CHANGES IN BODY CONDITION FROM SPRING MIGRATION TO REPRODUCTION IN THE GARDEN WARBLER *SYLVIA BORIN*: A COMPARISON OF A LOWLAND AND A MOUNTAIN POPULATION

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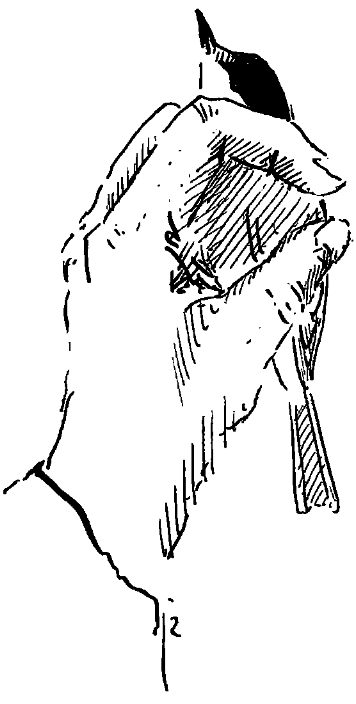

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Long-distance migrants often arrive on their breeding grounds with large fat stores. Two explanations for this phenomenon are (1) that large fat stores at arrival are needed to speed up the breeding schedule and to counteract possible time constraints, and (2) that they are used as insurance against adverse weather conditions during the days after arrival. We compared body condition (fat stores, breast muscle volume, body mass) and reproductive state (cloacal protuberance) at spring arrival of two Garden Warbler *Sylvia borin* populations living at different altitudes (200 m asl versus 1500 m asl) under completely different climatic conditions. Newly arrived individuals (predominantly males) of the lowland population carry slightly smaller fat stores at spring arrival than their mountain conspecifics. Furthermore, lowland males return with smaller fat stores than lowland females whereas in the mountains no sex differences seem to exist. For lowland females, which initiate reproductive activities soon after arrival, the fat stores are most likely used to boost these activities. For the mountain birds, the fat stores are presumably used as an insurance against adverse weather conditions upon arrival. According to the different physiological demands of endurance flight and reproduction, newly arrived birds show rapid changes in their body stores. Individuals recaptured during the transition phase from arrival to reproduction show a significant decrease of their fat stores within a few days, accompanied by shrinkage of the breast muscle. At the same time, the cloacal protuberance of males grows rapidly and females increase their body mass.

Key words: *Sylvia borin* - fat stores - spring migration - spring arrival

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INTRODUCTION

In spring, long-distance migrants return within a few weeks from their winter quarters to their breeding sites. In general, spring migrants are in a hurry to reach their destination. They use fewer stopover sites than in autumn and their overall speed of spring migration is generally much faster than in autumn (Pearson 1990; Pearson & Lack 1992; Fransson 1995). Spring arrival seems to be a fitness-relevant trait in that arriving too late has a fitness cost, as does arriving too early (Weber *et al.* 1998). The date of arrival on the breeding grounds has a strong influence on several breeding parameters such as breeding success which usually decreases as arrival date becomes later (Møller 1994; Aebischer *et al.* 1996). On the other hand, arriving too early may be costly, as harsh weather conditions such as snow cover or delayed vegetation development could cause food short-age and have a negative effect on body condition and the ability to breed (e.g. Whitmore *et al.* 1977).

It is well known that long-distance migrants often arrive on their breeding grounds with large fat stores. This 'overload phenomenon', which means that birds deposit larger fat loads than needed for covering the flight distance from the last stopover-site to the next destination, is characteristic for many migratory bird species. It has been predicted that it will be optimal to acquire extra energy reserves at the last stopover-site as long as the fat deposition rate, devaluated by the concomitant flight costs, is greater than the expected rate of energy gain at the breeding destination. The adaptive significance of this „overload phenomenon is generally considered as an insurance against unpredictable conditions at the breeding site or as an extra store to be utilised at the breeding grounds to speed up the onset of breeding (Gudmundsson *et al.* 1991). On the other hand, carrying extra fat loads could be costly by suffering higher mortality risk en route as a consequence of reduced flight manoeuvrability (Hedenström 1992; Kullberg *et al.* 1996).

Sandberg & Moore (1996) presented four, not mutually exclusive hypotheses about the significance of fat stores at spring arrival. They derived predictions from these hypotheses and considered possible costs associated with carrying such energy stores to the breeding grounds. One aim of our paper is to test predictions from two of the four hypotheses formulated by Sandberg & Moore (1996), namely the time-constraint hypothesis and the insurance hypothesis. The *time-constraint hypothesis* states that individuals that arrive on the breeding grounds with surplus fat stores are better able to offset time constraints than those without such stores. One of the predictions is that fat stores will be negatively correlated with the duration of the reproductive season and that females should arrive with larger fat stores than males. Moreover, large fat stores will provide more time for breeding by accelerating the start of reproduction. The *insurance hypothesis* says that fat stores will sustain the individual when environmental conditions upon arrival deteriorate and predicts (a) that early arriving individuals will carry larger fat stores than those arriving later and (b) that birds breeding in areas with a high risk of encountering harsh climatic conditions (less predictable food resources) on the breeding grounds will carry larger fat stores than birds living under favourable climatic conditions with more reliable food sources. The *breeding-performance hypothesis* (clutch size depends on pre-stored fat) and the *foraging-shift hypothesis* (females will benefit more than males from having previously accumulated fat stores since they have to produce the eggs) cannot be tested with our data.

The Garden Warbler, a typical long-distance migrant, shows an extensive latitudinal and altitudinal range of its breeding area, i.e. up to a latitude of 70°N in northern Scandinavia and an altitude of 2250 m asl in the Alps in SW- Switzerland (Hagemeijer & Blair 1997). Overall, the reproductive season is shorter and environments are more variable and less predictable with increasing altitude or latitude. Garden Warbler populations at higher latitudes as well as at higher altitudes are time-constrained by having a restricted breeding season. The laying period in the Central Swiss Alps at 1500 m asl is similar to that in southern Finland at 60°N and nearly a month shorter than in the lowlands of SW- Germany (Bairlein *et al.* 1980; Widmer 1998). Moreover, Garden Warbler populations of higher latitudes and higher altitudes arrive earlier on their breeding grounds with respect to vegetational phenology and air temperatures. Hence, early-arrived birds of these populations sometimes find very unfavourable conditions such as snowfall and temperatures down to freezing upon arrival (Glutz 1990).

In this paper we compare the body condition at spring arrival of two Garden Warbler populations that live at about the same latitude and have presumably the same migration distances but are separated by altitude (200 m asl versus 1500 m asl) and hence live under completely different climatic conditions. In detail, we measured fat stores, breast muscle volume and body mass as an indication of body condition and additionally the cloacal protuberance as an indication of reproductive state. The development of these body traits is described during the transition from arrival to reproduction on a population level and on an individual level by studying short-interval retraps.

STUDY SITES AND CLIMATE

The study area in the lowlands is situated in the Upper Rhine Valley in SW-Germany near Neuenburg am Rhein (47°49'N, 7°33'E; 200 m asl). It encompasses several small strips (total 32 ha) of riparian forest with open canopy along the Rhine. The forest consists mainly of willows *Salix* spp. and poplar *Populus* spp. trees as well as willow bushes in the understorey. Nettles *Urtica dioica* and brambles *Rubus fructicosus* dominate the undergrowth. The study site in the mountains is situated 150 km southeast of the lowland-area in the Urseren Valley in the Central Alps of Switzerland (46°36'N, 8°31'E; 1500 m asl). It comprises 18 ha of typical riparian subalpine scrub with various willows *Salix sp.* and Green Alder *Alnus viridis*.

The climate of the two study areas is completely different. The Upper Rhine Valley has one of the mildest climates in Central Europe, characterised by relatively high temperatures (mean May temperature 14.4°C) and little precipitation. The climate of the Urseren Valley is determined by relatively low temperatures (mean May temperature 6.5°C), large fluctuations of temperature within the breeding season, and frequent precipitation. In almost every breeding season there are periods of harsh weather with snowfall and temperatures down to freezing. The vegetation period in the mountain area is much shorter than in the lowlands and the onset of vegetation growth is delayed for several weeks (for details see Widmer 1993).

METHODS

This study is based on mist-net data collected in 1997 (n = 114) with additional data from 1994 to 1996 (n = 86). In 1997, at both study sites, the birds were trapped during exactly the same period, from the arrival of the first individual until 3 weeks after first arrival. In the lowland study area this was between 22 April and 12 May and in the mountain study area between 14 May and 4 June. In all other years, birds were trapped only on a few days in the arrival phase (lowland area 20 - 22 April, 3 - 5 May, 10 - 11 May 1995, 2 - 3 May, 9 - 11 May 1996; mountain area 21 - 22 May 1994; 24 - 26 May 1995, 22 - 23 May 1996). Trapping was conducted from dawn to mid-day and from late afternoon to dusk. In the lowland area we captured a total of 61 birds (six within-year retraps) during 30 trapping days and in the mountain area a total of 115 birds (18 within-year retraps) during 24 days.

All birds were banded with an aluminium ring and three colour rings for individual identification. We measured wing length and tarsus length and we assessed the subcutaneous fat deposits on the bird's abdomen and the interclavicular depression according to the detailed scale of nine main classes and 31 subclasses (Kaiser 1993). We estimate our accuracy of measurement to 1-2 subclasses or 0.25 - 0.5 main classes. The breast muscle volume was assessed by measuring the vertical difference from the sternum (measured in the central part) to the top of the convexly curved breast muscle at a horizontal distance of 2 mm (yields negative values; accuracy of measurement 0.1 mm; Biebach in prep.). Birds were weighed to the nearest 0.1 g with an electronic balance. For assessing the reproductive state of males, we estimated the volume of the cloacal protuberance (CP), a swelling of the cloaca which is caused by the growth of the seminal glomera that function as the site for storage and maturation of sperm (Birkhead & Møller 1992). The CP was assumed to be cylindric and its volume was calculated from its diameter at base and its height (measured with a piece of graph-paper). Some males could be sexed unequivocally by seeing the seminal glomera through the skin on the ventral side of the cloacal protuberance. Individuals with a rectangular cloacal protuberance (height ≥ 4 mm) were also sexed as males. All other individuals were provisionally classified as indeterminate. However, many colour-banded birds could be identified (or confirmed) later as males by seeing them performing territorial song. Some recaptured individuals with a flat cloaca in combination with a swollen abdomen could be identified as females.

In spring, it is impossible to determine the age of Garden Warblers by plumage characters (Svensson 1992). However, many retraps from former years allowed us to distinguish the two age-classes 'young' (unbanded, presumably 1 year old) and 'old' (caught in previous year and already banded, at least two years old). It is evident, that the first group also includes some older individuals that were not trapped in previous years.

Determining the standardised arrival date

Spring arrival dates (arrival of the first individual, median date of population arrival) differ between the two study sites and between years within a site. For comparing arrival dates from different sites and years we assigned the median date of arrival of the population, defined as the day when 50% of the territories are occupied, as the standardised arrival date. In this study all dates are expressed in relation to the standardised arrival date. In 1997, territory establishment at both study sites was monitored in detail by mapping the territories on the basis of simultaneously singing males every second or third morning. The first census was made some days before the expected first arrival date. To ascertain the final population size (*n* = 24 territories in both study areas), the last census was made three weeks after first arrival. By this method the median date of arrival (50% territories occupied) could be exactly interpolated. Because of the high speed of migration in Garden Warblers in spring (Fransson 1995), the possibility of confusing settling birds with singing migrants on passage is thought to be negligible. Moreover, many first-arrived individuals were still banded (trapped in former years) or their status as resident breeders was confirmed by retrapping them a few weeks later during the reproductive season.

RESULTS

In 1997, the arrival pattern was studied at both study sites in detail. In the lowland area we heard the first singing male on 23 April. The next day we counted a total of two males and on 25 April, six males were present. Five days after the first bird arrived we counted a total of twelve occupied territories, half of the 24 territories under observation (median arrival 28 April). Already on 3 May, ten days after first arrival, 22 territories were occupied (92%; Fig. 1). In the mountain area on 14 May (three days earlier than the average of the years 1990-1995; Widmer 1996) we observed the first individual, a male at least seven years old. Not until eight days later did we count twelve occupied territories, half of the total of 24 territories (median arrival 22 May). On 27 May, 13 days after the first male had arrived, 22 territories were occupied (92%; Fig. 1).

In the lowland area, males were trapped on average (± SD) a few days before females (2 May

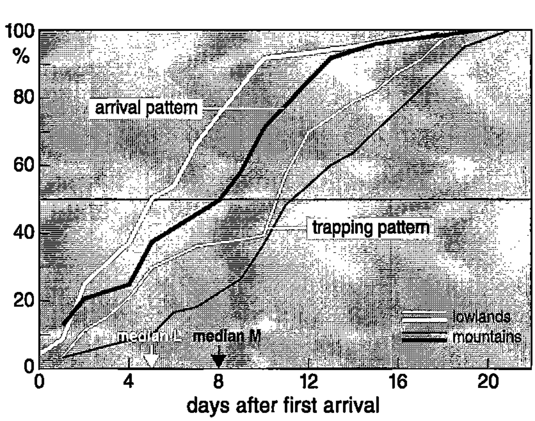

Fig. 1. Cumulative curve of occupied territories (bold lines) and trapped individuals (fine lines) in the lowlands (white lines) and in the mountains (black lines) in 1997. The arrows indicate the median dates of arrival (= 50% of territories occupied) in the respective populations.

Table 1. Body condition (body mass, fat score, breast muscle volume), body size (wing length, tarsus length) and CP- volume of early arrivals (date of capture before the median date of arrival) in the lowland- (L) and mountain (M) study area in 1997. The population mean values were tested with a non-parametric Wilcoxon-Test.

	Lowland population $n = 11$	Mountain population $n = 11$	Significance
Body mass (g)	17.8 ± 1.1	18.6 ± 1.4	$P = 0.18$
Fat score	2.3 ± 0.7	3.0 ± 1.0	$P = 0.08$
Breast muscle volume (mm)	-1.7 ± 0.4	-1.8 ± 0.2	$P = 0.29$
Wing length (mm)	79.4 ± 1.3	79.4 ± 2.2	$P = 0.82$
Tarsus length (mm)	20.4 ± 0.5	20.1 ± 0.5	$P = 0.17$
CP-volume (mm^3)	59.6 ± 20.9	52.4 ± 22.9	$P = 0.45$

± 5.4 days, $n = 15$ versus 8 May ± 3.7 days, $n = 6$; Mann-Whitney Test; $U = 15$; $P = 0.019$). In the mountain area the corresponding dates are 26 May ± 5.6 days ($n = 27$) and 30 May ± 2.6 days ($n = 7$; Mann-Whitney Test; $U = 57$; $P = 0.108$) respectively. For an age-related analysis, enough data were available only for the males of the mountain population. Older mountain males were trapped on average 6 days earlier than younger mountain males: 21 May ± 5.4 days ($n = 4$) versus 27 May ± 5.2 days ($n = 23$; Mann-Whitney-Test; $U = 18$; $P = 0.054$).

A comparison between the time course of territory establishment and the cumulative trapping curve shows that they do not coincide (Fig. 1). This demonstrates one of the fundamental problems of such studies. The trapping day is not necessarily the arrival day, since the median date of territory establishment is different from the median date of trapping. As the season progresses, the trapped birds are more and more a mixture of individuals that have just arrived and others that have been trapped some days after their arrival date. The ratio between these two groups will continuously change in favour of the latter group.

Body condition at arrival

Body condition parameters at arrival were evaluated only for birds trapped in 1997 (daily mist-netting) before the median date of arrival, when date of trapping is close to date of true arrival time. There is no indication of a clear difference in body size parameters between the two populations (Table 1). Garden Warblers of both study sites arrived on their breeding grounds with substantial fat stores. The first and foremost mountain birds arrive with slightly larger fat stores and a higher body mass than the lowland birds (predominantly males in both populations); however, the differences are statistically not significant. There is no difference in breast muscle volume and cloacal protuberance between the two populations (Table 1).

In the lowland population, females returned with larger fat stores (± SD) than males (2.3 ± 0.6, $n = 8$ versus 1.6 ± 0.7, $n = 19$), whereas no sex differences were found in the mountain population (1.8 ± 0.7, $n = 7$ versus 2.0 ± 1.0, $n = 37$; Table 2). In the mountain population, older (≥ 2 years) individuals arrived with much larger fat stores (3.0 ± 0.8, $n = 9$) than younger (≥ 1 year) individuals (1.7 ± 0.8, $n = 28$) and a similar trend also existed in the lowland population (Table 2). We found no evidence for a year-effect in either population.

Testing the time-constraint and the insurance hypothesis

The fat score decreased significantly with progressive season in both populations (lowland population: $y = 2.15 - 0.09x + 0.003x^2$; $R^2 = 0.127$; $F_{2,58} = 4.21$; $P = 0.02$; mountain population: $y = 2.24 - 0.08x + 0.003x^2$; $R^2 = 0.17$; $F_{2,107} = 10.90$; $P < 0.001$). No significant difference was found between the two populations; an ANOVA with the

Table 2. Analyses of covariance of the fat score of lowland population birds (Model $R^2 = 0.40$; $n = 27$) and mountain population birds (Model $R^2 = 0.43$; $n = 44$). Sources of variation are sex, age class and year as factors and the standardised arrival date as covariate. Two-way interactions were tested, but removed from the model if $P > 0.2$.

	df	MS	F	*P*
Lowland population				
Sex	1	4.699	12.086	0.002
Age class	1	0.928	2.387	0.137
Year	1	0.074	0.191	0.666
Standardised arrival date	1	2.056	5.287	0.031
Mountain population				
Sex	1	0.799	1.371	0.249
Age class	1	3.722	6.391	0.016
Year	2	0.513	0.440	0.647
Standardised arrival date	1	5.038	8.650	0.006

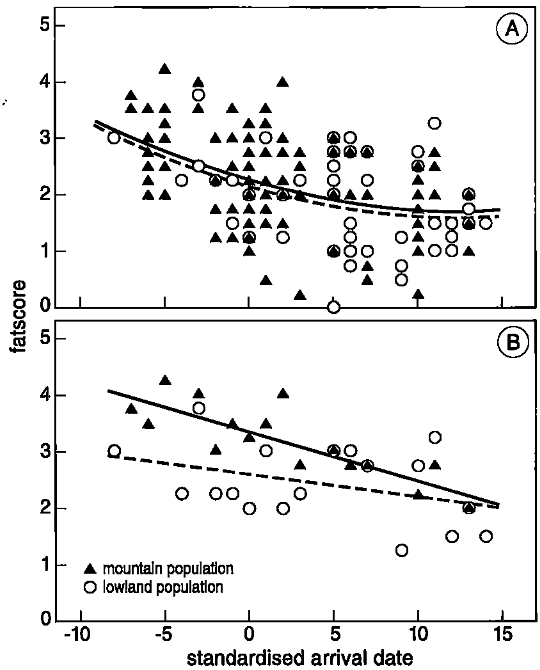

Fig. 2. (A) Fat score of Garden Warblers *Sylvia borin* from the lowlands (circles) and from the mountains (triangles) in relation to standardised arrival date. (B) Fat score (only the highest value per day per population) of Garden Warblers from the lowlands (circles) and from the mountains (triangles) in relation to standardised arrival date.

residuals of fat score to the overall quadratic regression as independent variable revealed no significant origin-effect ($F_{1,169} = 0.44$; $P = 0.506$; Fig. 2a). However, the data in Fig. 2a are extremely scattered, probably due to the fact that the dataset resembles a mixture of individuals trapped just after arrival and individuals trapped later. For individuals with a low fat score, we do not know whether these birds arrived with such low fat stores or whether they returned with higher fat deposits and depleted them during the interval between the true arrival day and the trapping day (see below). A way to solve this problem could be to calculate a regression only with the highest values of fat score per day. If a decrease of fat score with progressive time still exists, this would be a strong evidence for a real difference in the mean fat stores between early and late arrivals. In fact, an analysis with only the highest fat score values per day revealed not only a significant negative relationship of the fat score with time, but also a clear difference between the populations (Fig. 2b; Table 3).

Development of fat store, breast muscle volume and body mass of short-interval retraps

The data of short-interval retraps (within seven days at maximum) allowed us to study in detail

Table 3. Analysis of covariance (Model $R^2 = 0.54$, $n = 34$) of the fat score (only the highest value per day considered; Fig. 2b). Sources of variation are origin, standardised arrival date and the interaction term Origin*Standardised arrival date.

	df	MS	F	*P*
Origin	1	4.133	14.597	< 0.001
Standardised arrival date	1	4.716	16.656	< 0.001
Origin*Standardised arrival date	1	0.628	2.217	0.147

Table 4. Development of fat score (Kaiser 1993), breast muscle volume and body mass of individuals recaptured within one week. Shown are origin (lowland, L, or mountain, M), sex, arrival (early or late), the interval between first capture and recapture (days), the difference in fact score and the daily change in fat score, the difference in breast muscle volume (mm), and the difference in body mass (g). An early arrival date means that the bird was trapped before the median date of arrival, a late arrival date means that the bird was trapped after the median date of arrival.

Ringnumber	Origin	Sex	Arrival	Capt/recap interval	Difference fat score	Change fat score	Difference in breast muscle (mm)	Difference in body mass (g)
CX 26619	L	m	early	1 day	-0.25	- 0.25		- 0.9
CX 98012	L	m	early	4 days	-1.25	- 0.31		+0.1
CX 98054	L	f	late	2 days	-1.50	- 0.75	- 0.6	+1.4
E 811823	M	m	early	4 days	-2.25	- 0.56	- 0.5	- 1.4
E 982045	M	m	early	6 days	-1.50	- 0.25	- 0.2	- 1.8
E 982402	M	m	early	1 day	-0.75	- 0.75	- 0.3	- 1.2
E 982427	M	m	early	1 day	-0.50	- 0.50	- 0.1	+0.4
E 982463	M	?	late	4 days	-1.75	- 0.44	- 0.5	- 0.3
E 982482	M	m	late	6 days	-1.00	- 0.18	- 0.4	- 0.2
E 982483	M	?	late	1 day	-0.50	- 0.50	0.0	- 1.0
E 982489	M	f	late	7 days	-0.50	- 0.07	- 0.4	+2.8
E 982492	M	f	late	3 days	1.25	+0.42	+0.4	+0.3
E 982498	M	f	late	3 days	0.25	+0.08	- 0.4	- 0.6
N 43005	M	m	late	3 days	0.50	+0.17	- 0.3	0.0
N 43008	M	f	late	2 days	-0.75	- 0.38	- 0.4	+0.3

individual changes of fat stores, breast muscle volume and body mass after arrival. Early arrivals showed a rapid decrease of their fat stores by losing on average 0.44 fat-score units day^{-1}. This catabolism of fat stores is connected with a decrease in breast muscle volume and, apart from two exceptions, with a slight decrease in body mass (Table 4). The data from individuals trapped after the median date of arrival showed a more irregular pattern. Six out of nine birds decreased in fat stores and in breast muscle volume. Three out of these six individuals also showed a slight decrease in body mass while the other three individuals showed a substantial body mass increase, all of them females. Because of the brief period between arrival and reproduction, females are forced to accumulate body stores within a short time. In general, females increased their body mass before the egg-laying phase, whereas the body mass of males remained unchanged during the corresponding period (Widmer unpubl. data).

Growth of cloacal protuberance

The data from eleven retraps (eight mountain

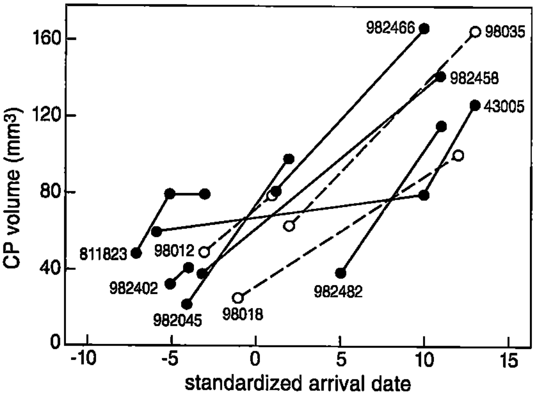

Fig. 3. Development of CP-volume of three lowland population-males (open symbols, dashed line) and eight mountain population-males (closed symbols, continuous line).

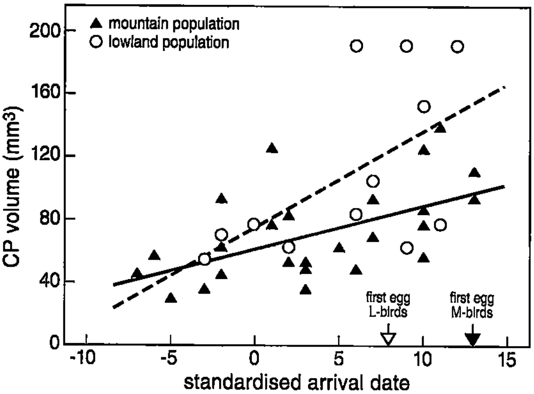

Fig. 4. CP-volume of lowland population-males (circles, dashed line) and mountain population-males (triangles, continuous line) trapped only once in relation to standardised arrival date. The arrows indicate the date of first egg in the two populations in 1997.

males, three lowland males) showed a two- to three-fold enlargement of CP- volume within two weeks after arrival in both populations (Fig. 3). These data and those from all first-recaptures in 1997 gave no evidence for a difference between the two populations (Table 5). On the other hand, there is a very weak indication of a more rapid growth in the lowland birds (Fig. 4). This is paralleled by a shorter interval between the median date of arrival and the onset of reproduction in the lowland birds. In 1997 in the lowland area the first egg was laid as early as the 5th of May, seven days after the median date of arrival or twelve days after the first arrived male. In the mountain area the corresponding intervals between arrival and onset of reproduction were 14 days and 21 days, respectively (first egg at 5 June; Fig. 4).

DISCUSSION

The arrival pattern did not differ substantially between lowland and mountain birds. At both study sites the arrival of the population took place very fast, so that within two weeks more than 90% of the territories were occupied. In both populations males seemed to arrive ahead of females and at least in the mountain population older birds (≥ 2-years old) returned a few days ahead of younger birds (≥ 1-year old). This reflects a well known pattern found in many passerines (Francis & Cooke 1986). Moreover, the small inter-individual variation in arrival time is typical of long-distance migrants with a restricted breeding season (e.g. Barred Warbler *Sylvia nisoria*, Neuschulz 1988).

The two study populations differed consistent-

Table 5. Analysis of covariance (Model R^2 = 0.44, n = 40) of CP volume of Garden Warbler males. Sources of variation are Origin, Standardised arrival date and the interaction term Origin*Standardised arrival date.

	df	MS	F	*P*
Origin	1	991.1	0.923	0.343
Standardised arrival date	1	18772.9	17.482	< 0.001
Origin*Standardised arrival date	1	2691.1	2.506	0.122

ly by three weeks in the median date of arrival. The ultimate explanation for this lies in the completely different climatic and phenological conditions at the two study sites. The proximate causes of this difference in arrival dates have been recently studied in the laboratory. It has been shown that lowland and mountain populations have different endogenously controlled spring migration programmes with a strong genetic basis (Widmer 1999).

Body condition at arrival

Garden Warblers arrived on their breeding grounds with substantial fat loads, which is typical of long-distance migrants (e.g. Sandberg 1996). Body mass and fat score of newly arrived birds of our study populations are considerably higher than those of passage migrants in the Mediterranean area. Especially on some Mediterranean islands, spring passage migrants have much lower body masses (mean values 15.6 – 17.4 g; Grattarola *et al.* 1999). In the Mediterranean area, a significant decrease of fat stores (mean fat score and mean body mass) with latitude was found, suggesting that Garden Warblers cross the Sahara and the Mediterranean Sea without substantial refueling in North Africa (Grattarola *et al.* 1999). However, at one site in northern Italy the authors found Garden Warblers with a mean body mass of 18.2 g, considerably higher than those at other trapping sites and comparable with our values. The authors suggest that these birds may have already started to replenish their fat stores prior to completing their northward migration. Our findings support this hypothesis. It is likely that Garden Warbler populations of Central Europe refuel their deposits in the northern part of the Mediterranean area before their takeoff to the breeding grounds. The distance from northern Italy to the breeding grounds is 250 – 400 km and is likely to be covered in one night-flight.

Testing the hypotheses

The finding that early arrivals carried larger fat stores than late arrivals is at first glance in agreement with one of the predictions of the insurance hypothesis (Sandberg & Moore 1996). However, there are some open questions. Do early arrivals carry larger fat stores because of their higher risk of encountering bad weather upon arrival, as Sandberg & Moore (1996) suggested? Garden Warbler populations arrive at their breeding territories with only a small overall variation in arrival dates. Consequently, the difference in the probability of encountering bad weather conditions between early and late arriving birds is very small and cannot completely explain the overall negative regression between fat score and time. The more likely explanation is that arrival date is confounded with the age of an individual. Early arrivals are older, more experienced individuals and later arrivals are presumably mainly one-year old birds. At least for the mountain birds, such an age-effect has been shown and age-dependent differences in arrival dates are a wellknown pattern in many migratory species (Francis & Cooke 1986). The age-effect is probably a more indirect one in that older birds migrate more directly and/or start with greater fat stores from the last stopover site than younger birds. We believe that variation in fat stores among newly arrived individuals within a site is more likely the result of differences in energy expenditure during the last spring migration journey than an adaptive strategy to a slightly higher risk of encountering bad weather conditions by arriving few days earlier.

Furthermore, newly arrived individuals (predominantly males) of the mountain population seemed to carry slightly larger fat stores at spring arrival than their lowland conspecifics, as predicted by the time-constraint and the insurance hypothesis. Two further predictions of the time-constraint hypothesis state that large fat stores will provide more time for breeding by accelerating the start of reproduction and that the more time-constrained sex (mostly females) should carry the larger fat stores. At least in the mountain birds, no sex differences in fat stores at arrival existed. Although mountain birds have a much more restricted laying period than lowland birds (58 days versus 84 days; Widmer 1998) and are therefore in general more time-constrained, they do not start reproduction earlier than lowland birds with respect to the arrival date. Just the opposite: in the mountains the interval between arrival and egg laying is on average 5 days longer and shows more between-year variation than in the lowlands (Widmer 1998). At higher altitudes, the onset of egg-laying clearly depends on the phenological state of the vegetation and in cold springs with underdeveloped vegetation and food supply the mountain birds have simply to wait until the conditions are favourable (Widmer 1993). Under these circumstances the value of large fat stores as an accelerator of the breeding schedule should be reconsidered for the mountain birds.

In the lowland population, where sex differences in arrival dates are more pronounced, females arrived with relatively larger fat stores than males. With respect to the phenological calendar, lowland females constantly arrive on their breeding grounds later than mountain females, at a moment when the vegetation is already fully developed. At least at the start of the breeding season, lowland females have probably less time than mountain females. The lowland females are forced to start with egg-laying as soon as possible and their fat stores are used to speed up the start of reproduction. In fact, the interval between the median date of arrival and the first egg in the population is shorter in the lowland population than in the mountain population (Widmer 1998; see also Fig. 4); moreover, the first clutches of lowland females are significantly larger than those of the mountain females (Widmer 1998).

Mountain birds most probably use their fat stores to better survive unfavourable weather conditions (snowfall, temperatures down to freezing) upon arrival (Widmer 1993). They are most likely an insurance to compensate for low food availability during the first days in the breeding territory. However, the difference in mean fat stores at arrival between mountain and lowland birds are not as large as one would probably expect from the different climates of the study sites. Mountain birds probably do not depend as much on large fat stores as birds of higher latitudes because of their opportunity to reach more favourable areas by altitudinal movements. However, such retreat movements have not yet been observed in mountain-dwelling Garden Warblers (Widmer unpubl.).

Development of body composition during the transition phase from arrival to reproduction

In general, newly arrived Garden Warblers of both study populations were in sufficiently good condition that, theoretically, they could have continued their flight. The first arrivals carried substantial fat stores, their breast muscle volume was high and body mass was higher than during the reproductive season. The data from the short-interval retraps clearly showed that fat stores were catabolized within a short time, connected with a shrinkage in the breast muscle volume and to a certain degree with a decrease in body mass. Simultaneously, males and females start to invest rapidly in their reproductive organs, shown by the rapid growth of the CP in males and by the body mass increase in females soon after arrival. These observations indicate a rapid alteration in body stores and body composition according to the completely different physiological demands of long-distance endurance flight and reproduction. A rapid decrease of fat stores connected with a slight decrease in body mass within few days after arrival has also been shown in a study of Willow Warblers in southern Sweden (Fransson & Jakobsson 1998).

The steep and rapid growth of the cloacal protuberance soon after arrival indicates a primarily exogenous control, in contrast to the gonadal growth which has a strong endogenous basis (Berthold *et al.* 1972). A rapid growth of the cloaca during the transition phase has also been found in the White-crowned Mountain-Sparrow *Zonotrichia oriantha* (Morton *et al.* 1990). More indications of an exogenous control of CP- growth come from an experiment with Bearded Tits *Panurus biarmicus*. In this study female presence positively influences the CP- size of males (Sax & Hoi 1998).

A rapid change in body composition after arrival on the breeding ground has also been shown in the Pied Flycatcher *Ficedula hypoleuca*. Ojanen (1984) found newly arrived females in a good body condition and observed a decrease in fat stores during the short period from arrival to the start of egg laying. Silverin (1981) found a significant increase in liver and spleen mass during the transition phase between spring arrival and reproduction.

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SAMENVATTING

Veel langeafstandstrekkers arriveren in de broedgebieden met een ruime vetreserve. Er zijn twee verklaringen voor dit fenomeen. Allereerst is een voldoende vetreserve belangrijk om onmiddellijk na aankomst tot broeden over te kunnen gaan. Een tweede reden is dat een zekere vetreserve noodzakelijk is om eventuele dagen met ongunstige voedselomstandigheden (bijvoorbeeld een 'laat voorjaar') de baas te kunnen. In het hier beschreven onderzoek wordt de lichaamsconditie (vetreserve, borstspiervolume en totale massa) en de broedconditie (zwelling van de cloaca) van zojuist aangekomen Tuinfluiters *Sylvia borin* in het voorjaar in twee verschillende populaties beschreven. De twee populaties, in een laagland gebied (200m boven zeeniveau) en in een berggebied (1500m boven zeeniveau), leven onder klimatologisch sterk verschillende omstandigheden. Pas aangekomen Tuinfluiters (bijna allemaal mannetjes) in het laagland hebben een iets minder grote vetreserve dan de in de bergen arriverende vogels. In het laagland keren mannetjes met een geringere hoeveelheid vet terug dan wijfjes, terwijl er in de bergen tussen beide seksen geen verschil kon worden gevonden. De vrouwtjes in het laagland, waar nestbouw en eiproductie vrijwel onmiddellijk na aankomst beginnen, worden de vetreserves kennelijk vooral voor het nestelen aangewend. Voor de Tuinfluiters in berggebieden geldt waarschijnlijk dat vooral de eerste dagen van overleving van betekenis zijn. Omdat er sterk verschillende fysiologische processen van belang zijn bij langeafstandstrek en reproductie, ondergaan de vogels onmiddellijk na aankomst enkele opmerkelijke veranderingen. Vogels die onmiddellijk na aankomst gevangen konden worden, en konden worden teruggevangen op het moment dat de broedtijd daadwerkelijk was begonnen, bleken dan niet alleen een veel kleinere vetreserve te hebben, maar ook een sterk in omvang geslonken borstspier. Tegelijkertijd bleken de cloaca's van mannetjes enorm gezwollen te zijn, terwijl het lichaamsgewicht van de wijfjes verder was toegenomen. (CJC)

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