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Large birds can migrate fast: the post-breeding flight of the Purple Heron *Ardea purpurea* to the Sahel

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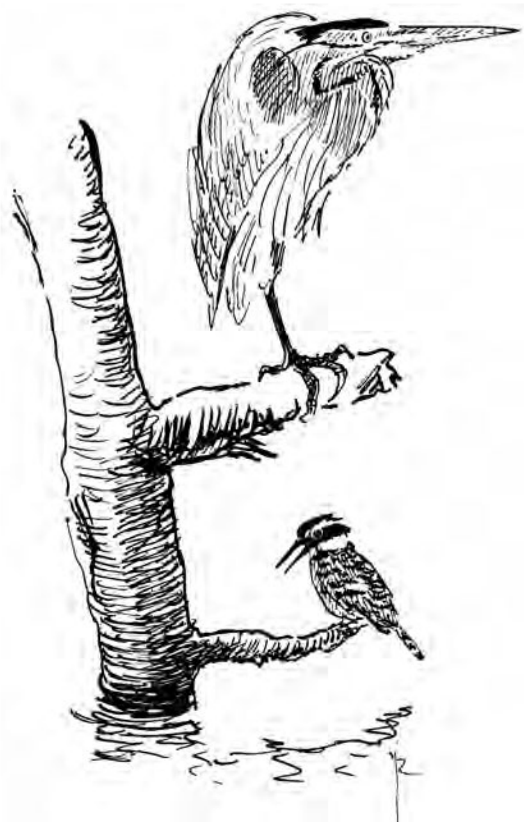

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Large and heavy birds usually use soaring flight during long-distance migration or make regular stopovers en route for substantial refuelling. Purple Herons are large, long-distance migrants. Because of their size, large herons migrating southwards from Europe to Africa were expected to make one or more stopovers to refuel. However, data from seven Purple Herons, fitted with satellite transmitters, showed that the herons were able to cover the distance into the Sahel of about 4000 km within 5–7 days. One individual even flew 5600 km non-stop, mostly over sea. The herons migrated mostly at night and partly during the day with a high travel speed indicative of flapping flight. The herons made few diurnal stops in Europe and North Africa. Substantial 'stopover' time was limited entirely to a period of several weeks before departure, and after arrival south of the Sahara. We assume that this is energetically possible for birds with a maximum wing load of 4–5 kg body mass per m^2 of wing surface. Larger wing loads as in storks or raptors prescribe soaring or refuelling with the consequence that most migratory journeys to African wintering grounds then take at least a month. The results emphasize the conservation importance of abundant and high-quality feeding habitat near the breeding areas for pre-migratory fuelling of this species. Furthermore, arrival habitat is likely to be more essential than previously expected. We suspect that the lack of suitable arrival habitat might explain the observed high adult mortality in dry Sahel periods better than 'winter' survival.

Key words: Purple Heron, satellite transmitters, migration, Sahara, conservation

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Long-distance migrating bird species have different migration strategies in which size plays an important role (Alerstam & Lindström 1990, Alerstam 1993, Alerstam & Hedenström 1998). Larger birds are constrained in the amount of fuel stores they can take along, and thus need to either economize on transportation costs by travelling by soaring, or they are required to make regular long refuelling stopovers. Large birds travelling by flapping flight like, geese and swans, typically make stopovers of one or more weeks to refuel (e.g. Andersson *et al.* 2001, Beekman *et al.* 2002). Other species like storks, raptors, cranes and pelicans use soaring during migration and regularly combine this with refuelling stopovers for periods of days or longer en route (Alerstam & Hedenström 1998, Shamoun-Baranes *et al.* 2003, Klaassen *et al.* 2008). Although soaring saves energy, many species travel by active flapping flight or use this flight mode in addition to soaring. Apparently, the advantage of conserving energy expenditure by travelling by soaring flight does not outweigh the disadvantage that soaring flight is limited to mainly midday hours, which implies relatively short daily flights (Hedenström 1993). Especially smaller birds maximize their overall migration speed by travelling by active flapping flight, despite the fact that it costs more energy (Hedenström 1993). Furthermore, active flight makes nocturnal migration possible with the additional advantages of minimising water loss and predation risk, and profiting from more stable air (Alerstam 2009, Klaassen 1996).

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Long-distance migrating herons use active flapping flight during both day and night (Maddock & Bridgeman 1992, Maddock & Geering 1993, Liechti & Schaller 1999, Kushlan & Hafner 2000). However, it was unknown whether herons make stopovers and if so, to what extent. In a previous satellite tracking study on juvenile Purple Herons *Ardea purpurea* (Jourdain *et al.* 2008), the birds could not be followed long enough to determine the migration strategy. Purple Herons are large herons with an average body mass of 900–1200 g. They breed as far north as 53° latitude in The Netherlands and spend the non-breeding period in wetlands of the Sahel region to as far south as coastal West Africa (Cramp & Simmons 1977, Zwarts *et al.* 2009). This implies a flight distance of at least 3500 km. As flapping flight comes with relatively high energetic costs we expected that a large long-distance migrant like the Purple Heron would make at least one long stopover of two to three weeks to refuel somewhere halfway along the journey from the breeding range to the Sahel. We equipped Purple Herons with satellite transmitters and found evidence for a previously undescribed long-distance travel strategy of herons. This is interesting from a biological as well as a conservation point of view.

METHODS

Five adult and three almost fully grown juvenile Purple Herons were equipped with satellite transmitters in three breeding colonies in The Netherlands in May–July 2007. The birds weighed between 960 and 1250 g at the time of capture. The transmitters were attached at the back of the herons using a lightweight Teflon backpack harness. Four adult birds were each equipped with a 30 g solar panel Platform Transmitter Terminal (ARGOS-PTT; Microwave Telemetry, USA)/GPS (Global Positioning System) and three juveniles and one adult with a 18 g solar panel ARGOS-PTT; making the total extra mass for the herons between 2 to 4% of the total body mass. The ARGOS-transmitters provide an accuracy of 100 m to more than 1500 m presented in the following classes: A, B, 1, 2, and 3 classes (see www.argos-system.org). Both types of transmitters provide information on location, however, the GPS-transmitters provide more accurate locations (±15 m) than ARGOS-transmitters and give additional information on flight altitude above-sea-level (±20 m), heading (±1°), and instantaneous speed (±1 km/h); all accuracy estimates provided by Microwave Telemetry Inc. Columbia, USA. The PTT duty cycle was programmed at 10 h on and 24 h off while the GPS-transmitter was set at a two hour log-interval. One juvenile bird was shot in Morocco, and because its transmitter did not work properly beforehand, it was excluded from the analyses.

Based on the results of a previous satellite transmitter project for Purple Heron (Jourdain *et al.* 2008) and additional tests with captive herons equipped with dummy transmitters, it was decided that it would be possible to equip Purple Herons with transmitters with acceptable risks. This was confirmed in the first months following the deployment of the transmitters as all birds behaved normally during the breeding season and no breeding failures were observed.

Data interpretation

The GPS-transmitters directly provide information on locations and speed. If instantaneous speed = 0 m/s birds were not flying. Other low speeds, which indicate e.g. walking, did not occur in the dataset. The number of logged GPS locations is strongly influenced by the battery load of the device. In cloudy circumstances or if feathers cover the solar panel the battery is insufficiently charged, resulting in gaps in information. For ARGOS-transmitters, birds were assumed resting if two subsequent positions were received within 10 km within at least a one-hour interval. If the transmitter did not move from its exact position for more than two days birds were assumed dead or the transmitter lost. The bird was also assumed to be dead if the behaviour before the last position pointed to a bad condition of the bird such as slow flight (< 10 km/h), regular stops in hostile environment (desert), and in some of our cases the presence of sandstorms just before the last positions (based on the Royal Netherlands Meteorological Institute weather reports and Google Earthcloud coverage).

We defined the 'start of migration' as the moment when birds actually took flight and started southward movements, so excluding the pre-migratory fattening period. If the exact onset of migration could not be recorded, the departure date was estimated based on average travel speed assuming an evening departure around sunset, a period with a distinct peak of migration onset (van den Bosch & Vlek 2006; van der Winden *et al.*, unpubl.). All of the studied herons moved to the region south of the Sahara and as this is the nearest regular wintering habitat (Cramp & Simmons 1977), we defined the 'end of migration' as the moment the herons reached this area and stopped flight movements for more than one day.

Instantaneous speed (km/h) was directly measured for birds with a GPS-transmitter. In addition, for these herons as well as herons with a ARGOS-transmitter,

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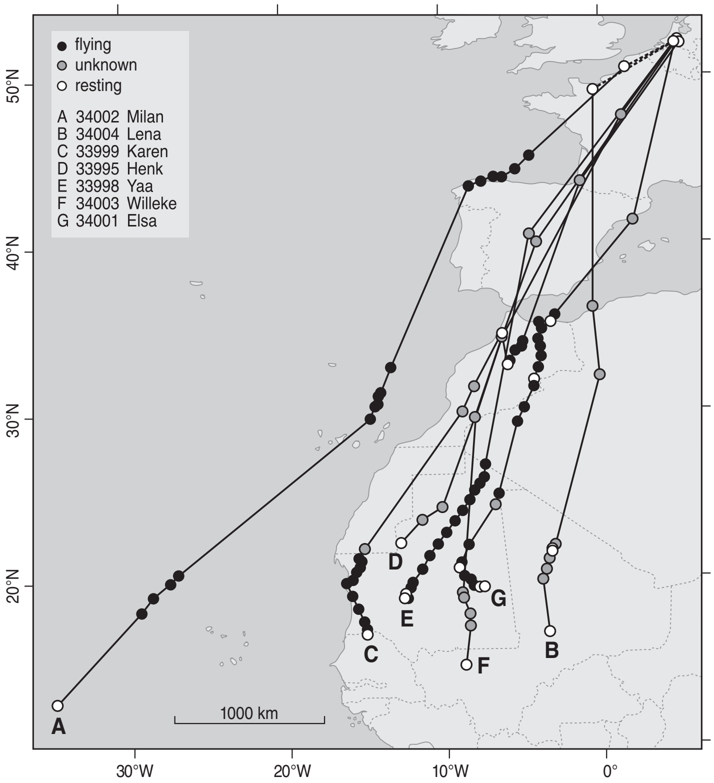

Figure 1. Migration routes of seven Purple Herons with satellite transmitters migrating from The Netherlands to Africa after breeding in 2007. The symbols distinguish between active flight, diurnal stopover or unknown (ARGOS-fixes, 1,2,3, A and B). ID 33995, 33998 and 34001 died in dust storms in the desert. Dotted line indicates dispersal movement of juveniles (A and B). Map in Equidistant Conic Projection with Africa as central median to prevent north-south distortion.

hourly travel speed (km/h) was derived by calculating distances between fixes during flight according to the shortest path between points (great circle distance). All fixes with high quality 1, 2 and 3 were used for this, as well as low quality fixes A and B if they coincided with the previous migration direction and speed based on high quality fixes. Since most of the distances were relatively short and predominantly north-south in orientation the differences with loxodrome distances (distances with a constant course on a globe) were minor. Migration speed (expressed as average n km/day) is defined as the speed from start to end of migration, including stops.

RESULTS

The eight Purple Herons started the southward migration between 28 August and 5 October (Table 1). Before these long-distance movements, adults stayed in feeding areas in The Netherlands within a few tens of km from the colonies for 30 to 82 days after breeding (van der Winden *et al.*, unpubl.). After fledging, two juveniles first moved to northern France and one juvenile moved northwards to a feeding area within The Netherlands (Fig. 1). We assume that this behaviour

Table 1. Migration statistics of seven Purple Herons (juveniles underlined) with satellite transmitters, migrating from The Netherlands to Africa in 2007. Travel time is the number of days for the entire migration and the intermediate position distance calculated as orthodrome or great circle distance. The migration speed is the average speed for the entire route excluding premigratory fuelling time at the breeding site and intra-African movements. ID 33999 suspended migration for 33 days and resumed migration afterwards and its migration parameters are calculated for the active migration period.

Bird ID	departure	Travel time (days)	Travel distance (km)	Migration speed km/day
33995GPS	4/09/07	5.2[a]	3708[a]	713
33998GPS	17/09/07	5.1[a]	4062[a]	796
33999GPS	7/09/07	13.0	4050	312
34001GPS	28/08/07	6.1[a]	3880[a]	636
34002	18/09/07	6.1	5571	913
34003	4/09/07	6.6	4038	612
34004	5/10/07	6.3	3309	525

[a] Not complete as birds most likely died en route.

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can be regarded as dispersal rather than actual migration because these juveniles moved to pre-migratory feeding areas. After arrival in such an area, they stayed at the location for a few weeks prior to actual migration, similarly to the adults.

Fast travellers

Seven herons succeeded in covering at least 3500 km (Fig. 1, Table 1). All but one bird showed a fast flight covering the route to the Sahel in 5–7 days (with an average migration speed of 699 km/day). The average instantaneous ground speed of three migrants was 45.9 km/h with a maximum of 80.0 km/h ($n = 35$) (Table 2). Instantaneous speed did not differ from travel speed (Table 2). Also the travel speed did not differ between day and night except for heron ID 33999 (Welch's *t*-test, $t = 5.537$, $df = 6.3$, $P = 0.0013$), which faced a strong headwind in Mauritania (http://www.wetterzentrale.de). Two adults died in the Sahara during sandstorms. Both birds slowed down flight speed significantly in a desert storm (confirmed by weather satellite pictures of the Royal Netherlands Meteorological Institute) and stopped moving in an extremely hostile environment (sand dunes). One other adult also slowed down flight speed substantially in the desert and stopped in a hostile environment for unclear reasons. One juvenile (ID 34002) flew in a westerly direction and ended up in the Mid-Atlantic Ocean, c. 2000 km west of Senegal and c. 1800 km northeast from the Brazilian coast, after a 5600 km non-stop flight. Based on the high average traject speed (48.3 km/h) and because of its continuous route over sea, stops were presumed impossible for this individual. Finally, we assume that it drifted for one day on the water surface (travel speed less than 2.4 km/h for at least 7 hours) and after this, the signals stopped. Lastly, two adults and one juvenile successfully reached the African wintering areas directly south of the Sahara.

Short diurnal stops

Due to problems with the batteries, GPS data were unfortunately very scarce, especially in Europe, resulting in little information on stopover time and habitat use. However, there were indications of short diurnal stops on a daily basis in Europe and North Africa (Fig. 1). For example, for one bird (ID 34001) the transmitter provided regular signals during a part of the journey from North Africa southwards (Fig. 1). This bird was flying over the Mediterranean north of Morocco around 10:00 on 1 Sept 2007. At 12:00 noon it landed in a river valley where it stayed until 16:00. This proved a short stop of about 4 hrs. At 18:00 it was flying 64 km west of this stopover point. At 10:00 on 2 Sept the bird landed again for a diurnal stop at a river valley for about 11 hrs and in the evening it took off for the flight over the Sahara.

Few other indications of stops in North Africa were obtained (Fig. 1); these stops were also diurnal. Only for one bird one stop was recorded in the Sahara (ID 34004), all other information pointed to non-stop crossings of the Sahara, based on the time of passage south of the Atlas Mountains, the time at the end position of the route in the Sahara or Sahel, and the average recorded GPS and travel speeds of around 45 and 43 km/h, respectively (Table 2). Because GPS fixes were lacking during parts of the journeys, especially in Europe, total travelling time (Table 1) could be used to reconstruct a daily stopover time based on average travel speeds and migration speed (Table 2). For four birds the non-stop crossings of the Sahara took on average 1.4 days, meaning that on average 4.3 days was spent on migration in Europe and North Africa.

Table 2. Diurnal and nocturnal flight speeds of three Purple Herons flying over Africa in 2007. Presented is instantaneous speed measured by the GPS satellite transmitter and calculated travel speed for the same transects for which GPS fixes were obtained. The diurnal and nocturnal flight speeds can be compared with the travel speed of bird 34002 (ARGOS-transmitter, so only travel speed available), which was flying continuously over water and could not stop. (n.d.) no data were available (no GPS).

Bird ID	*n* fixes	Instantaneous speed (sd) km/h	Travel speed (sd) km/h	Nocturnal travel speed (sd) km/h	Diurnal travel speed (sd) km/h
33998GPS adult	12	43.9 (10.9)	42.4(9.7)	39.2(14.1)	44.7(4.9)
33999GPS adult	10	42.9(11.9)	34.9(13.6)	50.3(1.0)	28.3(10.4)
34001GPS adult	13	50.0(13.7)	42.0(16.4)	43.5(16.6)	39.3(17.5)
34002 juvenile	17	n.d.	50.0(12.0)	50.5(8.6)	50.0(14.4)
Average		45.9(12.3)	43.3(13.8)	45.9(12.6)	41.2(14.6)

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Assuming the same average travel speed of around 45 km/h during this part of the journey, the herons must have stopped for about 47% of the time. Although GPS and ARGOS signals were scarce in Europe, the timing of passage of the birds indicates that this stopover time was evenly divided over the travel days, meaning mainly nocturnal migration alternated with diurnal stops taking less than the entire daylight period.

One adult heron (ID 33999) behaved differently to the other six herons in respect to its suspended migration halfway in Morocco. This bird encountered the same severe weather conditions in the Atlas region in which two adult birds died. However, this individual avoided the bad weather by returning north to the coast of Morocco where it suspended migration for 33 days. After this stopover it continued migration over the Atlas and Sahara non-stop like the other herons.

DISCUSSION

A fast travel to the Sahel

Our results show a yet undescribed and unexpectedly fast travel for Purple Herons, without a long stopover en route, from the breeding areas to the Sahel. In Europe and North Africa the herons flew throughout the night and part of the day, whereas the Sahara was crossed non-stop. Moreover, they travelled in continuous flapping flight and only short stops were made. Excluding the pre-migratory fattening period, the Purple Herons completed their journey of 3500–4000 km in just 5–7 days. This makes Purple Herons the fastest heavy migrants known so far covering such distance. Other large species like geese, swans, storks or raptors need 35–50 days to cover similar distances. Geese and swans need at least one long stopover en route (comparison with exclusion of the pre-migratory fattening period), while storks and raptors need thermals for soaring and can only cover about 450 km/day and therefore their migration speed is relatively slow (Meyburg *et al.* 2004, Shamoun-Baranes *et al.* 2003, Trierweiler *et al.* 2007, Newton 2008, Klaassen *et al.* 2008). Comparing Purple Herons to the Osprey *Pandion haliaetus*, another piscivorous species with a similar migration route, highlights the difference in travel strategy. Ospreys are slower than Purple Herons with an average travel speed of about 260 km/day, with a range of ground speeds of 17–47 km/h (Kjellén *et al.* 2001). The travel speed of Purple Herons, however, is lower than that of geese, who also use flapping flight and, in the case of Brent Geese *Branta bernicla* spp, can fly up to 1300–1900 km within 24 hrs (Dau 1992 in Newton 2008) compared to the close to 700 km per 24 hrs found for the herons in our study. This difference is mainly caused by the short diurnal stops made by the herons, and also by a lower flight speed. But as the Purple Herons flight:stopover ratio is 1:1 (excluding the pre-migratory fattening period) over a distance of 3500–4000 km, it results in a quicker overall journey than for Brent Geese covering a similar distance. Light-bellied Brent Geese *B. b. hrota* migrating from Greenland to the UK stop for at least two weeks in western Iceland in spring and autumn (Madsen *et al.* 1999) and Dark-bellied Brent Geese *B. b. bernicla*, which migrate 5000 km from the Wadden Sea towards northern Russia, stop also halfway, resulting in a flight:stopover ratio of 1:13 (without the pre-migratory fattening period) (Green *et al.* 2002). If pre-migratory fattening is included, these ratios are about 1:11 for Purple Herons and 1:25 for Brent Geese.

In this sense, the Purple Heron migration strategy resembles those of smaller long-distance migrant birds like Knot *Calidris canutus* or Bar-tailed Godwit *Limosa lapponica*, with few or no stopovers at travel distances of 4000 km or more, resulting in a fast travel (e.g. Piersma 1987, Gill *et al.* 2008). Such long-distance flights can only be accomplished by fattening substantially prior to migration. Based on the empirical data for Purple Heron, and the flight distance model of Pennycuick (1989, 1998), a fat mass of 0.217 kg (24% body mass) is estimated to be necessary to reach the winter quarters at a distance of 5000 km (Table 3). The assumed 24% is high for a large bird, so it is likely that the flight distance is more constrained by this, probably in the range of 3500–4000 km as was observed in six of the seven tracked birds. Further investigations should

Table 3. Flight characteristics and predicted fat fraction required for an assumed non-refuelling flight of 5000 km for Purple Heron (Pennycuick 2007, Flight model 1.18). Fat fraction is fat mass/body mass at departure.

Parameters	Purple Heron	Source/assumption
Empty mass (kg)	1.0	Alerstam *et al.* 2007/own data
Fat fraction	0.24	Model output
Wing span (m)	1.35	Alerstam *et al.* 2007
Wing area (m^2)	0.2488	Alerstam *et al.* 2007
Cruising altitude (m)	700	Based on average GPS data
True air speed (km/h)	50.8–64.8	Model output
Distance (km)	5037	Assumed distance
Flight time (h)	80.7	Model output

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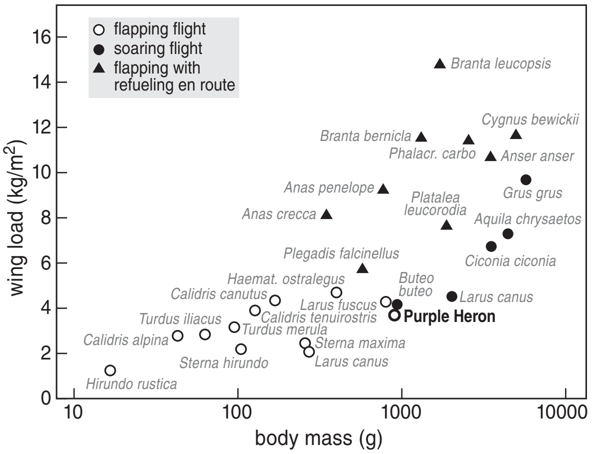

Figure 2. The relation between body mass and wing load in long-distance migrants bird species subdivided in birds with known strategies: active flapping flight with pre-migratory fuelling, (partly) soaring flights or active flapping flight with long en route refuelling stops. Data from Alerstam *et al.* (2007).

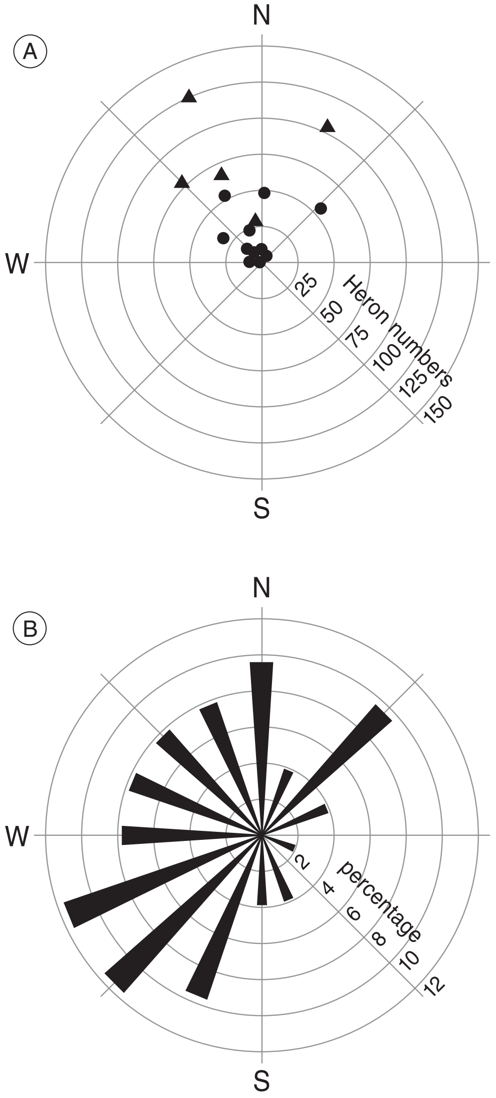

Figure 3. (A) The number of Purple Herons starting migration at a bird observatory at Ridderkerk in 2007 registered by visual counts (http://home.tiscali.nl/elzerman/vwgpureiger2.htm) in relation to the wind direction in the lower air layer. Triangles indicate days when also the herons with satellite transmitters started migration. (B) Wind directions (%) in the period 15 August to 5 October 2007 corresponding with Purple Heron departure period. Surface wind direction based on daily average surface wind direction for De Bilt, The Netherlands (www.knmi.nl).

be undertaken to get more information on the pre-migratory strategy of the Purple Herons. But it is unlikely that the 3–4 short diurnal stops en route during migration might be sufficient to store enough energy for such a flight. Moreover, indications for feeding during the (mostly) diurnal, relatively short stops are lacking.

Although many long-distance records of migrating birds using flapping flight are known, the ability of Purple Herons to use this migration strategy despite their large size may be a result of a relative low wing load compared to other large birds. So far, bird species with a maximum wing load of 4–5 kg/m^2 are known to be able to perform long-distance flights without long stopovers (Fig. 2). Covering long distances in flapping flight without prolonged stopovers is probably only just feasible for Purple Herons, given their size and wing loading (Fig. 2). In this regard, the even heavier Grey Heron *Ardea cinerea* and Great Blue Heron *A. herodias* may constitute the very limit of long-distance migration without the need for long stopovers. Accordingly, herons are potentially good colonisers, as they are capable of passing areas without refuelling opportunities and thermals, such as oceans. Our finding of the juvenile bird flying 5600 km non-stop supports this idea. The colonisation of the Americas by the Cattle Egret *Bubulcus ibis* from Europe further illustrates this point (Del Hoyo *et al.* 1992, Kushlan & Hafner 2000).

The question can be raised why herons make this long-distance migration without making long stopovers to restore reserves under way like other large birds? Perhaps migrant herons were forced into this strategy as they face insufficient and unpredictable habitat availability along their migration route in the Mediterranean and North Africa; such as during periods of summer droughts that result in wetlands of decreased size and thus increased competition with resident heron

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populations. This might have selected for a long prefattening period and a high migration speed rather than for a stopover strategy en route. The necessity of serious refuelling of at least a week or more in these regions might be risky.

Migration not possible without tailwinds?

Favourable tailwinds are essential for large long-distance migrants using active flight, especially at take-off when fat load is high (Alerstam 1979, Liechti 2006, Gill *et al.* 2008). Indeed, all Purple Herons, with or without transmitters started southward migration in evenings with favourable northerly tailwinds. At such evenings peak departures of hundreds of Purple Herons were registered at a bird observatory near Ridderkerk in The Netherlands (van den Bosch & Vlek 2006) (Fig. 3). This suggests that at least a convenient start for the herons might be important from an energetic perspective.

Conservation implications

This unexpected migration strategy shows the fragile balance between the choice for a high travel speed and the need for high quality premigratory fattening sites in the breeding range, and disturbance and hunting free sites in Spain and Morocco.

From a conservation perspective our findings imply that the quality of habitat (abundant food and rest) both in the departure areas and in the Sahel might be of crucial importance for replenishing reserves. In the nineteen-seventies, a severe dry period in the Sahel was clearly linked with a decrease in the Dutch Purple Heron population as a result of increased adult mortality (Den Held 1981). So far, the decline in surface area of foraging habitat in dry periods was assumed to have been the critical factor in adult mortality, although this was conflicting with the presence of abundant suitable wintering habitat further south in the tropical West African regions, where Purple Herons also commonly winter (Den Held 1981, Zwarts *et al.* 2009). But why is mortality high in the Sahel if abundant feeding habitat is present more to the south? We propose that the observed vicissitudes of mortality are better explained by a change in suitable habitat for arriving and (presumably) exhausted Purple Herons at the southern edge of the Sahara. Especially if, for this large species, the covered distances reported here are close to their physiological limit and particularly if wind conditions are not favourable throughout. If this is true, most fatalities of migrants might be expected at the far end of the route, which was the case for three of the studied herons. Although the reason for the fatalities is not known, severe weather occurred in two cases. It cannot be excluded that the transmitters hindered additionally, although other herons migrated successfully over the Sahara. At this stage no information is available if our relatively high loss of 3 adults in the Sahara was accidental or not. The study results might also explain the paradox of the correlation of winter mortality with Sahel droughts while substantial numbers of Dutch Purple Herons winter further south in areas without droughts. It will be very interesting to test this hypothesis in more detail and for more species.

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SAMENVATTING

Grote zware vogels kunnen relatief weinig reserves meenemen tijdens lange trekvluchten. Zij maken daarom veelvuldig gebruik van zweefvluchten of lange tussenstops om op te vetten. Purperreigers *Ardea purpurea* zijn grote vogels die actief vliegen tijdens de trek van Europa naar Afrika. Wij vermoedden daarom dat ze onderweg een of meer lange tussenstops zouden maken om op te vetten. De gegevens van zeven Purperreigers die met een satellietzender waren uitgerust, laten echter zien dat deze reigers snelle trekkers zijn die in 5 tot 7 dagen 4.000 km kunnen afleggen. Eén individu vloog, voornamelijk over zee, met de wind in de rug zelfs non-stop 5.600 km. De reigers trokken meestal gedurende de nacht en ook wel overdag, met slechts korte stops overdag. Ze verbleven alleen lang aan de grond voorafgaande aan de trek en na aankomst in de Sahel. Wij denken dat deze trekstrategie energetisch mogelijk is voor vogels met een maximum draaggewicht van 4–5 kg lichaamsgewicht per m^2 vleugeloppervlak. Vogelsoorten met een hoger draaggewicht, zoals ooievaars en kraanvogels, moeten gebruikmaken van thermiek, waardoor de reis meer dan een maand duurt. Door hun gunstig draaggewicht kunnen Purperreigers sneller trekken dan veel andere grote vogels en daarmee mogelijk slechte habitats overslaan. Dit betekent wel dat er voorafgaande aan de trek goede gebieden moeten zijn waar zij kunnen opvetten, omdat ze voldoende vetreserves moeten meenemen. Ook moet er voldoende geschikt habitat (wetlands) zijn als ze in Afrika aankomen. Omdat de vliegduur gelimiteerd is voor deze soort, is een gebrek aan geschikt habitat bij aankomst in de Sahel mogelijk een betere verklaring voor de hoge sterfte in droge jaren dan de winteroverleving, omdat de meeste Nederlandse Purperreigers ten zuiden van de Sahel overwinteren, waar droge perioden nooit zo invloedrijk zijn. Dit zou ook de onduidelijkheid kunnen verklaren die er bestaat over de correlatie tussen wintermortaliteit en regenval in de Sahel.

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