ספרות אורות

המאמרים במערכת הדפסים זו מוגנים על-פי חוק זכויות יוצרים.

d下面是小冊 tấtואלי של לימוד וחפירה.

אינני מענה על כל שימור מסחרי למאמרים.
Blackcapped *Sylvia atricapilla* stopping over at the desert edge: physiological state and flight-range estimates

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Migrating Blackcapped *Sylvia atricapilla* were mist netted at the desert edge in northern Israel and in Elat (southern Israel) during spring and autumn migrations between 1970 and 1991. Birds in spring in northern Israel were representative of birds that had completed the crossing of the Sahara, while those in Elat still had to cross the 150 km of the Negev Desert, which separates Elat and northern Israel. In autumn, birds captured in northern Israel were representative of those about to cross the Sahara Desert, while those in Elat had already started to cross the desert. The data allowed analysis of seasonal and location differences in the physiological state of Blackcaps before and after crossing the Sahara. Data analysed included body mass, visible fat score and calculated fat content. Autumn migrants were in better physiological condition than spring migrants at both locations, probably as a consequence of their migration route through fertile areas in autumn compared with the crossing of the Sahara in spring. Body mass was less variable after the Sahara crossing in spring than before the crossing in autumn. In spring, 71% and 67% of the birds were fat depleted (fat scores 0 and 1) at Elat and in northern Israel, respectively, while in autumn 34% and 42% were fat depleted. Blackcaps at Elat were 1.6 g lighter than those in northern Israel in autumn and 1.9 g lighter in spring. Potential flight ranges were estimated on the basis of meteorological conditions and flight altitude of passerines above the Negev in Israel (northern Sahara edge) during migration and on a simulation model that considered both energy and water as potential limiting factors for flight duration and distance. The simulation model predicted that half of the Blackcaps that stopped over in Elat and the majority of those that stopped over in northern Israel could not make a nonstop flight over the Sahara Desert in autumn without the assistance of at least an 8 m per s tailwind. Such a wind would still not be sufficient for 34% of the birds in Elat and 42% in northern Israel, and clearly they had insufficient fat reserves to cross the Sahara in a single flight. Although the fattest Blackcaps had accumulated sufficient fat to enable them to traverse the Sahara in a single flight, they probably faced dehydration by at least 12% of their initial body mass when they reached the southern Sahara edge. These birds should use intermittent migration with stopovers at sites with drinking and feeding potential. Their decision to stop over during the day in the desert at sites with shade but without food and water would be beneficial if the meteorological conditions during daytime migration imposed greater risks of dehydration than at night. Spring migrants could not reach their breeding areas in Europe without feeding, but those examined in Elat could cross the remainder of the desert in a single flight.

How do passerine migrants cross the ecological barrier of the Sahara Desert? The "single nonstop flight" hypothesis postulated by Moreau (1961, 1972) was recently challenged on the basis of the physiological state (energetic and water balance considerations) of migrating birds, leading to the conclusion that an intermittent migratory strategy is more appropriate when weather conditions are unfavourable (Baillie 1985, 1992, Biebach 1990, 1992). The amount of fat deposition prior to trans-Saharan flight may indicate the possibility of nonstop flying, and some theoretical energetic considerations demonstrated such ability (Gladwin 1963, Moreau 1972, Bibby & Green 1981, Wood 1982a, Biebach 1990). Nevertheless, water rather than energy may be the limiting factor for long flights, as suggested originally by Yapp (1956, 1962). A simulation model, taking into consideration energy and water balance during migration and developed by Carmi et al. (1992, 1995), predicted that water may limit flight duration of small passerines over the Sa-
hara, and therefore they should fly only at night and rest during the day. When evaporative water loss would be high-
est, their model was based on a 10-g Willow Warbler Phyl
miscus trochilus with 30% fat and 50% water, and the model
has not yet been used to analyse migration limits of other
species based on field data representing the full spectrum of
physiological states of migrants just before crossing the Sa-
hara.

Weather conditions, especially wind speed and direction,
have been considered vital for successful migration over the
Sahara (Alerstam 1990, Biebach 1990). However, data on
the altitude choice of passerines during migration and me-
teorological conditions at these altitudes have only recently
become available (Bruderer 1994, Bruderer & Liechti 1995,
Bruderer et al. 1995). These new data, combined with the
new simulation model for flight range estimates that takes
into consideration the physiological state (energy and water)
of migrants (Carmi et al. 1992, 1995) and field data on the
actual physiological state of migrants on the desert edge,
now enable more realistic and accurate flight range esti-
mates and can therefore be used to evaluate the possibility
for a single nonstop flight over the Sahara.

Israel is a major stopover of many migrating birds be-
tween the western Palearctic and East Africa. Furthermore,
northern Israel is also located on the Negev Desert edge,
which is adjacent to the Sahara Desert belt, and is the last
opportunity for migrants to refuel before crossing the Negev
and the Sahara in autumn and the first feeding opportunity
after the desert crossing in spring (Fig. 1). Many species of
migrant birds pass through Elat (Safril 1968, Shinarai &
Gellert 1987) which is the southernmost point in Israel,
located 150 km south of the northern Negev edge (Fig. 1).
Comparison of the physiological state of migrating pass-

Figure 1. (A) Map of Israel with the location of Blackcap trapping sites (triangles). Northern Israel zone is hatched: (B) Map of the eastern Sahara Desert with the location of Israel and Elat. The stippled area shows rainfall <100 mm per year.

ines at different distances from the desert edge in Israel and
between seasons should throw some light on their migration
strategy. The Blackcap Sylvia atricapilla is one of the most wide-
spread nocturnal migrants that breeds in the western and central
Palearctic and migrates to tropical Africa (Curry-
Lindahl 1981). The migratory behaviour of the Blackcap
and its genetic basis have been studied extensively (Berthold
1986, 1988b, Helbig 1991a,b). Genetic factors play an im-
portant role in the control of migratory processes in this
species (see Berthold & Helbig 1992, Helbig 1994). The
Blackcap is a transient in Israel, although recently a few
were found wintering in northern Israel (I. Izahkai, pers.
obs.). It is assumed that the Blackcap, as with most passer-
ines, cross the Mediterranean Sea and the Sahara-Saudi-
Arabia desert belt on broad fronts with more intensive mi-
gration through the eastern and western Mediterranean ba-
sin (Wood 1982b, Berthold 1988a, Helbig 1994). In the
Middle East, the Blackcap is much more numerous in spring
than in autumn (Flint & Stewart 1983, Yom-Tov & Ben-
are more likely to stop over at Elat in spring, after crossing
about 2000 km of desert, than in autumn, after crossing
more fertile areas and only 150 km of the Negev Desert.
Elat appears to be an essential stop in the spring, especially
for lean birds, being one of the first fertile areas migrants
encounter after crossing the Sahara (Maitav & Izahkai 1994).

The aim of this study was to identify the migration strat-
egy of the Blackcap based on field data of birds trapped in
Israel just before and after trans-Saharan migration. To as-

ess the ability of stopover migrants to terminate their jour-
ney from northern Israel and Elat in each migrating season
without refueling, with respect to the hypothesis of a non-
<table>
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<th>$b_1$ (time)</th>
<th>$b_2$ (date)</th>
<th>$b_3$ (year)</th>
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<th>d.f.</th>
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</table>

* Equations are $y = a + b_1 x_1 + b_2 x_2 + b_3 x_3$, where $a$ is the $y$-intercept. $b_1$, $b_2$, and $b_3$ are partial regression coefficients and $x_1$, $x_2$, $x_3$ are the independent variables. $b_1$ is body mass (g) gained per hour. $x_1$ is time; $b_2$ is body mass difference per 1 day along each season. $x_3$ is the date; $b_3$ is body mass difference per 1 year. $x_3$ is year. $F$-statistics and corresponding $P$-values indicate how well regression models fit data. $r^2$ expresses the proportion of the total variability in $y$ attributable to the dependence of $y$ on $x_1$, $x_2$, $x_3$.

* All values were significant at the $P < 0.001$ level except $b_3$ for northern Israel in autumn. Where $P < 0.05$.

stop trans-Saharan crossing (Wood 1982b) v an intermittent migration strategy (Safriri & Levie 1988, Levie & Safriri 1989, Bieblin 1992, Carmi et al. 1992), we compared the physiological state (body mass and fat score) of Blackcaps trapped before and after the desert edge (northern Israel and Elat, respectively) within and between spring and autumn migrations.

**STUDY AREAS**

The data were gathered by mist netting in different locations throughout Israel. For this study, data were grouped into two zones: (1) Elat (29°33′N, 34°57′E), which is located at the northern tip of the Gulf of Aqaba (Fig. 1) and (2) northern Israel, which included all catchers between the southern Judean Mountains (31°48′N) in the south (250 km north of Elat) and Mount Hermon (33°29′N) in the north (440 km north of Elat). The dimensions of this zone are c. 175 km × 60 km (Fig. 1).

Elat is a green spot on the desert route between the Saharan Desert and northern Israel, located 150 km south of the northern Negev Desert edge (Fig. 1). Mean annual rainfall in Elat is only 25 mm, and the maximum temperature in the summer months reaches 47°C (Jaffe 1988). Elat resembles the conditions of a desert oasis, with several habitats, such as open water reservoirs, fields, cultivated gardens, a marsh and a salt marsh, concentrated in a small area (Shiri & Gellett 1987).

The northern Israel area includes different habitats such as mountains and plains, sandy and rocky beaches, fields and groves and steep and shallow river banks. This area is part of the temperate region and is characterized by relatively high humidity, cloudiness and precipitation and relatively low temperatures and solar radiation. The minimal mean annual rainfall is 400 mm in the southern Judean Mountains and the maximum is 1000 mm in Upper Galilee in the north (Jaffe 1988). It is expected that these areas would provide better foraging opportunities than in Elat because of the richer natural vegetation.

**METHODS**

The data for this study were gathered from capture records provided by the International Bird Centre in Elat, by The Israel Ornithology Centre of the Society for Protection of Nature in Israel and by A. Roshman, Z. Abramsky and U.N. Safriri. Mist netting was carried out during spring and autumn migrations between 1970 and 1991 at 36 locations in northern Israel (Fig. 1) and in Elat (southern Israel). Each captured bird was given a numbered ring and was sexed by plumage characteristics. Maximum wing cord was measured to the nearest millimeter and body mass was determined with a Pesola 50-g spring balance to the nearest 0.5 g. Visible fat was quantified according to an ordinal scale developed by Helms and Drury (1960).

Before analysing the effect of zone, season and sex on body mass, the masses were corrected. This correction was based on the linear relationships between body mass and (1) time (hour) of capture, (2) date (day and month) of capture and (3) year of capture. Four regression equations were calculated, each for a different zone-season combination (Table 1). Body mass was positively correlated with all three variables in all zone-season combinations except in Elat in spring where date was negatively correlated with body mass (Table 1). The effect of these three independent variables on body mass was greater in autumn than in spring (Table 1). All body masses were corrected to 12.00 h (Cherry 1982). All body masses were corrected to 1 October 1985 in autumn and to 1 April 1985 in spring. At Elat in autumn, the effects of time of day and year were not significant, and body masses were corrected only for the
date (Table 1). In northern Israel in autumn, the effect of date was not significant, and therefore body masses were corrected only for time of day and year (Table 1).

Very few birds (1.7% in spring and 1.3% in autumn in both zones) were recaptured after the day of their first capture. Furthermore, no Blackcaps that was ringed at any site in northern Israel was recaptured at any other sites in northern Israel or in Gat and vice versa (Lachman & Langer 1991, 1992). Hence, many birds that stop over in Elat in spring probably overfly northern Israel, and those that stop over in northern Israel in autumn probably overfly Elat. These data suggest that most Blackcaps departed within a day or night of their arrival and did not accumulate fat elsewhere, in Elat or in northern Israel. Therefore, we assumed that body mass and fat score which were measured in the field are adequate representations of body condition in departure for migration.

A three-way analysis of variance was employed to analyse the effects of zone, season and sex on the corrected body mass. The three-way ANOVA test was performed by GLM (SAS Institute Inc. 1988), analysing separately each main effect and adjusting for the effect of every other, before assessing the effects of two-way and then three-way interactions.

We calculated the estimated possible nonstop flight ranges (without refueling) of Blackcaps from Elat and from northern Israel in both seasons with the use of a computer-simulation model published by Carmi et al. (1992) and including modifications (Carmi et al. 1995). Part I of this model was based on Penncuick (1989) and treated energy as the only limiting factor in migration, while part II treated water as the limiting factor and separated water and fat loss. The first model used the Penncuick default values, and the input data included meteorological conditions and body-related measurements.

Meteorological data were based on a recent publication (Bruderer et al. 1995) of altitude choice of nocturnal passerine migrants in the Arava Valley in the Negev, Israel (Fig. 1). The weather data, as well as the migration altitudes, refer to a site which is 150 m below sea level (Bruderer 1994, Bruderer et al. 1995). Most autumn migrants flew in a height zone between 200 m and 1400 m above ground level (a.g.l.; Bruderer 1994: fig. 5). Therefore, the height of 700 m a.g.l. was chosen as a representative value for autumn migrants. The average height distribution of Blackcaps on spring migration was estimated as 2000 m a.g.l. (Bruderer et al. 1995:fig. 6). The average temperature, humidity and pressure at these altitudes were 21°C, 54% and 970 mb, respectively, in autumn, and 10°C, 52% and 840 mb, respectively, in spring (Bruderer et al. 1995:fig. 1). These meteorological conditions were measured in the middle of the night during the migration season.

The body-related measurements for the model included wing span (0.2 m, calculated according to Buggot 1986), fat amount and fat-free body mass. Two independent estimates were made for fat and fat-free body mass: (1) Minimal estimate. Fat was extracted with the use of petroleum ether (I. Izhaki, 1986; unpublished PhD thesis, The Hebrew University of Jerusalem; using the procedure of Moreau & Dolph 1970) from a sample of Blackcaps caught in northern Israel during migration. Then an equation was calculated for the relationships between extractable fat (FAT), fresh body mass (BM) and wing-length (WING). FAT = 75.735(BM/WING)^1.8198 (r^2 = 0.53, P < 0.001, n = 74). Fat-free body mass was calculated as body mass minus fat. The equation for fat estimation gives an increase of 1 g body mass corresponding to an increase of 0.51 g fat, which is 9–24% lower than in other published equations (see below). This equation was used for minimal estimation of fat, and a second method was used for maximal estimation of fat. (2) Maximal estimate. Fat amount was calculated from the differences between body mass and the minimum fat-free body mass found in this study. Minimum fat-free body mass of Blackcaps was defined as the mean body mass of the lowest quartile of birds in Elat in spring after a desert crossing (mean = 13.31 g, n = 982). A change of 1 g in body mass in Garden Warblers Sylvia borin and Willow Warblers Phylloscopus trochilus corresponded to a change of 0.60 g and 0.75 g in fat content, respectively (Biebich 1990, see also Kolier 1992). The average value of 0.68 g, which is 17% higher than the values obtained from the first equation, was used. Thus fat was estimated from the equation FAT = (BM - 13.31) × 0.68.

RESULTS

Body mass and fat load of captured Blackcaps

In general, Blackcaps landing in Israel during autumn were 27% heavier than in spring (mean ± s.d. = 20.01 ± 3.58 g, n = 1032, v = 15.78 ± 2.02 g, n = 6132, respectively). V = 37.5, P < 0.0001; data were pooled from both zones and sex). Those making a stopover in northern Israel were 1.9 g and 1.6 g heavier than those in Elat in spring and autumn, respectively (sexes pooled). A three-way ANOVA indicated that, after correcting body mass for time of day, date and year of capture (Table 1) and also correcting for zone and sex, the difference in body mass between seasons was 4.3 g (Table 2). After correcting for season and sex, Blackcaps stopping over in Elat were lighter than those in northern Israel by 2.58 g. There was no significant mass difference between sexes.

Although there were significant differences in average body mass between seasons and zones, the frequency distributions of body mass were relatively similar between zones within each season (sexes pooled, Fig. 2). In both zones, the distribution was much narrower in spring than in autumn, indicating that body masses in spring, after desert crossing, were more homogeneous than in autumn, before the desert crossing. Autumn mass distributions were bimodal in both zones and more prominent in Elat, indicating that one mode was of lean Blackcaps, but another important group was of relatively fat Blackcaps (Fig. 2).

Frequency distributions of fat class scores at each zone and sex combination demonstrated large proportions of lean
Table 2. Three-way ANOVA comparing body mass of Blackcaps by migration season (spring and autumn), zone (Elat and northern Israel) and sex. The results of F-tests for main effects (season, zone and sex) and interactions are given. Also given are the average deviation of each category from the grand mean (mean of all individuals regardless of category, see bottom line of table) and sample size of each category. Body masses were corrected to time, date and year of capture before analysis (see Methods).

<table>
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*The deviation of mass and wing-length in each category from the grand mean was calculated after adjusting for the other main effects. For example, the body mass grand mean of 556.1 Blackcaps was 16.39 g; 1012 of these blackcaps were captured in autumn, and Blackcaps in autumn tended to exceed the grand mean by 3.49 g after accounting statistically for variation in mass attributable to zone and sex. Since there were significant interactions, the deviations must be considered as only approximations.

birds in spring and fat birds in autumn, with more extreme distributions at Elat (for statistical analysis, see Fig. 3). At Elat, the fattest Blackcaps (fat class 3) in autumn were 50% of the total trapped birds, while in northern Israel, the fattest birds in autumn were only 41% of the total trapped birds (Fig. 3). The highest proportion of fat-depleted birds (fat class 0) in spring was detected in Elat, where 45% were in this group: in northern Israel, this group was 40% of the trapped birds (Fig. 3).

Although there was a positive correlation between fat class and body mass for each zone and season combination, the average body mass of Blackcaps that were in the same fat class was different between seasons in each zone as well as between zones in each season (Fig. 4). The average lean bird (fat class 0) weighed 14.3 g in Elat in spring and 15.7 g in autumn, while in northern Israel, the average lean bird weighed 16.1 g in spring and 17.2 g in autumn. The average fat bird (fat class 3) weighed 17.8 g in Elat in spring and 21.3 g in autumn, while in northern Israel, it weighed 19.5 g in spring and 23.5 g in autumn (for statistical analysis, see Fig. 4).

Fat content
Fat content (sexes pooled) estimated from the correlation with body mass and wing-length (minimal estimate) was 37-58% lower than fat content estimated from the differences between body mass and the average body mass of the lower quartile of fat-free birds (fat class 0) in Elat in spring (13.3 g, maximal estimate). Accordingly, the minimal estimation yielded lower values of fat index (fat content/body mass) and higher values of fat-free body mass than the maximal estimate (Table 3).

The minimum fat index was found in Blackcaps with fat class 0 which stopped over in Elat in spring (3.2% and 4.7% by these two methods), and the maximum fat index was found in birds with fat class 3 in autumn in northern Israel (21.5% and 25.9% by the two methods; Table 3).

Still-air flight range estimate
The still-air flight ranges according to their fat classes were calculated for spring and autumn migrants (sexes pooled) alighting at Elat and in northern Israel (Table 3). First, the maximum range was estimated using the assumption that energy is the only limiting factor. The predicted flight distances based on the two different methods of fat estimation were greater in autumn than in spring and were longer for Blackcaps in stopover in northern Israel than at Elat (Table 3, Fig. 5). The estimated flight potential of Blackcaps alighting in Elat in autumn before desert crossing indicates that
the lean birds with fat classes 0 and 1 may accomplish less than 500 km (flight duration of 5–11 h with flight speed of 10.1 m/s), while the birds with fat class 3 may accomplish 740–1200 km (19–32 h, 10.5–10.7 m/s, depending on the estimation method; Table 3). The estimated flight range in northern Israel in autumn of the lean birds with fat classes 0 and 1 is 400–800 km (10–22 h, 10.2–10.3 m/s) and of birds with fat class 3, it is 940–1430 km (24–37 h, 10.6–10.9 m/s, depending on the estimation method; Table 3, Fig. 5). The maximum nonstop flight in spring was for birds with fat class 3 in northern Israel, and they could fly 1000 km (26 h, 10.8 m/s; Table 3).

Estimated total water loss during these flights indicated that birds in all fat classes would lose <10% of their initial body mass. The exceptions were Blackcaps with fat class 3 in northern Israel (both seasons) and Blackcaps in Eliat in autumn that lost >10% of their initial body mass (maximal estimate; Table 3, Fig. 5).

**The effect of winds on flight range estimate**

The trade winds (from the northeast) in autumn in the Arava were found at 500–1500 m a.g.l. to have an average speed of 4–4.5 m per s (Bruderer et al. 1995), and trade winds of 8 m per s were reported at 1000 m above the Sahara (Griffith & Soliman 1972). Although the first values seem to be appropriate for our simulation (since the flight altitude of Blackcaps that we chose was 700 m a.g.l.), the

**Figure 2.** Frequency distributions of body mass (sexes pooled) of migrating Blackcaps according to zone (Eliat and northern Israel) and season. Arrows indicate mean body mass in each distribution.

**Figure 3.** Frequency distributions of fat classes of migrating Blackcaps according to zone (Eliat and northern Israel), sex and migration season. Distributions differed between sexes for each zone-sex combination (Eliat, males: $x^2 = 156, n = 2194, P < 0.001$; Eliat, females: $x^2 = 189, n = 2044, P < 0.001$; northern Israel, males: $x^2 = 91, n = 1171, P < 0.001$; northern Israel, females: $x^2 = 122, n = 1175, P < 0.001$).

**Figure 4.** Relationships between mean body mass (g, ± s.d.) and fat score for Blackcaps migrating during spring and autumn in Eliat and in northern Israel. Sample sizes are given in parentheses. One-way ANOVA indicated significant differences between the 16 fat class-zone-season combinations ($F_{15,108} = 9.36, P < 0.001$). Means with the same letter above them are not significantly different ($P < 0.05$, Duncan’s multiple range test).
Table 3. The estimated still-air flight range for Blackcaps in different fat classes stopping over in Elat and northern Israel in spring and autumn, based on a computer-simulation model (Carmi et al. 1992, 1995).* Fat and fat-free body mass were estimated by (two methods for details, see Methods)

<table>
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<tr>
<th>Zone</th>
<th>Method I—Minimal estimate</th>
<th>Method II—Maximal estimate</th>
</tr>
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<tr>
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<td>Body mass (g)</td>
<td>Fat (g)</td>
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* The followed climatic values were assumed for the model: flight altitude, 2000 m, 700 m; air temperature, 10°C, 22°C; air pressure, 840 mb, 970 mb; relative humidity, 57%, 54%; (values for spring and autumn, respectively calculated from Frasier, 1997). The following default values were used: air density, 1.35 kg per m³; energy density of fat, 3.9 × 10³ J per kg, conversion efficiency, 0.23; induced power factor, 1.2; circulation/respiration factor, 1.1; profile power ratio, 1.2 (Carmi et al. 1992). wing span, 0.2 m (calculated from Bodenagel 1986).

* Minimal estimate—fat amount was calculated from the following equation (I. Ishak, 1986, unpublished PhD thesis, The Hebrew University of Jerusalem): Fat = 75.735 (body mass/ wing²) - 2.195 (body mass = wet body mass [g], wing is wing chord length [mm]).

* Maximal estimate—fat amount was calculated from the following equation: Fat = (body mass - 13.31) × 0.68. Minimum fat-free body mass (13.31 g) was the average of the lower quartile of body mass of Blackcaps with fat class 0 in spring in Elat after desert crossing; 68% of body mass increase was assumed to be related to fat change (calculated from Biebich 1992).

* Percentage of fat from (wet) body mass.
* Percentage of water loss from initial body mass.
value of 8 m per s (which is the maximum reported value over the Sahara) was chosen as the tailwind speed in the simulation model to reduce the probability of underestimation of flight range. In spring, 10-m per s anti-trade winds (from the southwest) were detected above 2000 m a.g.l. (Bruderer et al. 1995), and this value was used to represent tailwind speed in spring.

Using tailwinds during the entire flight would increase the estimated still-air flight range of birds in all fat classes by 71–76% in autumn and by 89–93% in spring as calculated by both methods, assuming that fat is the only limiting factor (Fig. 5).

**DISCUSSION**

**Condition at stopover**

Fat-depleted migrants should predominately at the first available habitats following the Sahara crossing in spring, and fat migrants should predominately at the same habitats just before desert crossing in autumn. The results were consistent with these expectations in spring, and 71% and 67% of the Blackcaps were fat depleted (fat classes 0 and 1, sex pooled), while 66% and 58% of the Blackcaps in autumn were relatively fat (fat classes 2 and 3, sex pooled) at Elat and at northern Israel, respectively (Fig. 5). Blackcaps’ decision to land in northern Israel and at Elat in autumn before entering the eastern Sahara which has few oases and nearly no vegetation (Biebach et al. 1986), appeared to be similar to the decision made by migrants flying over large oases in the Sahara and is related to their low fat reserve and high probability of successfully foraging in these fertile areas.

Only 350 km separates the centre of the northern Israel zone and Elat; the most southern 150 km are the Negev Desert (<300 mm annual precipitation; Fig. 1). Nevertheless, Blackcaps in Elat were 8% and 12% lighter than those that stopped over in northern Israel in autumn and spring, respectively. Differences in body size between these two zones could not account for these differences since wing-lengths of Blackcaps stopped over in Elat were significantly larger than those stopped over in northern Israel in both seasons (I. Izhaki & A. Maitav, unpubl. data). Thus, the differences in body mass were likely a result of differences in fat deposition. Elat may attract lean birds needing to rebuild their fat stores in one of the last oases before the Sahara crossing, and the high proportion of lighter birds in autumn may reflect this situation. The between-zone differences in body mass in spring were probably an outcome of the higher probability of birds to refuel in the more productive habitats in northern Israel, although Blackcaps stopped over in Elat in spring, especially the leaner ones, tended to increase their body mass as well (Maitav & Izhaki 1994).

Average body mass of autumn-migrating Blackcaps was 20% and 24% heavier than of spring-migrating Blackcaps in northern Israel and Elat, respectively (see also Yom-Tov & Ben-Shahar 1995). It is likely that the differences in body mass between seasons were fundamentally a result of the fact that in autumn the birds were caught before crossing the ecological barrier (Mediterranean Sea and/or Sahara Desert), while in spring, they were caught after the trans-Saharan journey (Izhaki & Safriel 1985, Yom-Tov & Ben-Shahar 1995). The two peaks in the bimodal distribution of body mass in autumn in both zones might represent different populations with different body sizes. Differences in body masses might indicate the passage of two subspecies of Blackcap: Sylvia atricapilla atricapilla and S. a. dammehi (Yom-Tov & Ben-Shahar 1995).

**What limits flight range?**

What is the minimum distance that southward migrants should accomplish from Elat and northern Israel before reaching habitats suitable for replenishing their energy and water? The Sahel zone in Sudan, bounded approximately by the 75-mm and 300-mm isolates, is attractive to many au tumnal passerines including Blackcaps (Hogg et al. 1984). Therefore, for this discussion, we assume that the minimal direct flight routes from northern Israel and Elat to the northern Sahel boundary (20°N) would be 1200 km and 1550 km, respectively (Fig. 1). These flight routes represent the lower range of the 1500–2500 km suggested for Saharan crossing (e.g. Biebach et al. 1986, Lavee & Safriel 1989, Alerstam 1990). Since no ecological barrier characterizes the northward spring passage of Blackcaps from northern Israel and only 150 km of desert separate Elat from northern Israel, the following discussion will focus mainly on autumn migration.
Estimated still-air flight range in autumn, if energy was the only limiting factor, showed that only Blackcaps with fat class 3 were able to cover the minimal 1200 km necessary to complete the Sahara crossing from Elat (only by the maximal estimate: Fig. 5). None of the Blackcaps which stopped over in northern Israel was able to cover the 1550 km to the southern Sahara edge in still air as well. If energy was the only limiting factor, encountering an 8-m per s tailwind would enable birds with fat class 2 in Elat and fat classes 2 and 3 in northern Israel to accomplish a nonstop journey over the Sahara in autumn (maximal estimate only: Fig. 5). Therefore, energetic consideration revealed that only the fattest birds in Elat (fat class 3) would be able to cross the Sahara without favourable tailwinds. Furthermore, only birds with fat classes 2 and 3 (66% and 58% of the Blackcaps stopped over in Elat and northern Israel, respectively) were able to complete their autumnal desert crossing with the assistance of 8-m per s tailwinds. Ground speed of migrants over the Mediterranean Sea in autumn is between 15 m per s (Casement 1966) and 18 m per s (Adams 1962), which is 4-8 m per s faster than the calculated flight speed of Blackcaps (Table 3). Indicating that migrants actually profit from tailwinds in autumn and, as suggested by Bibbach (1992), may rely on this wind for successful desert crossing.

Those Blackcaps that had established large fat reserves for desert crossing were probably unable to use all the fat in a single flight because of the threat of dehydration. Thus, it seems that dehydration is the most important physiological constraint for the most obese Blackcaps (Carmi et al. 1992). It is still not clear how much dehydration passerine birds can tolerate. Carmi et al. (1992) used the least restrictive assumption that the maximum allowable amount of net water loss is 10% of the bird's pre-flight water content. Since they assumed that the 10-g body mass of the Willow Warbler contained 5 g water and 3 g fat, the permissible dehydration in their simulation model was 15% of the initial body mass or 21% of fat-free body mass. A much more restrictive value of 5% of initial body mass was assumed for pigeons (Nachtschall 1990). If the tolerable dehydration of migrating Blackcaps is 10% of their initial body mass, the most obese birds (fat class 3 in both zones, maximal estimate) in autumn would likely face high dehydration when completely utilizing their fuel reserves (Fig. 5).

Spring transients in Elat did not face dehydration and were only energy limited, while the most obese birds (fat class 3) in northern Israel probably faced dehydration because they lost 12% of their initial body mass (Table 3). The ability of birds to carry out their nonstop journey over the Sahara without dehydration risk in spring but not in autumn is principally related to the air temperature at their flight altitudes. While spring migrants over the Negev at 2000 m altitude encounter air temperatures of about 10°C, autumn migrants at 700 m encounter much warmer air of 22°C (Bruderer et al. 1995). Although such high temperatures probably increase evaporative water loss, the majority of the autumnal migrants over the desert edge did not choose the 2500-m flight altitude, which has the expected preferable temperature of 10°C (Biebach 1990), probably because of the anti-trade winds at this altitude (Bruderer et al. 1995). The finding that temperature profile has no influence on height distribution of nocturnal passerine over the Negev was probably an indication that the wind regime was the predominant factor in flight altitude (Bruderer et al. 1995), although it may have placed them at risk of dehydration. Water measurements of migrants in the desert are scarce, but so far, there is no evidence to support the notion that small passerines in the desert are dehydrated (Biebach 1990). These conclusions are valid only if the meteorological conditions and flight altitudes that have been measured in the desert edge (Negev in Israel; Bruderer et al. 1995) also characterize the remainder of the migration route over the Sahara.

Flight strategy

As indicated from the estimated flight range, only a minority of the Blackcaps that stopped over in Israel could cross the Sahara in single flight with tailwind assistance and without dehydration threat. Are the others doomed to perish during attempted crossings of the Sahara? Different flight strategies are expected for each of the following two distinctive groups of migrants.

(1) Blackcaps with insufficient fat reserves could not achieve one nonstop flight to the southern Sahara edge. Therefore, these birds most likely apply either an intermitent migratory strategy or a gradual migratory movement along the Nile (Biebach et al. 1986, Biebach 1990, I. Tahal, 1986, unpublished PhD thesis. The Hebrew University of Jerusalem). In any case, the chosen stopover sites in the desert should supply food in order to rebuild fat reserves of these lean birds (but see Carmi et al. 1992). The proportion of migrants that stop over in oases is still unknown, and no mass migration has been recorded along the Nile Valley (Biebach 1990). Although most studies pointed out the importance of east Africa as wintering quarters of Blackcaps, there is evidence that some may winter in the Nile Valley in Egypt (Curry-Lindahl 1981, Goodman & Meninger 1989, Cramp 1992). Another possibility is that lean Blackcaps that stop over in Israel take a southwestern route of c. 400 km to the Nile Delta and Valley.

(2) Blackcaps with sufficient fat reserves but under threat of dehydration could accomplish a nonstop flight over the Sahara with tailwind aid by terminating their flight on the desert edge before reaching fat exhaustion. For example. Blackcaps with fat score 3 in northern Israel could cross the 1550 km to the Sahel edge in 23.5 h, with 8 m per s tailwind, with net water loss of 7%, rather than depleting their total fuel reserve by flying 37 h with net water loss of 12%. The option to terminate the journey on the desert edge rather than fully utilizing energy reserves seems to fit all birds with fat score 3 in Elat and in northern Israel. However, the water budget for such nonstop flights of these birds probably leaves only a narrow margin of safety to successfully cross
the Sahara (Carmi et al. 1992). Studies that observed the phenomenon of fat migrants that stopped over in the desert where food and water were not available (Barlein 1985, 1992, Biebach et al. 1986, Biebach 1990) did not elucidate how these birds could regain their net water loss.

Finally, broad generalization from the data that were gathered in northern Israel and Elat to all birds setting up to cross the desert, especially in autumn, depends on whether or not this sample was representative. Since the number of Blackcap transients in Israel was much less in autumn than in spring, perhaps in autumn only the less fit individuals were unable to continue their journey, stopping over in Israe1 when the majority continued their flight into the desert without stopping. Our interpretation will probably remain suggestive until sufficiently small transmitters are available for using satellite telemetry in small migratory passerines.

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