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PHILOPATRY TO STOPOVER SITE AND BODY CONDITION OF TRANSIENT REED WARBLERS DURING AUTUMN MIGRATION THROUGH ISRAEL[1]

KOBI MEROM
Kibbutz Nir David, Bet Shean Valley, Israel

YORAM YOM-TOV[2]
Department of Zoology, Tel Aviv University, Ramat Aviv 69978, Israel, e-mail: yomtov@post.tau.ac.il

ROBIN MCCLERY
Department of Zoology, South Parks Road, Oxford OX1 3PS, U.K.

Abstract. Philopatry to stopover site and changes in body condition of migrating Reed Warblers *Acrocephalus scirpaceus* were studied in Bet Shean Valley, Israel, where warblers were netted throughout the year. Although the majority of birds were seen only once, the proportion of transients seen twice or more in different years is comparable to the figure for summer residents returning between years, indicating a high degree of philopatry among transients. Transients get heavier with longer duration of stay, up to about 15 days, after which body mass increase appears to level off at about 3 g. Change in body condition, taken to be body mass divided by wing length, also was noted, albeit of less significance. The mean date of arrival in the autumn of birds in their first year was about 20 days later than that of older birds. Reed Warblers use their time effectively to replenish their body mass and improve their condition before starting the dangerous crossing of the Sahara Desert.

Key words: Acrocephalus scirpaceus, *body condition, philopatry, Reed Warbler, stopover.*

Philopatry or home-site fidelity for both breeding and wintering grounds is a well known phenomenon among birds (Baker 1978, Sokolov 1988, Cuadrado 1992). The advantages of philopatry include familiarity with the physical and biological conditions of the site, which may increase foraging efficiency and improve breeding site selection. Site fidelity for stopover sites is less well known (Winker et al. 1991, Cantos and Telleria 1994, Rimmer and Darmstadt 1996). However, it seems logical to assume that birds that make stops during migration will similarly benefit from replenishing their reserves in localities whose resources are familiar to them.

Moreau (1972) assumed that migrating small Palearctic passerines fly without stopping from their breeding grounds to their winter destination in Africa and back. Recent data suggest that this does not apply to many small passerines, which in fact make stopovers of various lengths. Stopovers offer an opportunity to replenish energy and water reserves, and avoid harsh weather conditions. Recent studies have shown that whereas individuals of several species increase their body mass and improve body condition (Winker et al. 1992, Morris et al. 1996), sometimes showing an average daily gain of about 1.5% of body mass (Otahal 1995, Yong and Finch 1997), others may undergo a decline in energetic condition during stopover (Winker et al. 1992, Parrish 1997).

Palearctic Reed Warblers (*Acrocephalus scirpaceus*) breed in Eastern Europe and Asia and over winter in East Africa as far south as Zambia (Cramp 1992). Reed Warblers are abundant in reed beds, swamps, and near fish ponds in central and northern Israel, are easily captured in mist nets, and many individuals tend to return to the same locality every year. Two subspecies of the Reed Warbler occur in the western Palearctic: *A. s. fuscus,* which breeds in Russia, the Near East, and Iran, and *A. s. scirpaceus,* which breeds in Europe. The distinction between the two subspecies is based on feather coloration and is difficult to determine under field conditions (Dement'ev and Gladkov 1968), especially as geographical variation is slight and the races may intergrade in Turkey (Cramp 1992) and probably elsewhere in the Middle East. In Israel, both subspecies are common transients, passing through during spring and autumn, but *A. s. fuscus* also commonly breeds in Israel between April and June (Hovel 1987, Merom et al. 1999). Reed Warblers are seen in Israel between mid-February and October, but some individuals may be seen in November. Both subspecies winter in sub-Saharan Africa where they finish their molt (Dowsett-Lemaire and Dowsett 1987).

We report on philopatry for stopover site and changes in body condition of migrating Reed Warblers.

METHODS

Reed Warblers were trapped in mistnets by one of us (KM) in a fish pond area in Bet Shean Valley, northern Israel during 1986–1994. Netting took place about three times weekly between the end of February and the end of May and between August–October, and about twice weekly during the rest of the year. Nets (36 m) were erected for 2.5–3 hr, either during the morning, starting 30 min before sunrise, or during the evening, until about 30 min after sunset. All captured individuals were fitted with numbered aluminum rings, weighed with a Pesola spring balance to an accuracy of 0.1 g, and their wing cord measured to 0.1 mm using calipers. Age was noted according to the EURING code to the following categories: (0) birds of the

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[2] Corresponding author.

TABLE 1. The number of birds captured and seen again in subsequent years.

Status	Years seen 1	2	3	4	5	6	7	All
Summer breeders	5,013	563	156	47	4	1	2	5,786
Transients	2,470	96	26	3	1	0	0	2,593
Wintering	1,508	9	0	0	0	0	0	1,517
Ambiguous	94	37	4	2	2	0	0	139
Total	9,085	705	183	52	7	1	2	10,035

year, (1) first calendar year, (2) second calendar year, etc. Birds of the year are easily recognized by their fresh plumage, dark legs and eyes, and two white spots on the back of the tongue, and second and third calendar years birds by their paler legs and eyes which gradually turn brown. Body condition was calculated by dividing body mass by wing length. No individuals, whether summer breeders or transients, could be sexed.

We divided the captured specimens into four groups: summer breeders, transients, wintering, and ambiguous based on the date of their first capture. Broadly, to qualify as a summer visitor, birds had to be seen in May, June, or July, but were not disqualified if seen up to the end of August, although they could not be seen in September–November. To qualify as a transient, the bird had to be seen between 16 August and 30 November, with no other observations after 1 May or before 1 August. Both summer visitors and transients seen between 1 December and 1 May retained their defined status, except for those seen only outside the winter period, which were classified as "wintering." Birds observed in both summer and autumn were classified as "ambiguous;" the majority of these were seen only in August. Table 1 presents these categories and the number of observed individuals in each.

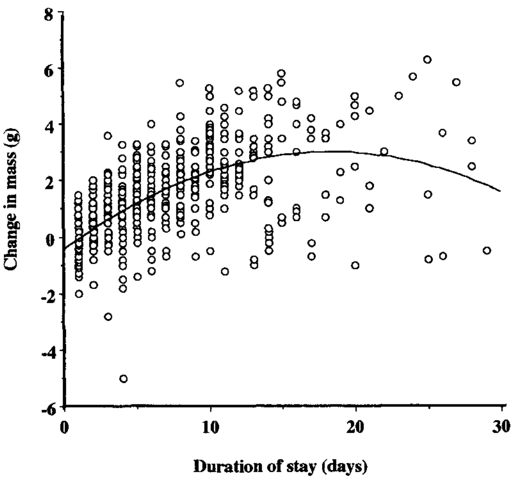

FIGURE 1. Daily body mass change of Reed Warblers staying at Bet Shean Valley during autumn migration. Polynomial regression $F_{1,65} = 29.45$, $P = 0.001$. For sample sizes see text.

It was not possible to make meaningful comparisons between "spring" and "autumn" migrations as the majority of the 177 birds seen during early spring appeared to be summer residents. Only nine definite transients were observed, and only one of these was captured more than once during the same season, implying that transient individuals did not remain for very long in the study area during spring migration. Hence, the results of this study are from summer breeders and autumn transients.

We analyzed the data using *t*-test, χ^2 test, polynomial regression, and ANOVA.

RESULTS

SITE FIDELITY

A total of 9,085 warblers were captured and ringed between 1986–1994. Although the majority of birds were seen only once, an appreciable number of transients (123/2,593) were seen in subsequent years. If one considers only those specimens observed more than once, the proportion of transients (27/123, or 22%) seen more than twice is comparable to the figure for summer residents (210/773 or 27%). These proportions do not differ significantly (χ^2 test pooling 3 or more years of return, $\chi^2_2 = 0.6$, $P = 0.72$). Although the vast majority of birds were seen only during one season, the pattern for those seen over at least two seasons shows that roughly the same proportion of transients return as residents (pooling 5 or more returns, $\chi^2_3 = 3.0$, $P = 0.38$). Thus, although fewer transient than resident individuals were caught, the proportion of each seen repeatedly remained the same.

BODY MASS GAIN AND BODY CONDITION

From wing length measurements (means ± SE: summer breeders 63.7 ± 0.4 mm, ambiguous 63.3 ± 1.6 mm, transients 66.1 ± 0.6 mm, wintering 66.3 ± 0.7 mm), it would appear that "winter" birds are probably "transients," whereas "ambiguous" individuals are more likely to be late migrating summer individuals. The longer wing length of transients is probably related to the fact that they breed farther north than summer breeders, and conforms with Allen's rule. In most of the following we have discarded winter and ambiguous individuals and use only the definite transients.

Transients get heavier with longer duration of stay, up to about 15 days, after which body mass increase appears to level off at about 3 g (Fig. 1), an average (± SE) gain of 0.17 g (± 0.01) day^{-1}, which is equiv-

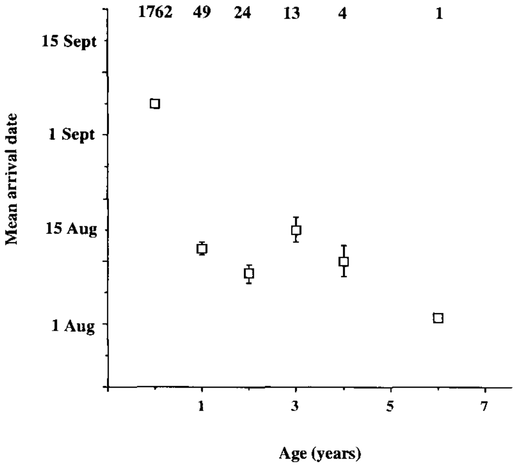

FIGURE 2. Mean (± SE) arrival date of Reed Warblers caught at Bet Shean Valley during autumn migration. Birds of the year (marked 0) arrive significantly later than all other age classes, and are the only ones caught during October–November. Sample sizes are given above each data point.

alent to 0.2% of mean body mass (polynomial regression $F_{1,660} = 396.2$, $P = 0.001$). The condition (body mass/wing) on arrival of birds who stayed > 10 days was significantly worse than that of birds staying 1–10 days (we omitted birds seen only once in a season from this analysis; $t_{252} = 4.46$, $P < 0.001$; we use an unpooled test here as the variance of the 1–10-day group was about twice that of the long stay group). This difference was entirely due to differences in body mass between the groups—they did not differ in wing length ($t_{705} = 0.93$, $P = 0.93$).

There was a very slight tendency for birds arriving later in the season to be heavier by about 0.01 g day^{-1} ($F_{1,2606} = 80.7$, $P = 0.001$).

We determined the first arrival date for those birds which could be aged accurately, and sought a correlation between arrival dates in successive years. The mean date of arrival of birds in their first year was about 20 days later than that of older birds (Fig. 2). In fact, nearly all adult transients were seen in late August and September, with only birds of the year being seen in October and November.

There was a weak correlation between date of arrival in the first year of life and that of the following year ($r = 0.31$, $n = 41$, $P < 0.05$). There were no significant correlations in any other pair of ages, but this could be due to the very small sample size for birds over the age of two.

DISCUSSION

The similar proportion of transient and summer resident warblers recaptured at the same site (a single small reedbed), indicates a high degree of philopatry among transients. Reed Warblers are known to be philopatric to both their breeding (56% in a Jersey, United Kingdom, population; Long 1975) and wintering grounds (13.6% in an Ugandan site, Pearson 1972, Dowsett-Lamaire and Dowsett 1987). If they also are generally philopatric to their stopover sites, as shown in this study, this may indicate that they spend most of their lives in familiar sites during breeding, wintering, and even stopover sites during migration.

Adult Reed Warblers arrive earlier than juveniles, probably because they already know where they are going, while juveniles are finding their way, foraging as they go. Some support for this view comes from the fact that fat scores of juveniles increased from September to November. Another factor which may contribute the late arrival of juveniles is competition with adults in stopover sites, which may reduce foraging efficiency of juveniles. The almost total temporal separation of juveniles and adults in stopover sites (adult transients were seen in late August and September, with only birds of the year being seen in October and November) means that there is no competition between these two groups.

Similar to some other species in various countries (Morris et al. 1996, Yong and Finch 1997), Reed Warblers use their time effectively to replenish their body mass and improve their condition before starting the dangerous crossing of the Sahara Desert.

The very small recapture rate during spring migration may indicate that there is a selective advantage for migrants to make the return spring journey faster than the autumn one. This is probably due to the need to occupy a territory and ensure successful breeding. Shorter stay at stopover sites during spring also is possible because of the increased availability of suitable habitats as the birds travel farther north from the desert belt and into the Mediterranean region (Yom-Tov and Ben Shahar 1995), whereas during autumn, birds tend to stop longer in order to accumulate fat reserves for the desert crossing.

The accumulating evidence that individuals may use the same stopover sites during successive migrations has important implications for conservation (Yom-Tov 1993, Cantos and Telleria 1994). This is especially true for birds with narrow habitat requirements, and those living in marshes, lakes, and other water-related habitats. For Palearctic species, access to water is particularly important before crossing the Sahara. Hence, wetlands and oases are crucial for the survival of many birds. In Israel, the number and size of wet habitats, such as swamps, rivers, and even temporary water pools, decreased considerably during this century (Yom-Tov and Mendelssohn 1988), and similar phenomena occurred elsewhere throughout the Middle East. Thus, the intensive use of water resources throughout the Mediterranean region and the draining of swamps for agricultural use, threaten not only local avifaunas but also migratory birds.

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FLIGHT COSTS AND FUEL COMPOSITION OF A BIRD MIGRATING IN A WIND TUNNEL[1]

MARCEL KLAASSEN
Max-Planck-Institut für Verhaltensphysiologie, D-82346 Andechs, Germany, and Netherlands Institute of Ecology, Centre for Limnology, P.O. Box 1299, 3600BG Maarssen, The Netherlands, e-mail: klaassen@cl.nioo.knaw.nl

ANDERS KVIST AND ÅKE LINDSTRÖM
Department of Animal Ecology, Lund University, Ecology Building, S-223 62 Lund, Sweden

Abstract. We studied the energy and protein balance of a Thrush Nightingale *Luscinia luscinia*, a small long-distance migrant, during repeated 12-hr long flights in a wind tunnel and during subsequent two-day fueling periods. From the energy budgets we estimated the power requirements for migratory flight in this 26 g bird at 1.91 Watts. This is low compared to flight cost estimates in birds of similar mass and with similar wing shape. This suggests that power requirements for migratory flight are lower than the power requirements for nonmigratory flight. From excreta production during flight, and nitrogen and energy balance during subsequent fueling, the dry protein proportion of stores was estimated to be around 10%. A

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