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Fuel deposition and potential flight ranges of Blackcaps *Sylvia atricapilla* and Whitethroats *Sylvia communis* on spring migration in The Gambia

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Abstract

Spring migration of Palaearctic passerines was studied on Ginak Island in The Gambia, as part of the European Science Foundation network " Palaearctic-African Songbird Migration". In this paper data collected from Blackcaps *Sylvia atricapilla* and Whitethroats *Sylvia communis*, which in late March-early April prepare for the crossing of the Sahara desert, are analysed. On a diet of mainly *Maytenus senegalensis* berries these warblers put on up to 3–4 % body mass per day and when ready for take off 35–40 % of their mass consists of fuel for the trip. According to conventional flight-range calculations this gives them flight ranges in still air of maximum 1200 km, which will not take them unaided across the desert. But predictable tailwinds, usually found at altitudes above c. 2500 m, may help them to central Morocco or beyond. In addition, recent wind-tunnel experiments have suggested a distinctly reduced drag coefficient for use in the flight-range calculations, and this may extend the still-air range to more than 2500 km. In that case the desert crossing would be possible also without the help of tailwinds.

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The main hazard for spring migrating palaearctic birds wintering in tropical Africa is the crossing of the Sahara desert (e.g. Moreau 1972) where, with the exception of a few scattered oases (e.g. Ash 1969, Bairlein 1988, 1992), water and food is in principle unavailable for 1500–2000 km. How the birds, at the height of the dry season south of the desert, prepare for and thereafter carry out this passage has for long interested ornithologists, and through the years a number of studies have been carried out (e.g. Ash 1969, Fry *et al.* 1970, Dowsett & Fry 1971, Stoate & Moreby 1995, and the overview of the question by Moreau 1972). This problem is also central in the network program "Spatio-temporal course, ecology and energetics of Western Palaearctic-African songbird migration", organized by the European Science Foundation (Bairlein 1993).

As part of the ESF- program trapping and ringing of palaearctic migrants have been carried out on Ginak Island in The Gambia, West Africa, during the springs of 1995 and 1996, organized by J.M.B. King. The scope of this paper is to describe and discuss the pre-migratory fuel-deposition in Blackcaps *Sylvia atricapilla* and Whitethroats *Sylvia communis,* based on data from 1995.

Working area and methods

Ginak Island (Fig. 1) is a 2–4 km wide and 10 km long coastal spit, stretching northwards from the mouth of the Gambia River. Its northern end reaches into Senegal. The vegetation is a coastal variety of Guinea savanna, with a fringe of mangrove on the inland side.

Our work was based on the Madiyana Lodge, situated close to the Senegalese border, among largely inactive sand dunes covered with scrubby Acacia woodland, with Tamarisk scrub in the moister depressions between the dunes. The shrub *Maytenus senegalensis* was common and its fruits constituted a major part of the diet of the palaearctic migrants, including the two species discussed here.

In 1995 work started 3 March and ended 6 April. The trapping was carried out within a few hundred

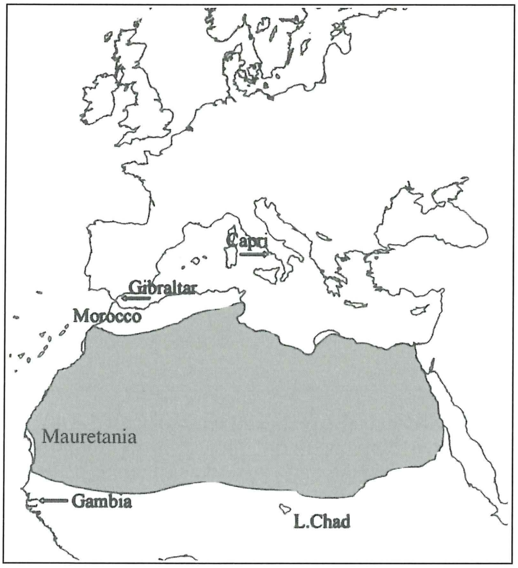

Fig. 1. Map of Africa and the western Palaearctic, with the Sahara desert shaded

Afrika och västra Palearktis, med Sahara skuggat

meters of the lodge, both in Acacia woodland and Tamarisk scrub, using a maximum of 12 60´(18 m) mist-nets. The nets were used every day from before dawn to about 11 am, and sometimes also for about 3 hours before sunset. Between 3–5 persons were involved at the same time and the grand total of palaearctic migrants ringed was 278, representing 17 species. Among these were 87 Blackcaps and 73 Whitethroats.

The birds were weighed with a Pesola balance and visible fat was scored using the 8 class (0–7) scale of Kaiser (1993). Ageing and sexing was done according to Svensson (1992) and Jenni & Winkler (1994), wing length measured according to the maximum method (method 3) of Svensson (1992).

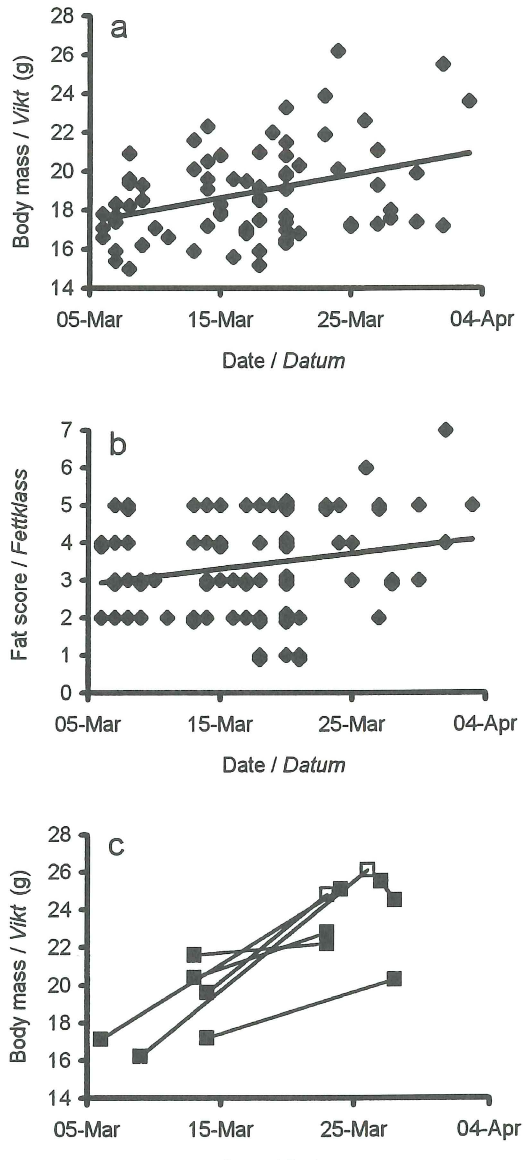

Fig. 2. (a) Body mass measurements in relation to trapping date and the general mass gain trend ($y=0.12x + 16.78$, $r^2=0.12$, $p=0.002$, $n=77$) for Blackcaps during spring 1995. (b) Fat-score measurements in relation to trapping date and the general fattening trend ($y=0.04x + 2.69$, $r^2=0.05$, $p=0.059$, $n=78$) for Blackcaps during spring 1995. (c) Retraps, showing body mass changes in individual Blackcaps during spring 1995. Filled squares represent birds trapped in the morning, open squares corrected values (see text) for birds trapped in the afternoon.

(a) Vikt i förhållande till fångstdatum hos svarthättor våren 1995, samt regressionslinjen och den statistiska signifikansen för sambandet mellan vikt och datum. (b) Fettklass i förhållande till fångstdatum hos svarthättor våren 1995, samt regressionslinjen för sambandet mellan fettklass och datum. (c) Viktutvecklingen hos svarthättor som kontrollerades en tid efter ringmärkningen våren 1995. Fyllda symboler visar vikter från fåglar fångade på morgonen, öppna symboler korrigerade kvällsvikter (se texten).

Results

Of the Blackcaps all birds were sexed (62% males) and 77 (89%) aged (10% ad.). Of the Whitethroats 32 birds (44%) were sexed (61% males), almost all of them after 24 March, and 65 (89%) were aged (20% ad.). Of the total of 87 Blackcaps and 73 Whitethroats trapped, 7 (8%) and 18 (25%) respectively were retrapped one or more times.

The distribution over time of body mass and fat-score, and the body mass developement of individual retrapped birds, are shown in Fig. 2 for the Blackcap, and in Fig. 3 for the Whitethroat. Birds which were originally trapped in the afternoon (8 Blackcaps and 18 Whitethroats) are excluded from all analyses of body mass and fat scores – except for the analyses of retraps, where a correction for the time of day has been applied.

Body mass and fat scores in relation to trapping date

In the Blackcap body mass increased significantly with date of trapping, but the relationship between date and the more open ended fat score was not fully significant (Fig. 2). Body mass, but not fat score, was significantly higher in the second half of the study period (after 20 March) than in the first: body mass 20.0 ±3.0 (SD) g *vs.* 18.5 ±2.1 g, fat score 3.9 ±1.6 *vs.* 3.2 ±1.8 (body mass, t_{75}=2.4, p=0.02; fat score, t_{76}=1.9, p=0.067). There were no effects of either age or sex on the relationship between body mass and fat score, respectively, and date (ANCOVA, effect of age on body mass $F_{[1,65]}$=0.1, p=0.70, on fat score $F_{[1,65]}$=0.1, p=0.74; effect of sex on body mass $F_{[1,73]}$=0.2, p=0.64, on fat score $F_{[1,73]}$=0.4, p=0.52).

In the Whitethroat both body mass and fat score increased significantly with date (Fig. 3). Birds were significantly heavier and fatter after 20 March than before: body mass 17.3 ±2.9 (SD) g *vs.* 15.2±1.8 g, fat score 4.3 ±1.8 *vs.* 2.8 ±1.6 (body mass, t_{53}=3.3, p=0.002; fat score t_{53}=3.0, p=0.004). As in the Black-

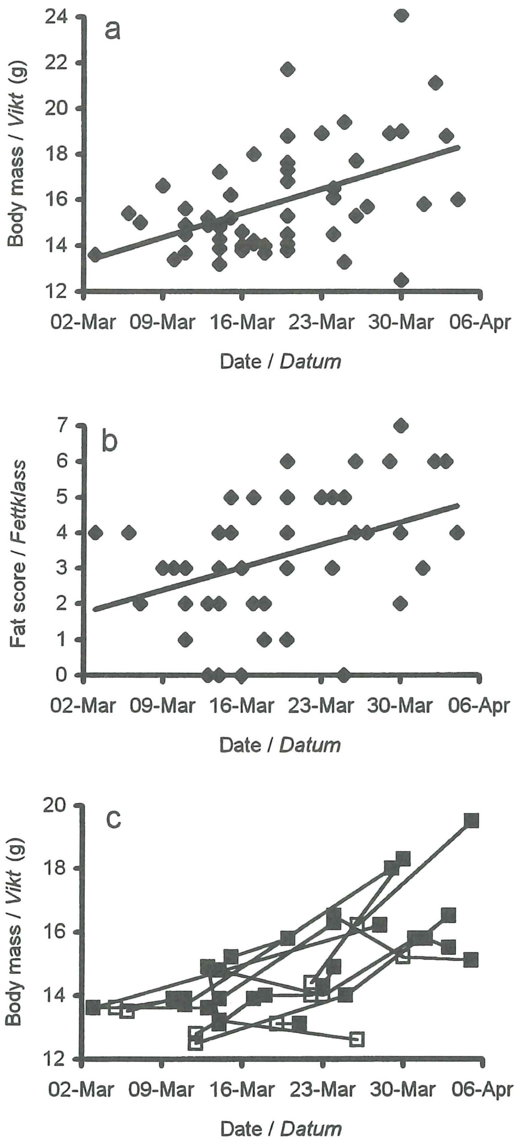

Fig. 3. (a) Body mass measurements in relation to trapping date and the general mass gain trend (y=0.15x + 13.00, r^2=0.24, p<0.001, n=55) for Whitethroats during spring 1995. (b) Fat-score measurements in relation to trapping date and the general fattening trend (y=0.09x + 1.58, r^2=0.15, p=0.003, n=55) for Whitethroats during spring 1995. (c) Retraps, showing body mass changes in individual Whitethroats during spring 1995. Filled squares represent birds trapped in the morning, open squares corrected values (see text) for birds trapped in the afternoon.

(a) Vikt i förhållande till fångstdatum hos törnsångare våren 1995, samt regressionslinjen och den statistiska signifikansen för sambandet mellan vikt och datum. (b) Fettklass i förhållande till fångstdatum hos törnsångare våren 1995, samt regressionslinjen för sambandet mellan fettklass och datum. (c) Viktutvecklingen hos törnsångare som kontrollerades en tid efter ringmärkningen våren 1995. Fyllda symboler visar vikter från fåglar fångade på morgonen, öppna symboler korrigerade kvällsvikter (se texten).

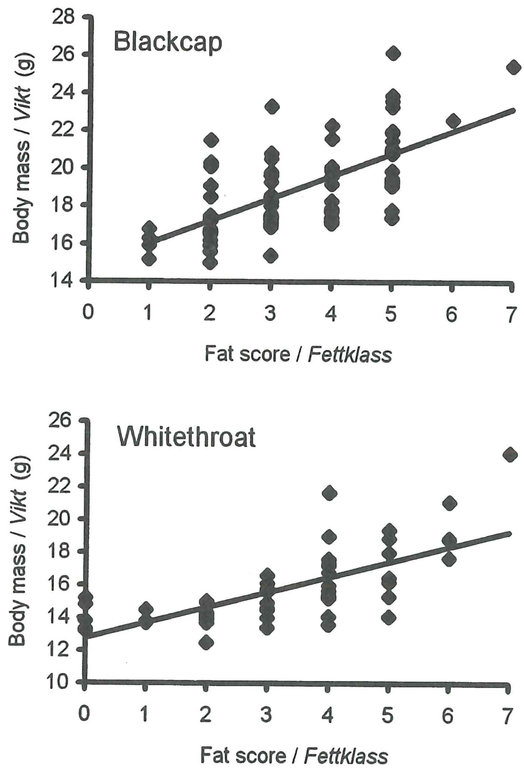

Fig. 4. (a) The body mass / fat score relationship ($y=1.20x + 14.83$, $r^2=0.43$, $p<0.01$, $n=77$) in Blackcaps. (b) The body mass / fat score relationship ($y=0.93x + 12.76$, $r^2=0.50$, $p<0.01$, $n=55$) in Whitethroats.
(a) Relationen mellan vikt och fettklass hos svarthätta. (b) Relationen mellan vikt och fettklass hos törnsångare.

cap there was no effect of age on the relationship between body mass and fat score, respectively, and date (ANCOVA, effect of age on body mass, $F_{[1,44]}=0.02$, $p=0.90$, on fat score $F_{[1,44]}=0.6$, $p=0.45$). Too few birds were sexed to test any corresponding effect of sex on body mass and fat score.

Body mass and fat score relationships

For both species the relationship between body mass and fat score was highly significant (Fig. 4). Including all trapping occasions, Blackcap body masses in 1995 varied between 15.0 and 27.6 g and fat scores between 1 and 7. The corresponding figures for the Whitethroat were 12.5–24.1 g and 0–7.

Retraps

Six out of seven retrapped Blackcaps increased in mass (Fig. 2c). Two of these were first trapped in the morning and retrapped in the afternoon. To compensate for the within-day mass increase we subtracted 1.5 g from the afternoon weights of these two birds. The other birds were both ringed and retrapped in mornings or evenings, respectively. The average mass increase was 0.4 g/day (on average 4.9 g over an average period of 13 days, n=6). Assuming a lean body mass of 15 g (the mean of 11 fat-score 0 Blackcaps weighed in early spring 1996 was 15.4 g), the average rate of mass increase was 2.4% of lean mass/day (1996 values are used in this particular case as, due to the later start of ringing in 1995, there were no 0 measurements for Blackcaps that year, and very few for Whitethroats). The two highest rates of increase (corrected values) were 9.9 g in 17 days and 5.2 g in 9 days. For both these birds the average mass increase was 0.6 g/day, corresponding to 3.5% of lean mass/day.

Many Whitethroats were ringed in the morning and retrapped in the afternoon, or vice versa (Fig. 3c). To make the body mass values comparable we subtracted 1.2 g from all afternoon weights, assuming this to be a reasonable within-day mass increase. Several birds were retrapped more than once (up to three times). Fifteen out of 18 retrapped birds had increased in mass when retrapped the last time. If retrapped more than once, we included only the occasions when mass increased up to the last trapping. The average mass increase for the Whitethroats was 0.2 g/day (on average 1.7 g over an average period of 9 days, n=15). Assuming a lean body mass of 12 g (the mean of 15 fat score 0 Whitethroats weighed in early spring 1996 was 12.2 g.; 1996 values used here, as for the Blackcap, see explanation above), the average rate of mass increase was 1.7 % of lean mass/day. The two highest increases were 3.9 g in 8 days (0.5 g/day or 4.1% of lean body mass/day) and 0.9 g in 2 days (0.5 g/day and 3.8% of lean mass/day).

Discussion

Different starting areas?

The fuel deposition patterns of the two species, as indicated by the retraps, seem slightly different. Five out of 7 retrapped Blackcaps showed distinct increases in mass (Fig. 2 c), and the other two remained at the same level (one of these in the maximum fat score class 7, when retrapped after only one day). In contrast 4 out of 18 Whitethroats started with loosing fat and mass (Fig. 3c). This indicates that many Whitethroats trapped by us may just have arrived from further south in Africa (cf. Mehlum 1983, Hansson & Pettersson 1989). A similar conclusion was drawn by Fry *et al.* (1970) for weight-loosing Whitethroats at Lake Chad. Thus most of the Blackcaps trapped by us may have wintered in The Gambia – or moved into the area earlier in the season – whereas many of the Whitethroats may have been transients.

The gradual northward exodus of both species around the shift from March to April is indicated by the decreasing numbers of birds trapped (Figs. 2a and 3a), with trapping efforts remaining largely constant.

Fuelling rates and flight ranges

In the Blackcap, an increase with one fat-score class means an average body mass increase of about 1 g (Fig. 4a). The calculated average mass increase was 0.4 g/day (maximum 0.6 g/day) and the average rate of mass increase 2.4%/day (maximum 3.5%/day). The latter figure is only one third of the maximum fat deposition rate given for the Blackcap by Langslow (1976; see also Lindström 1991, fig. 3).

An increase from fat score 0 to 6 means that a Blackcap accumulates about 7 g fuel and an increase to class 7 about 8 g. In the latter case c. 35% of the body mass in birds ready for take-off consists of fuel for the trip.

A fat score class 7 Blackcap may weigh as much as 25 g and a class 0 bird 15 g. Using Pennycuick´s calculation manual (Pennycuick 1989, program 1, version 1:1, 1992 update), with a measured average wingspan value of 20 cm (n=5) and with an approximate small bird aspect ratio of 4.8, such a class 7 Blackcap should have a flight range in still air of c. 1600 km. If we also consider that only c. 70% of the fuel load is fat, the rest being less energy rich protein (Klaassen & Biebach 1994), this range may have to be reduced to c. 75%, which corresponds to a flight range of 1200 km. In still air this will not bring the bird to refuelling areas in Morocco, only to the barren wastes of northern Mauretania.

In the slightly smaller Whitethroat, an increase with one fat-score class means a weight increase of about 0.85 g (Fig. 4b). The calculated average mass increase was 0.2 g/day (maximum 0.5 g/day) and the average rate of mass increase 1.7%/day (maximum c. 4%/day).

A fat-score class 7 Whitethroat may weigh 20 g and carries 7–8 g more fuel than the class 0 bird. This means that for these birds c. 40 % of their body mass is fuel. Using the same rough way of calculating flight ranges as for the Blackcaps (with a measured average wingspan value of 20 cm (n=4) and the aspect ratio 4.8, a decrease from class 7 to class 0 from 20 – 12 g (Fig. 4b) and a reduction of the calculated range to 75% (due to fat vs. protein mobilization rates), we find that under still air conditions a class 7 Whitethroat, like the Blackcaps, would only be able to travel c. 1200 km – which is not sufficient for the desert crossing.

The above calculations would thus seemingly lead to the conclusion that these warblers cannot manage the desert crossing without either refuelling en route, or using tailwinds.

As to the refuelling, Bairlein (e.g 1988, 1992) showed that some migrants do refuel in the few and scattered Saharan oases. But the limited number of such places and the somewhat limited numbers of birds encountered there indicates that this is not the strategy adopted by the bulk of migrants.

As to the tailwinds, Biebach (1992), after calculating flight-ranges for autumn migrants trapped in the Mediterranean area and at desert sites south thereof (using Rayner´s (1990) formula), came to the conclusion that they could not make the crossing without the aid of tailwinds. He also noted that in autumn the wind regimes normally allow the birds to profit from tailwinds. Piersma & van de Sant (1992), studying West African spring wind patterns in relation to wader migration, noted that birds which fly high (usually above 2500 m) and which adapt their flight altitude to the best winds, can profit from tailwinds of on average 15 km/h. If we put the Blackcap´s and Whitethroat´s air speed at 30–35 km/h (e.g Alerstam 1990, Biebach 1992) that tailwind means a range extension of 40–50%. That should get the birds into viable refuelling areas in Morocco.

However, very recent wind-tunnel experiments (Pennycuick *et al.* 1996) have indicated that the drag coefficient hitherto used in the flight range calculations (Pennycuick 1989, and 1992 upgrade) has been grossly overestimated. It may indeed be only about 10% of what was earlier believed. If the new empirically derived coefficient is used, the still air flight ranges for both the Blackcap and Whitethroat will exceed 2500 km – which is more than needed to cross the Sahara without tailwinds!

Different populations with different timing?

When comparing our material with other spring migration data sets from sub-Saharan Africa we can, for the better studied Whitethroat, note that weights for April–May in Ethiopia (means 15–16 g, ranges between 11.3–22.1 g; Ash 1994) were largely similar to ours from The Gambia (Fig. 4b). The large Whitethroat material collected at Lake Chad in 1967–68 (Fry *et al.* 1970, Dowsett & Fry 1971) showed similar spring weights (mean 15.8, range 12.0–23.5 g). The latter study, as already mentioned, also found that retrapped Whitethroats at Lake Chad had a tendency to initially loose weight, indicating (as for our birds) arrival to a stopover site after migration from the south. But whereas the Whitethroats in The Gambia seem to have their maximum fat deposition and take-off period in late March– early April, the Lake Chad birds reached that period first about one month later, at the end of April and in early May. The mean fat deposition rate at Lake Chad was 0.6 g/day (Fry *et al.* 1970, p. 69), which is higher than our maximum rate from The Gambia. The later fattening and take-off probably indicates a more northerly, later available goal for Lake Chad birds than for the Whitethroats passing through The Gambia.

That the Whitethroats passing through The Gambia aim for more southerly breeding areas than those at Lake Chad is also indicated by the generally small wing lengths of the birds trapped in The Gambia (second year males 71.5 mm, n=12; second year females 71.3 mm, n=11; after second year males 70.3 mm, n=9; after second year females 72.3 mm, n=3). No wing lengths were given for the birds studied by Fry et al. (1970) at Lake Chad, but according to the recovery map in Glutz von Blotzheim & Bauer (1991, p. 859) they may be the same birds which en route northwards pass Capri in Italy in early May. These have on average 2–3 mm longer wings (Pettersson *et al.* 1990) than the Gambian birds.

The above conclusion is further substantiated by winter recoveries of British Whitethroats in Senegal (da Prato & da Prato 1983) and by the fact that in spring British birds arrive to their breeding areas some 3 weeks earlier than Swedish Whitethroats (Fransson 1995).

From a study at a spring stopover site in a southern Moroccan oasis, of birds which had covered most of the desert passage, Ash (1969) reported a mean mass for Blackcaps of 14.1 g. Using our data, this means a mean fat-score class around 0. The mean mass for Whitethroats in Morocco was 13.7 g, which according to our data corresponds to a mean fat-score of between 0–2.

Conclusion

Blackcaps and Whitethroats which in spring (largely through feeding on *Maytenus* berries) put on fuel in The Gambia before the trans-Saharan passage may gain between 3 and 4% of their fat-free body mass per day. When ready for take-off about 35% of a Blackcap´s and 40% of a Whitethroat´s body mass consist of fuel for the trip. According to conventional flight-range calculations this gives them flight ranges in still air of around 1200 km, which will not take them unaided across the desert. But predictable tailwinds, usually found at altitudes above 2500 m, may help them to reach central Morocco or beyond. In addition, recent wind-tunnel experiments have suggested that a distinctly reduced drag coefficient should be used in the flight-range calculations. This may extend the still air range to more than 2500 km – allowing a desert crossing also without the help of tailwinds.

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Sammanfattning

Fettupplagring och möjliga flygsträckor hos svarthättor och törnsångare på vårflyttning i Gambia.

Inom ramen för ett sameuropeiskt forskarnätverk kring fågelflyttningen mellan Palaearktis och Afrika har brittiska och svenska ornitologer sedan 1995 bedrivit ringmärkning på Ginak Island i Gambia. Fångstmiljön är ett kustnära äldre dynlandskap, numera bevuxet med acacior och diverse buskar och med tamarisksnår i fuktigare områden. Här förbereder sig många palaearktiska flyttfåglar för passagen över Sahara, vars södra gräns ligger blott 300 km norrut. Av största vikt för bränslepåfyllningen (fettupplagringen) inför ökenpassagen är bären på den vanligt förekommande busken *Maytenus senegalensis*.

Svarthättor och törnsångare som rastade på Ginak under uppladdningsperioden kring skiftet mars/april 1995 ökade sin kroppsmassa (vikt) med upp till 3–4 % per dag och när de var redo att ge sig iväg norrut (vid fettklasstatus 5–7 på en åttagradig skala som börjar med 0) bestod de till 35–40 % av bränsle – i huvudsak pålagrat fett. Enligt hittills använda normer för beräkning av fåglars potentiella flygsträcka skulle detta ge dem en räckvidd i vindstilla väder på ungefär 1200 km. Detta är emellertid inte tillräckligt för att ta dem över den 1500–2000 km breda öknen,

där komplettering med föda och vatten sällan låter sig göras. Enda lösningen för fåglarna vore att utnyttja den medvind som normalt blåser på ca 2500 m höjd. Med hjälp av medvind skulle de med de observerade bränslereserverna kunna nå över öknen till acceptabla rastområden i Marocko. Dessa vindar är dock inte helt förutsägbara och medvind kan mer eller mindre utebli vissa år, något som då borde leda till populationskrascher av en storleksordning som sällan eller aldrig noterats.

Därför kunde man undra om beräkningarna verkligen var korrekta, och nu visar också vindtunnelförsök i Lund att den friktionskoeffecient som använts i de tidigare beräkningarna troligen är kraftigt överskattad. Ett nytt, empiriskt och avsevärt mindre friktionsvärde ungefär fördubblar svarthättornas och törnsångarnas räckvidd i vindstilla väder, till mer än 2500 km. Detta räcker för att flyga över Sahara, även utan hjälp av medvind!