revealed that nocturnal flights are very uncommon among raptor species, and most often closely linked with long sea crossings (e.g. Cochran 1985, Fuller *et al.* 1998, Martell *et al.* 2001, Hake *et al.* 2003, Alerstam *et al.* 2006, Decandido *et al.* 2006, Strandberg *et al.* 2008). Radar observations at the Spanish south coast detected nocturnal sea cross-

ings, in this case of small falcon species such as Common Kestrel *Falco tinnunculus*, Eurasian Hobby *Falco subbuteo* and Lesser Kestrel *Falco naumanni* (Meyer *et al.* 2003). Regular nocturnal migration over land has so far only been shown for one diurnal raptor, the Levant Sparrowhawk *Accipiter brevipes* (Stark & Liechti 1993, Spaar *et al.* 1998). It was estimated that about 5–10% of the population crossed the Negev Highlands in Israel during the night.

In this paper, we analyse the daily travel schedules of the Hobby in different regions along its long-distance migration route between northern Europe and southern Africa. This small raptor is not as strongly dependent on thermal soaring migration as larger raptor species, a fact that is well known from field observations (Kjellén 1997, Chapman 1999) and also expected for aerodynamic reasons because of its relatively small size (Pennycuik 1989, Hedenström 1993). We expect that the difference in the balance of gain from thermals and from fly-and-forage migration between the small Hobby and larger raptors will be associated with differences in daily travel schedule, and we aim to test the following predicted differences between the Hobby (with a comparatively low profitability associated with thermal migration but a potentially high profitability associated with fly-and-forage migration) and larger raptors represented mainly by the Osprey (Klaassen *et al.* 2008):

(1) We expect the Hobby to primarily be a diurnal migrant, exploiting the advantage of a fly-and-forage migration strategy in combination with opportunistic soaring in thermal air. Because of its habits of regularly hunting not only during the day but also during dawn and dusk (Chapman 1999, Bijlsma & van den Brink 2005), we predict that the daily travel period of the Hobby includes early morning and late evening hours in addition to the daily thermal time window.

(2) In the Sahara Desert, where we assume that foraging is not possible, we predict that Hobbies will travel during a large number of both day and night hours (Alerstam 2009), summing up to a longer migration period per 24 h than for the Osprey flying only in the daily thermal time window (Klaassen *et al.* 2008) as well as to a faster total speed per 24 h across the desert compared with the Osprey.

(3) We predict that the Hobby, as other smaller raptors, is generally more prone than larger thermal dependent raptors to performing nocturnal migratory flights over land when foraging possibilities are poor (Alerstam 2009). As suggested by Strandberg *et al.* (2009), the equatorial evergreen rain forest could, beside the Sahara Desert, be a potential barrier for migrating Hobbies on their routes to southern Africa.

## METHODS

From 2005 to 2007 four adult Hobbies (three females and one male) were captured at their breeding sites in southern Sweden (55.7–55.9°N, 13.4–14.2°E) and equipped with Solar PTT-100 satellite transmitters (Microwave Telemetry Inc.), which were attached as backpacks. The transmitters weighed 9.5 g which comprised on average 4.1% of the Hobbies' body mass. The weight of the transmitters had no visible effects on flight behaviour and hunting performance (own observations) or timing of migration (e.g. Beaman & Galea 1974, Kjellén 1992).

The transmitters were programmed to operate on a transmission cycle of 10 h on and 24 h off and tracked by CLS/Service Argos in Toulouse, France. Depending on satellite orbits and local conditions we received 0–15 positions per 10-h period. Hence, the initiation of the 10-h transmission period shifted backwards by 4 h/day, which means that every day a slightly different part of the daily cycle was sampled. The evaluation of positions differing in accuracy was the same as described by Hake *et al.* (2001): we primarily used high quality positions (ARGOS-class 1–3, accuracy is most often within 1 km). Low quality positions (ARGOS-class 0, A, B, accuracy is unspecified) were only used when the locations seemed reasonable and were in agreement with typical travel rates and directions. For the autumn migration, the complete data set comprised 786 positions, of which 32% were high quality locations (for further information about ARGOS-classification see <http://www.argos-system.org>).

We assumed that the Hobbies had initiated their autumn migration the day they moved >50 km away from their nesting area. When the Hobbies were stationary for more than one week in the southern Hemisphere we assumed that they had arrived at their wintering quarters.

Daily travel schedules were analysed by calculating flight speeds for 'short-interval segments', which are segments with time intervals of 1–8 hours. By using a minimum of 1 hour the possible effect of low quality positions is reduced. Within each 10-h transmission period as many non-overlapping segments were defined as possible. Only data from travel days were used in our analyses, while stopover days (when the bird remained at the same site during one or more 24-h periods) were excluded. If there were several positions within one hour, we always used the highest quality position to define the segment. The speeds for the short interval segments were plotted in relation to the time of day for three main geographic regions along the migration

route: Europe (north of the Mediterranean Sea); Sahara (36–30°N to 17–15°N, depending on longitude), and tropical Africa (south of Sahara).

Short-interval segments were subsequently classified in two groups, indicating active travel (segment length >5 km) or stationary behaviour (segment length <5 km; 1 h segments shorter than 5 km are best classified as stationary primarily due to variation in location accuracy). The mid-interval times for every segment were used to obtain the distribution of travelling and stationary periods throughout the 24 hours of the day, which reflects a simple daily time budget (cf. Klaassen *et al.* 2008).

The number of daily travelling hours in the different main geographic areas were estimated in three different ways: (1) by dividing the mean speed of migration on travelling days (km/24 h; based on locations between different transmission periods) by *mean* short-interval speeds (km/h; including only segments >5 km), (2) by dividing the mean speed of migration on travelling days (km/24 h; based on locations between different transmission periods) by *median* short-interval speeds (km/h; including only segments >5 km) and (3) by calculating the number of hours with active travel from the daily time budgets (i.e. the cumulative sum of hours with active travel from the hourly frequencies of travelling and stationary segments).

Times are given in local daily exact time (thus calculated by correcting location times in GMT for the longitudinal time difference). The exact local time of sunrise and sunset was obtained for every location from the website of the Astronomical Applications Department of the U.S. Naval Observatory (<http://aa.usno.navy.mil>).

We compared the travel speed in the three different geographical regions in a GLM mixed model (SPSS 16.0) with individual included as random factor. Separate tests were conducted with hourly flight speed (as obtained from the short-interval segments) and daily migration speed as dependent variables, respectively. Post hoc tests were used to reveal differences in speed between the three regions.

## RESULTS

We recorded autumn migrations of four adult Hobbies, one track for each bird, with all birds passing the equator, but only three reaching the wintering grounds in southern Africa (Table 1). The journey lasted on average 61 days of which 39 were travel days. The mean distance travelled was 9223 km (for a presentation and

analysis of the routes of the falcons, see Strandberg *et al.* 2009).

### Regional variation in travel hours

In Europe, the Hobbies were travelling from 4:00 am to 6:00 pm (Fig. 1, Fig. 2) and the average daily flight time on travel days was 7.9–10.5 hours (Table 2). Three of four morning tracks starting around or before sunrise were associated with water crossings (two over the Baltic Sea and one departing for the Mediterranean Sea).

Of the 22 segments recorded in the Sahara Desert, 16 were recorded during active flight. The estimated flight time on travelling days was 11.7–14.6 hours (Table 2) and flights were evenly spread out over the daylight hours (Fig. 2). Two flights were recorded before sunrise and two ended after sunset (Fig. 1).

The majority of positions were received from tropical Africa, for which we can thus construct the most detailed time budgets (Fig. 2). The average daily flight time on travel days was 10.1–13.0 hours (Table 2). The great majority of flights were recorded from 5:00 am to 6:00 pm. In total 18 active flight segments started before sunrise and seven ended after sunset, with additionally seven flight segments recorded during dark hours only (Fig. 1). The latter flights were made by three out of the four Hobbies north and south of the equatorial rain forest belt between 7.5–6.9°N (Nigeria) and 1.2–6.2°S (Congo).

### Regional variation in travel speeds

The hourly speeds differed significantly between the three different regions (GLM mixed model,  $F_{2,163} = 6.79$ ,  $P = 0.001$ ). A post hoc test revealed that hourly speeds in Sahara (mean = 33.4 km/h, SD = 21.4,

$n = 16$ ) were different (Tukey B test,  $P < 0.05$ ) from speeds in tropical Africa (mean = 19.9 km/h, SD = 12.7,  $n = 123$ ) and Europe (mean = 23.8 km/h, SD = 14.9,  $n = 27$ ), whereas no significant differences (Tukey B test,  $P > 0.05$ ) existed between Europe and tropical Africa.

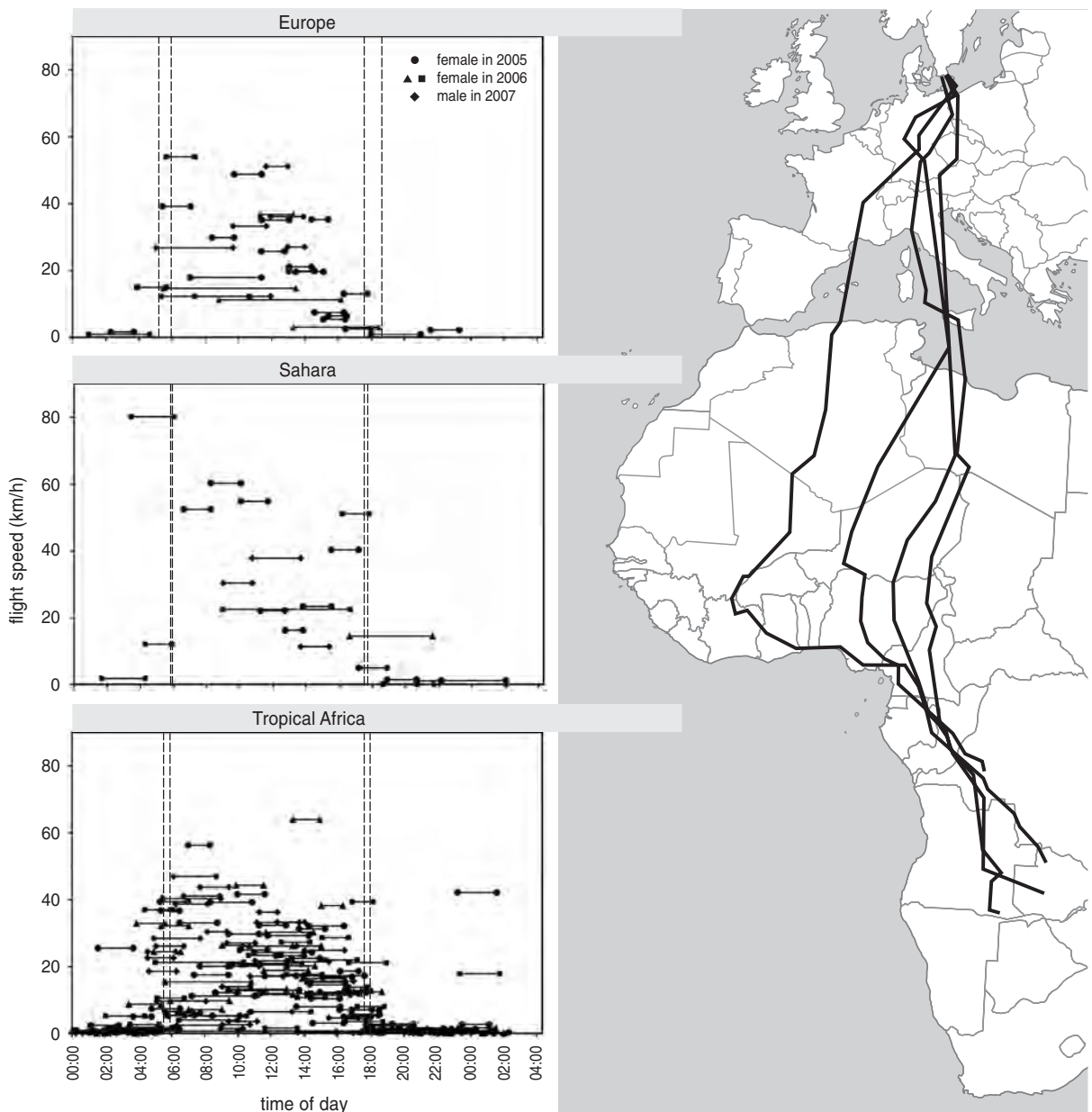
In Europe, the three fastest flights (>45 km/h) were recorded on the first migration days, and in two cases this occurred during the crossing of the Baltic Sea

**Table 2.** Speed on travel days and number of daily travelling hours of four Eurasian Hobbies in different geographical regions during autumn migration. Segments are 1–8 h. Mean daily travel speed = mean values based on daily travel distance divided by number of travel days (mean number of travel days used for calculations: Europe = 7; Sahara = 4; tropical Africa = 20). The number of daily travelling hours (per 24 h) was estimated in three different ways; (1) by dividing daily travel speed with mean segment speed, (2) by dividing daily travel speed with median segment speed and (3) from the proportion of segments in Fig. 2 (cf. Methods).

|                                      | Europe | Sahara | Tropical Africa |
|--------------------------------------|--------|--------|-----------------|
| Mean segment speed (km/h)            | 23.8   | 33.4   | 19.9            |
| Median segment speed (km/h)          | 21.0   | 26.9   | 17.9            |
| <i>n</i> segments                    | 27     | 16     | 123             |
| Mean daily travel speed (km/day)     | 188.6  | 391.3  | 200.2           |
| Estimated no. daily travelling hours |        |        |                 |
| (1)                                  | 7.9    | 11.7   | 10.1            |
| (2)                                  | 9.0    | 14.6   | 11.2            |
| (3)                                  | 10.5   | 12.3   | 13.0            |

**Table 1.** Timing, duration and distance of autumn migration of adult Eurasian Hobbies tracked during 2005–2007. Departure = departure date from the breeding area. Arrival = arrival date to the wintering area. Duration = total number of days from departure to arrival. Distance = the distance travelled. Travel = number of travel days (movement >50 km/day). Median values are given for departure and arrival dates for all birds. Mean values are given for duration, distance and travel days of all birds. The second female (data in italics) did not complete migration and is not included in the median arrival date and mean values. Note that the end position is not equivalent to wintering site, because the Hobbies are nomadic during this period.

| Sex           | Departure          | Start position        | Arrival       | End position         | Duration (days) | Distance (km) | Travel (days) |
|---------------|--------------------|-----------------------|---------------|----------------------|-----------------|---------------|---------------|
| Female        | 9 Sept 2005        | 55.9°N, 14.2°E        | 9 Nov         | 12.1°S, 24.6°E       | 62              | 11226         | 43            |
| <i>Female</i> | <i>4 Sept 2006</i> | <i>55.9°N, 14.2°E</i> | <i>27 Oct</i> | <i>4.2°S, 19.0°E</i> | <i>54</i>       | <i>7987</i>   | <i>37</i>     |
| Female        | 8 Sept 2006        | 55.9°N, 14.1°E        | 5 Nov         | 16.0°S, 20.0°E       | 59              | 8540          | 38            |
| Male          | 7 Sept 2007        | 55.7°N, 13.4°E        | 6 Nov         | 15.7°S, 25.6°E       | 61              | 9139          | 37            |
| All birds     | 7 Sept             |                       | 6 Nov         |                      | 61              | 9223          | 39            |



**Figure 1.** Daily distributions of speeds during short-time intervals (1–8 h) for adult Eurasian Hobbies during autumn migration in three geographical areas; Europe (top), Sahara (middle), tropical Africa (bottom). The dashed vertical lines show the sunrise and sunset periods, which differ slightly with latitude and season.

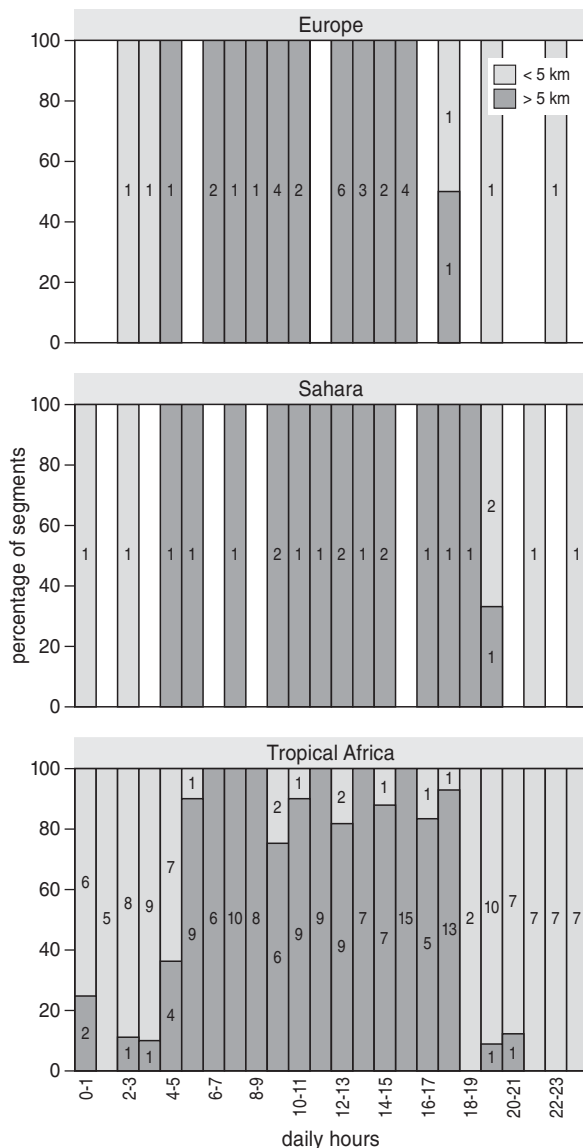
(Fig. 1). All high-speed segments (>35 km/h) in the Sahara were directed to the southwest, which may be related to the dominating easterly winds in this zone (Erni *et al.* 2005).

In the tropics, the highest speeds were predominantly achieved during morning hours (Fig. 1) and were made either over the equatorial rain forest of

Cameroon and Congo or in the nearby areas, except for one segment in western Zambia, when the bird was approaching the wintering area.

The three regions also differed in the daily travel speed (GLM mixed model,  $F_{2,8} = 14.10$ ,  $P = 0.002$ ). A post-hoc test revealed that the highest speed achieved in the Sahara (mean = 391.3 km/day) was signifi-

cantly different (Tukey B test,  $P < 0.05$ ) from the speeds accomplished in Europe and tropical Africa (mean = 188.6 km/day and 200.2 km/day, respectively). Within tropical Africa the speed during the crossing of the rainforest was noticeably high (249.9 km/day), but not significantly different from the speed in the rest of tropical Africa, which was only 191.3 km/day ( $P = 0.056$ ,  $t$ -test).



**Figure 2.** Daily distributions of stationary (<5 km of movement) and active migration (>5 km of movement) segments, based on mid-interval times for adult Eurasian Hobbies during travel days in Europe (top), Sahara (middle), tropical Africa (bottom).

## DISCUSSION

The adult Hobbies we studied adapted their flight speeds and flight hours to the local environmental conditions. Instead of avoiding geographical barriers along their routes to southern Africa they travelled with increased speed over adverse areas such as the Baltic Sea, Sahara Desert and equatorial rain forest (the latter also regarded as a barrier according to Strandberg *et al.* 2009).

While some of our predictions about travel schedules of the Hobbies were supported by the results, there were also important discrepancies between predictions and observations, especially concerning the birds' behaviour during the crossing of the Sahara Desert (prediction 2). As the sample size of our study is small our results should be interpreted with care. However, the four individuals (from three different years) behaved in a similar way with respect to speed and daily timing of migration, indicating that they showed the typical migratory behaviour for the species.

(1) *Diurnal migration with many travel hours.* The daily distributions of speed and activity (Figs 1 and 2) showed that the Hobbies were primarily diurnal migrants in Europe and in tropical Africa. They started migration earlier than raptors that are more specialized in thermal soaring flight (e.g. Osprey, cf. Klaassen *et al.* 2008). The number of daily travel hours were 8–11 in Europe and 10–13 in tropical Africa (Table 2), which exceeds the number of flight hours (about 5) in the daily time budget of migrating Ospreys in Europe (Klaassen *et al.* 2008). This is in accordance with our predictions. The Hobbies started their daily migration already at or before sunrise and reached the fastest travel speeds in the first half of the day. Still, the variation in short-interval speeds was very large, probably because of a large variation in the amount of foraging that is combined with their migratory flights.

The mean flight speed of a Hobby in active cruising flight is close to 40 km/h (similar means of 11.3 and 10.9 m/s reported by Bruderer & Boldt 2001 and Heiko Schmaljohann pers. comm., respectively). Faster speeds thus indicate that the Hobbies have travelled with tailwinds, while slower speeds indicate flight into headwinds or that the birds have made deviations or interruptions associated with a fly-and-forage strategy (Strandberg & Alerstam 2007). Also thermal soaring behaviour may have contributed to reduce the resulting speeds. Travel speeds decreased in the afternoon in Europe and tropical Africa, which was unexpected. This pattern may be due to increased foraging intensity towards the end of the day, higher flight cost for flapping

flight in relation to an increase in air turbulence throughout the day and/or to preparations for the birds' settling for the coming night.

(2) *Travel time during the Sahara passage.* The Hobbies had the longest travel days (with 12–15 h of travel time, Table 2) during the crossing of the Sahara Desert, as predicted. However, they still seemed to travel primarily during daytime and not very much during the night, a result that was in disagreement with the predicted behaviour of a distinct increase in nocturnal travel time during the desert crossing. There were only six short-term intervals indicating stationary periods in Sahara and all of these took place during the night between 6:00 pm and 4:00 am. This indicates that Hobbies tended to interrupt the desert crossing mainly at night, but there were also four short-time intervals to show that they sometimes continued to fly during the dark hours. It should be kept in mind that data are limited with only 22 short-time intervals available from the Hobbies' crossing of Sahara, and further data are necessary to evaluate the relative occurrence of diurnal and nocturnal flight more accurately.

As a result of the fast short-interval travel speeds in combination with long travel days, the total average daily travel distance reached close to 400 km for the Hobbies crossing Sahara. This exceeds daily average travel distances by typical thermal soaring migrants like Osprey and Honey Buzzard during their crossing of the Sahara Desert (with average speeds on travel days of 200–300 km/day; Hake *et al.* 2003, Alerstam 2003, Klaassen *et al.* 2008).

It is difficult to understand why the Hobbies during the desert crossing did not increase the number of daily travelling hours even further to include nocturnal flight to a larger degree (cf. Alerstam 2009). They appeared to travel both before and after the thermal time window (9:00 am – 5:00 pm) used by the Osprey (Klaassen *et al.* 2008) so resort to thermal soaring migration cannot provide the full explanation. Travel speeds were fast during the desert crossing, possibly indicating that the Hobbies were flying more consistently in their migratory direction without much deviations and interruptions for foraging. Further studies are needed to investigate if Hobbies can benefit in a sufficient way from thermal soaring and from foraging during their flights across Sahara to explain why they seem to travel mainly during the daytime in this region. The behaviour of the Hobbies stands in stark contrast to the well-defined nocturnal travel schedules used by many songbirds during their Sahara crossings (Biebach *et al.* 1986, Bairlein 1988, Biebach 1990, Biebach *et al.* 2000, Schmaljohann *et al.* 2007).

(3) *Possible nocturnal flights when foraging conditions are poor.* The most extensive data set was obtained from the Hobbies' travel schedules in tropical Africa south of Sahara. A striking feature was the early start of migration, well before sunrise. A small proportion of observations (seven out of 69 short-time intervals between 7:00 pm and 4:00 am) showed that also true nocturnal flights may occur occasionally. This pattern was in reasonable accordance with predictions, even if the decreasing activity and speeds during the afternoon and the low frequency of nocturnal flights were unexpected.

The nocturnal flights recorded in the tropics were mainly undertaken in association with degraded forest areas north and south of the rain forest belt. If these areas represents bad foraging habitats for the falcons we do not know, but we can suspect that the intact forests do. The daily rains associated with this habitat may also limit the foraging hours for the falcons and that might explain why they increase speed over and close to the forest.

## CONCLUSIONS

The daily migration schedules of the Hobby differed from those of thermal soaring migrants like the Osprey by extending flights outside the thermal time window (especially by the early morning start of migration) and by reaching a morning peak in speed. The Hobby schedules also differed from those of diurnal migrants not using thermals, like pigeons, pipits, wagtails and finches (cf. Alerstam 1990) by the extended duration of travel throughout the afternoon. We attribute the special characteristics of the daily travel schedules of Hobbies primarily to their use of a fly-and-forage strategy, possibly in combination with preparedness for exploiting thermals during the daily thermal time window.

Further studies are needed to show if the Hobby type of daily travel schedule is typical among birds using a fly-and-forage migration strategy. For such migrants one should expect that the daily travel schedule would change when migrating through regions where foraging is no longer possible, e.g. during the crossing of the Sahara Desert (Alerstam 2009). From the limited data available it seems like the Hobbies keep to a dominantly diurnal travel schedule during this crossing, in stark contrast to the vast numbers of songbirds that avoid evaporative water losses by a nocturnal schedule for their flights across Sahara (Schmaljohann *et al.* 2007). Perhaps there are after all



enough possibilities for hunting during daytime in the desert (e.g. pursuing the songbirds that land in the desert during the day) to make diurnal migration favourable for the Hobbies?

It is a challenging task to evaluate the primary selection factors determining daily travel schedules among migrating birds. Temporal analyses based on detailed tracking of individual birds over a larger range of species could provide crucial information about the daily travel schedules among different ecological categories of migrants and about the variability of schedules in different regions. For example, it would be very interesting to make a detailed comparison between Hobbies, which do not travel so much during the night, and Levant Sparrowhawks, which regularly travel during night (Stark & Liechti 1993, Spaar *et al.* 1998). Are Hobbies better in exploiting thermals during migration than the sparrowhawks, or is fly-and-forage migration more important for Hobbies than for Levant Sparrowhawks? Such detailed information and knowledge will be necessary for an understanding of the adaptive values of these important temporal aspects of migration ecology.

## ACKNOWLEDGEMENTS

We are grateful to Mikael Hake for supervising and participating in the capturing of birds, to Mikael Svensson for his climbing efforts during field season 2005 and to Anthony Chapman and Mikael Hake for encouraging discussions about Hobby ecology. We also thank Heiko Schmaljohann and an anonymous reviewer for constructive comments on the manuscript. We are grateful for support and excellent equipment from Microwave Telemetry Inc. The study was approved by the Ethical Committees in Uppsala (C92/6) and Malmö/Lund (204-06). Permission to capture the birds was obtained from the Swedish Environmental Protection Agency (412-429-05 Nf). This research was financed through grants from the Swedish Research Council (to T.A. and to R.K.) and from the Niels Stensen Foundation (to R.K.).

## REFERENCES

- Alerstam T. 1990. Bird migration. Cambridge University Press, Cambridge.
- Alerstam T. 2003. Bird migration speed. In: Berthold P., Richardson E. & Sonnenschein E. (eds) Avian migration. Springer-Verlag, Berlin.
- Alerstam T. 2009. Flight by night or day? Optimal daily timing of bird migration. *J. Theor. Biol.* 258: 530–536.
- Alerstam T., Hake M. & Kjellén N. 2006. Temporal and spatial patterns of repeated migratory journeys by ospreys. *Anim. Behav.* 71: 555–566.
- Bairlein F. 1988. How do migratory songbirds cross the Sahara? *Trends Ecol. Evol.* 3: 191–194.
- Beaman M. & Galea C. 1974. The visible migration of raptors over the Maltese Islands. *Ibis* 116: 419–431.
- Biebach H. 1990. Strategies of trans-Sahara migrants. In: Gwinner E. (ed.) Bird Migration. Springer-Verlag, Berlin.
- Biebach H., Friedrich W. & Heine G. 1986. Interaction of body mass, fat, foraging and stopover period in trans-Sahara migrating passerine birds. *Oecologia* 69: 370–379.
- Biebach H., Biebach I., Friedrich W., Heine G., Partecke J. & Schmidl D. 2000. Strategies of passerine migration across the Mediterranean Sea and the Sahara Desert: a radar study. *Ibis* 142: 623–634.
- Bijlsma R.G. & van den Brink B. 2005. A Barn Swallow *Hirundo rustica* roost under attack: timing and risks in the presence of African Hobbies *Falco cuvieri*. *Ardea* 93: 37–48.
- Bruderer B. & Boldt A. 2001. Flight characteristics of birds: 1. Radar measurements of speeds. *Ibis* 143: 178–204.
- Chapman A. 1999. The Hobby. Arlequin Press, Chelmsford.
- Cochran W.W. 1985. Ocean migration of Peregrine Falcons: is the adult male pelagic? In: Harwood M. (ed.) Proc. Hawk Migr. Conf. IV. Hawk Migration Assoc. N. Am.
- DeCandido R., Bierregaard R.O. Jr., Martell M.S. & Bildstein K.L. 2006. Evidence of nocturnal migration by Osprey (*Pandion haliaetus*) in North America and western Europe. *J. Raptor Res.* 40: 156–158.
- Dorst J. 1962. The migrations of birds. Windmill Press, Kingswood, Surrey.
- Erni B., Liechti F. & Bruderer B. 2005. The role of wind in passerine autumn migration between Europe and Africa. *Behav. Ecol.* 16: 732–740.
- Fuller M.R., Seegar W.S. & Schueck L.S. 1998. Routes and travel rates of migrating peregrine falcons *Falco peregrinus* and Swainson's hawks *Buteo swainsoni* in the Western Hemisphere. *J. Avian Biol.* 29: 433–440.
- 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* 103: 385–396.
- 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. The University of Chicago Press, Chicago.
- Kerlinger P. & Moore F.R. 1989. Atmospheric structure and avian migration. In: Power D.M. (ed.) Curr. Ornithol. Plenum Press, New York.
- Kjellén N. 1992. Differential timing of autumn migration between sex and age groups in raptors at Falsterbo, Sweden. *Ornis Scand.* 23: 420–434.
- Kjellén N. 1997. Importance of a migratory hot spot: proportion of the Swedish population of various raptors observed on autumn migration at Falsterbo 1986–1995 and population changes reflected by the migration figures. *Ornis Svecica* 7: 21–34.
- Kjellén N., Hake M. & Alerstam T. 1997. Migration strategies of two Ospreys *Pandion haliaetus* between Sweden and tropical Africa revealed by satellite tracking. *J. Avian Biol.* 28: 15–23.
- 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 observations, radar and satellite tracking. *J. Avian Biol.* 32: 57–67.
- Klaassen R.H.G., Strandberg R., Hake M. & Alerstam T. 2008. Flexibility in daily travel routines causes regional variation in bird migration speed. *Behav. Ecol. Sociobiol.* 62: 1427–1432.
- Martell M.S., Henny C.J., Nye P.E. & Solensky M.J. 2001. Fall migration routes, timing, and wintering sites of North American ospreys as determined by satellite telemetry. *Condor* 103: 715–724.
- Meyer S.K., Spaar R. & Bruderer B. 2003. Sea crossing behaviour of falcons and harriers at the southern Mediterranean coast of Spain. *Avian Sci.* 3: 153–162.
- Pennycook C.J. 1989. Bird flight performance: a practical calculation manual. Oxford University Press.
- Rudebeck G. 1950–51. The choice of prey and modes of hunting of predatory birds with special reference to their selective effect. *Oikos* 2: 67–88, 3: 200–231.
- Schmaljohann H., Liechti F. & Bruderer B. 2007. Songbird migration across the Sahara: the non-stop hypothesis rejected! *Proc. R. Soc. B* 274: 735–739.
- Spaar R., Stark H. & Liechti F. 1998. Migratory flight strategies of Levant sparrowhawks: time or energy minimization? *Anim. Behav.* 56: 1185–1197.
- Stark H. & Liechti F. 1993. Do Levant sparrowhawks *Accipiter brevipes* also migrate at night? *Ibis* 135: 233–236.
- Strandberg R. 2008. Migration strategies of raptors – spatio-temporal adaptations and constraints in travelling and foraging. PhD thesis, Lund Univ., Lund.
- Strandberg R. & Alerstam T. 2007. The strategy of fly-and-forage migration, illustrated for the osprey (*Pandion haliaetus*). *Behav. Ecol. Sociobiol.* 12: 1865–1875.
- Strandberg R., Klaassen R.H.G., Hake M., Olofsson P., Thorup K. & Alerstam T. 2008. Complex timing of Marsh Harrier *Circus aeruginosus* migration due to pre- and post-migratory movements. *Ardea* 96: 159–171.
- Strandberg R., Klaassen R.H.G., Hake M., Olofsson P. & Alerstam T. 2009. Converging migration routes of Eurasian hobbies *Falco subbuteo* crossing the African equatorial rain forest. *Proc. R. Soc. B* 276: 727–733.
- Thiollay J.-M. 1989. Distribution and ecology of Palearctic birds of prey wintering in West and Central Africa. In: Meyburg B.-U. & Chancellor R.D. (eds) *Raptors in the Modern World*. WWGBP, Berlin.
- Walter H. 1979. *Eleonora's falcon: adaptations to prey and habitat in a social raptor*. Chicago University Press, Chicago.

## SAMENVATTING

In dit artikel wordt met behulp van satellietmetrie nagegaan hoe Boomvalken *Falco subbuteo* tussen Europa en zuidelijk Afrika trekken. Door de afstand tussen opeenvolgende posities gedurende de dag (met tijdsintervallen van 1 tot 8 uur) te bepalen, is de treksnelheid gemeten. Snelheden waren boven de Sahara significant hoger dan boven Europa en tropisch Afrika. Boven de Sahara vlogen de valken van 's morgens vroeg tot 's avonds laat. Het aantal vliegreizen dat ze dagelijks maakten, was daardoor groter dan bij roofvogels die grotendeels afhankelijk zijn van thermiek. Door de hoge vliegsnelheden en 'lange werkdagen' legden de valken per dag veel meer kilometers af dan zwevende roofvogels. Boven Europa en tropisch Afrika varieerde de vliegsnelheid sterk gedurende de dag. Vooral in de middag was de snelheid daar vaak laag. De lage snelheden suggereren dat de valken trekbewegingen afwisselen met voedsel zoeken (vlieg-en-foerageerstrategie). Onze voorspelling dat de valken geregeld gedurende de nacht zouden trekken, in het bijzonder boven ecologische barrières zoals woestijnen, werd niet door de gegevens ondersteund. Boven de Sahara vlogen de valken vrijwel uitsluitend gedurende de dag. In tropisch Afrika viel echter 10% van alle bewegingen gedurende (een deel van) de nacht. De valken begonnen daar vaak al voor of gedurende zonsopgang te trekken. De speciale manier waarop Boomvalken over de verschillende regio's trekken, wordt vooral toegeschreven aan de vlieg-en-foerageerstrategie en de neiging om in de loop van de dag van thermiek gebruik te maken. De vraag waarom Boomvalken 's nachts niet trekken als ze de Sahara oversteken, vraagt om verder onderzoek. We veronderstellen dat de trekstrategie van Boomvalken een typisch voorbeeld is van een trekvogel die trek afwisselt met voedsel zoeken. Deze strategie verschilt sterk van dat van andere dagtrekkers zoals grotere roofvogelsoorten (die sterk afhankelijk zijn van thermiek) en piepers, kwikstaarten, duiven en vinken (die vrijwel uitsluitend gedurende de ochtend vliegen).

*Corresponding editor: Yvonne I. Verkuil*

*Received 23 September 2008; accepted 18 May 2009*

# ARDEA

TIJDSCHRIFT DER NEDERLANDSE ORNITHOLOGISCHE UNIE (NOU)

*ARDEA* is the scientific journal of the Netherlands Ornithologists' Union (NOU), published bi-annually in spring and autumn. Next to the regular issues, special issues are produced frequently. The NOU was founded in 1901 as a non-profit ornithological society, composed of persons interested in field ornithology, ecology and biology of birds. All members of the NOU receive *ARDEA* and *LIMOSA* and are invited to attend scientific meetings held two or three times per year.

## NETHERLANDS ORNITHOLOGISTS' UNION (NOU)

**Chairman** – J.M. Tinbergen, Animal Ecology Group, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands

**Secretary** – P.J. van den Hout, Royal Netherlands Institute for Sea Research (NIOZ), P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands (hout@nioz.nl)

**Treasurer** – E.C. Smith, Ir. van Stuivenbergweg 4, 6644 AB Ewijk, The Netherlands (ekko.diny@planet.nl)

**Further board members** – E. Boerma, G.J. Gerritsen, J. Komdeur, J. Ouwehand, G.L. Ouweneel, J.J. de Vries

**Membership NOU** – The 2010 membership fee for persons with a postal address in The Netherlands is €42 (or €25 for persons <25 years old at the end of the year). Family members (€9 per year) do not receive journals. Foreign membership amounts to €54 (Europe), or €65 (rest of the world). Payments to ING-bank account 285522 in the name of Nederlandse Ornithologische Unie, Sloetmarke 41, 8016 CJ Zwolle, The Netherlands (BIC: INGBNL2A and IBAN: NL36INGB0000285522). Payment by creditcard is possible.

Correspondence concerning membership, payment alternatives and change of address should be sent to: Erwin de Visser, Sloetmarke 41, 8016 CJ Zwolle, The Netherlands (nou ledenadmin@gmail.com).

**Research grants** – The NOU supports ornithological research and scientific publications through its Huib Kluijver Fund and the 'Stichting Vogeltekstation'. Applications for grants can be addressed to the NOU Secretary. Donations to either fund are welcomed by the NOU treasurer.

**Internet** – [www.nou.nu](http://www.nou.nu)

## ARDEA

**Editors of ARDEA** – Rob G. Bijlsma, Wapse (Editor in chief); Christiaan Both, Groningen; Niels J. Dingemanse, Groningen; Dik Heg, Bern; Ken Kraaijeveld, Leiden; Jouke Prop, Ezinge (Technical editor); Julia Stahl, Oldenburg; B. Irene Tieleman, Groningen; Yvonne I. Verkuil, Groningen

**Dissertation reviews** – Popko Wiersma, Groningen

**Editorial address** – Jouke Prop, Allersmaweg 56, 9891 TD Ezinge, The Netherlands (ardea.nou@planet.nl)

**Graphics** – Dick Visser, Haren

**Artwork** – Jos Zwarts, Bunnik

**Internet** – [www.ARDEAJournal.nl](http://www.ARDEAJournal.nl)

**Subscription ARDEA** – Separate subscription to *ARDEA* is possible. The 2010 subscription rates are €36 (The Netherlands), €42 (Europe), and €50 (rest of the world). Institutional subscription rates are €53, €69, and €78, respectively). Papers that were published more than five years ago can be freely downloaded as pdf by anyone through *ARDEA*'s website. More recent papers are available only to members of the NOU and subscribers of *ARDEA*-online. Receiving a hard-copy with additional access to *ARDEA*-online costs €55 (The Netherlands and Europe), €70 (rest of the world), or €110 (institutions). Subscriptions to *ARDEA*-online (without receiving a hard copy) cost €40 (individuals worldwide), or €85 (institutions). Payments to ING-bank account 125347, in the name of Nederlandse Ornithologische Unie, Ir. van Stuivenbergweg 4, 6644 AB Ewijk, The Netherlands (BIC: INGBNL2A and IBAN: NL16INGB0000125347). Correspondence concerning subscription, change of address, and orders for back volumes to: Ekko Smith, Ir. van Stuivenbergweg 4, 6644 AB Ewijk, The Netherlands (ekko.diny@planet.nl).

**Exchange of publications** – All periodicals sent in exchange for *ARDEA* should be addressed to: Library of the Netherlands Ornithologists' Union (NOU), c/o Tineke Prins, Institute of Systematics and Population Biology, Zoological Museum, P.O. Box 94766, 1090 GT Amsterdam, The Netherlands.

**Books for review** – should be addressed to: *ARDEA* Secretariat, c/o J. Prop, Animal Ecology Group, Biological Centre, P.O. Box 14, 9750 AA Haren, The Netherlands. After review, the books will be deposited in the NOU Library in Haren.

**NOU Library (journals)** – Mauritskade 57, Amsterdam, Mo–Fr 10:00–16:00 (to check in advance by telephone + 31 20 525 6614).

**NOU Library (books)** – Library Biological Centre, Kerklaan 30, Haren (G.), Mo–Thu 09:00–17:00 (to check at [www.rug.nl/bibliotheek/locaties/bibfwn/index](http://www.rug.nl/bibliotheek/locaties/bibfwn/index)).

© Nederlandse Ornithologische Unie (NOU), 2009

Layout by Dick Visser, Haren, The Netherlands

Printed by Van Denderen, Groningen, The Netherlands, October 2009

Downloaded From: <https://complete.bioone.org/journals/Ardea> on 18 Feb 2025

Terms of Use: <https://complete.bioone.org/terms-of-use>