

Stopover behaviour of spring migrating Wood Warblers *Phylloscopus sibilatrix* on the Island of Capri, Italy

Rastningsbeteende hos vårflyttande grönsångare Phylloscopus sibilatrix på ön Capri, Italien

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Abstract

Migratory birds are assumed to be under strong selection pressure during migration. It is generally assumed that many species are maximizing speed of migration because of the benefits from arriving early at the breeding grounds. Males' incentives are to occupy the best territories before they are occupied by competitors. Females breeding early usually have a greater reproductive success. In this study, the stopover behaviour of the Wood Warbler is studied on Capri, a Mediterranean island in southwest Italy. Movements of birds on the island are from higher elevations with sparse vegetation, where they presumably arrive, to low elevations with more dense vegetation. Males were found to migrate earlier than females, but were also staying much shorter

time than females on the island. Males were estimated to stay on average slightly more than one hour whereas females stayed on average thirteen hours. The results suggest that Capri is not an important refueling site for the Wood Warbler and that males are more inclined to quickly leave this poor stopover site than females.

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Introduction

The migration is a significant part of many birds' lives, both in terms of the time and the energy it requires (Holmgren & Hedenström 1995). It entails a great risk of mortality for birds: predation risks increases when the birds are exposed to predators during flight and during foraging at stopover sites. The birds are also at greater risk of mortality as a consequence of starvation or of severe weather during flight (Alerstam 1988).

The stopover, during which the birds replenish their energy reserves, is the most time-consuming part of the migration, and hence is under strong selection (Alerstam & Lindström 1990). Optimal migration theory suggests that birds should take into account current stopover site conditions, such as local food abundance and current wind, for its decision to stay or leave (Weber et al. 1998). They should also take into account their expectations in the near future of migratory barriers, expected food density at stopover sites along the route (Gudmundsson et al. 1991), and search and

settling time at the next stopover site (Alerstam & Lindström 1990). A bird's condition, in terms of energy reserves, protein, water, and sleep deprivation (Schwilch et al. 2002), is also important for the bird to consider.

Because of the risks during migration, and the benefits from arriving early on breeding grounds (see below), birds on spring migration are expected to maximise migration speed (Alerstam & Lindström 1990). While doing this optimization of spring migration, the birds have to consider the conditions mentioned above. The mass gaining rate of birds is usually a function of local food density, but it may also vary between individuals e.g. because of differences in dominance (Lindström et al. 1990) or in foraging efficiency. The dominance situation may change during the stopover at one site (Rappole & Warner 1976), whereas foraging efficiency will have the same effect on a birds intake rate at all its stopover sites. If birds are speed maximizers, and intake rate varies between individuals as an effect of local conditions, a positive correlation between energy deposition

rate and departure body mass is expected among birds (Alerstam & Lindström 1990).

During spring, speed of migration is crucial for males. Those males that arrive early benefit from occupying the best territories on breeding grounds (Forstmeier 2002; Smith & Moore 2005). Male Wood Warblers are polyterritorial and some will pair with multiple females (Temrin et al. 1984). Females start to arrive 7–10 days after most males have settled at the breeding grounds (Temrin 1986). In a population of Wood Warblers in central Sweden, secondary females of polygynous males fledged as many young as females of monogamous males and primary females of polygynous males (Temrin et al. 1996). For females, speed of migration is expected to be less critical than for males, because the mating opportunities increase as the number of established males increase. It is still unclear if males depart earlier than females from the wintering grounds or if males migrate faster than females. Little is known about the differences between the sexes on migration. Here we report on fat scores, stopover duration, and changes in body mass of the Wood Warbler *Phylloscopus sibilatrix* at a spring stopover site on Capri, a Mediterranean island in southwestern Italy.

Methods

In 1993, birds were captured and ringed at two sites on Capri, 40°33' N, 14°13' E. One site was located at Castello Barbarossa on a small hilltop of the island, c 400 m above sea level. The other site was located approximately 100 m downhill in typical Mediterranean macchia vegetation with some pine trees, *Pinus* spp. The vegetation gradually became higher and denser down the slope. The ringing at the hilltop was part of “the small island project” (Progetto Picole Isole; Pilastro et al. 1998) of the Italian national ringing centre, Bologna, undertaken from 16 April to 15 May 1993 (Messineo et al. 2001). The ringing on the slope was undertaken from 22 April to 11 May in order to study the stopover behaviour of the birds.

The birds were ringed, measured and weighed immediately after capture. Wing length was measured using maximum chord to the nearest mm (Svensson 1984). Tarsus length was measured with 0.1 mm accuracy, including the folded adjoining joints. Fat score was estimated visually, following a ten-graded scale from 0 to 9 (an extension of the Pettersson & Hasselquist 1985 method). Body mass was weighed to 0.1 g accuracy. Some birds were also recaptured before leaving the island. To

control for body size in the statistical analyses, wing length and tarsus length were used as indirect predictors. One may on theoretical grounds argue that a linear relationship with body mass is achieved if wing length and tarsus length are raised to the power of three to reflect the volume of the body. These were tested as alternatives to the linear measurements in multiple regressions but there were only small differences between the alternatives (data not shown).

Stop-over lengths were analysed in two ways. Minimum stopover lengths (MSL), i.e. the time between ringing and last recapture were for each individual recaptured. MSL was used in correlations with initial body mass (IBM), last recapture body mass (LBM), and body mass changing rate (BCR). It is well known that many birds initially lose body mass at a stopover site before they start to gain body mass (see discussion). Birds may be captured and recaptured at any time of their stay at a stopover site. When analyzing recovery data, the obtained measurements of MSL and BCR may therefore depend on IBM as an indicator of when the bird was first captured in relation to its arrival. We could not find any significant correlation between BCR and IBM ($r_p = -0.11$, $t_{45} = -0.76$, $p = 0.45$, partial correlation correcting for minimum stopover length). On the other hand, there was a negative correlation between MSL and IBM ($r_p = -0.32$, $t_{45} = -2.30$, $p = 0.026$, partial correlation correcting for body-mass change rate) indicating that birds with IBM closer to their goal departure body mass stayed shorter than other birds. Since IBM may have an effect on MSL and LBM we controlled for IBM in the tests of optimal stopover theory.

The real stopover length was estimated for all Wood Warblers using the adjusted Jolly-Seber method of Holmgren et al. (1993). The method is developed for analyzing data of birds that are recaptured at least once, and assumes a constant daily stopover probability. Maximum likelihood estimates are given for the mean daily stopover probability and the variance of the estimated mean.

Results

In total for both the hilltop site and the slope site, 774 Wood Warblers were ringed. The Wood Warbler was the most common species on the slope site, with 331 birds being ringed. The body mass of the birds ranged from 6.7 g to 12.5 g, with ninety-five percent of the birds within the range 7.2 g

Table 1. Multiple regression of wing length, tarsus length, and fat score on body mass. Regression coefficient value, the squared semi-partial regression (the proportion of the total variance in body mass explained by this variable), the t-statistics and the probability are shown. The degrees of freedom are 326.

Multiple regression av vinglängd, tarslängd och fettklass mot vikt. Regressionskoefficient, förklaringsgraden på variationen i vikt, t-värde och signifikansvärde anges. Antalet frihetsgrader är 326.

Variable	Coeff.	Prop. Var.	t	p
Intercept	-4.92		-3.20	0.001
Wing length	0.104	0.077	8.09	<0.001
Tarsus length	0.193	0.010	2.95	0.003
Fat score	0.488	0.519	21.0	<0.001

Table 2. Results of univariate linear regressions of wing length, tarsus length, fat score, and body mass over the time of season.

Linjär regression av vinglängd, tarslängd, fettklass och vikt mot tid på säsongen.

Variable	coeff.	t	n	p
Wing length	-0.130	-4.16	331	<0.001
Tarsus length	0.004	0.69	331	0.49
Fat score	0.030	1.92	331	0.055
Body mass	0.015	1.23	330	0.22

to 10.5 g. The body mass of the warblers depended on fat score, wing length, and tarsus length (Multiple $R = 0.78$, $F_{3,326} = 173$, $P < 0.001$, multiple regression). The strongest dependence was by the fat score, which alone explained more than fifty percent of the variation in body mass (Table 1). Wing length explained eight percent, whereas tarsus length explained only one percent of the variation in body mass.

All birds, whether recaptured or not or moving between the sites, were included in the analyses of differences between birds ringed at different sites or different times of the year. Only the measurements taken at ringing were included, and birds were assigned to the site of where they were ringed. The average body mass when ringed (at first capture) at the hilltop, 8.80 g was no different from that on the lower slope, 8.71 g ($F_{1,761} = 1.7$, $P = 0.19$). There was no difference between the birds ringed at the different sites regarding fat score, both having an average score of 3.4 ($F_{1,761} < 0.1$, $P = 0.97$; Figure 1). Neither was there any difference in average wing lengths between the hilltop, 76.3 mm, and the slope site, 76.6 mm ($F_{1,761} = 2.0$, $P = 0.15$). Wing length of captured birds decreased over the season, probably because of a gradually increased proportion of caught females

over the course of the season. Fat score exhibited a tendency to increase over the course of the season, whereas tarsus length and body mass showed no such tendency (Table 2, Figure 2).

The ringing yielded 48 recaptures. None of the Wood Warblers ringed on the hilltop site were recaptured at the same place. Eight (8) Wood Warblers ringed at the hilltop were later recaptured at the slope site. The majority of the recaptures were Wood Warblers ringed and recaptured within the slope site. Only one (1) recapture was of a bird moving the slope site up to the hilltop site ($P < 0.001$, Fisher's exact, recaptures grouped by site and whether recaptures are within or between sites).

Predictions from optimal stopover theory

According to optimal migration theory, some birds may maximize speed of migration (see introduction). The accumulation of fat reserves is the most time-consuming part of a bird's migration. To speed up the migration, birds that accumulate fat reserves at a faster rate than generally expected on a stopover site, should take the opportunity to stay longer and put on larger reserves than on an average stopover site. Under the assumption that birds

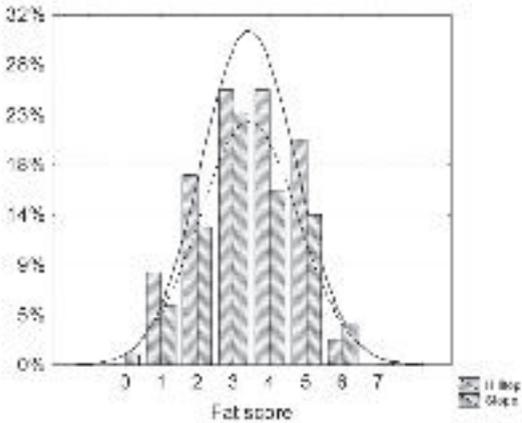


Figure 1. The frequency distribution of fat scores of Wood Warblers ringed at the hilltop and the slope site. The curves depict fitted normal distributions.

Frekvensfördelning i fettklasser av grönsångare ringmärkta på bergstoppen respektive i sluttningen. Kurvorna visar anpassade normalfördelningar.

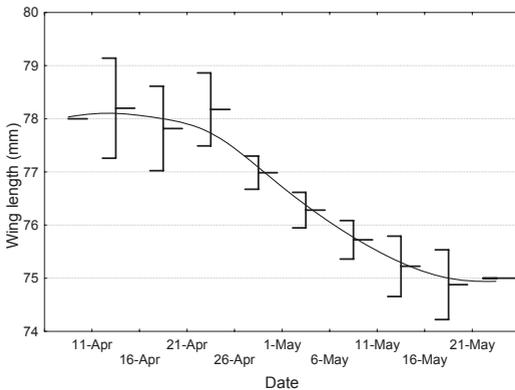


Figure 2. Wing lengths of Willow warblers ringed over the spring migration period. The bars depict the mean and 95% confidence interval of warblers ringed within 5-day periods (dates at tick labels indicate last day of the period). The curve is a second-order polynomial fitted to the means by minimising least squares.

Vinglängder på ringmärkta grönsångare i femdagars-intervall (datumen på x-axeln är sista datum i varje period) under vårflyttningen på Capri. Symbolerna anger medelvärde och 95 procentigt konfidensintervall. Kurvan är ett andraders polynom anpassat med minsta-kvadratmetoden.

at a stopover site have similar expectancies of fat accumulation rates at alternative stopover sites, or that these expectancies are uncorrelated with fat accumulation rates at a specific stopover site, we would predict that the BCR is positively correlated with both MSL and LBM. Among the 48 recaptured Wood Warblers, 22 lost body mass between ringing and last recapture, 18 had their body mass unchanged, and only 8 increased their body mass. There was no significant correlation between MSL and BCR ($r_p = 0.16$, $t_{45} = 1.10$, $p = 0.28$, partial correlation correcting for IBM; Figure 3a). However, LBM was positively correlated with BCR ($r_p = 0.62$, $t_{45} = 5.30$, $p < 0.001$, partial correlation cor-

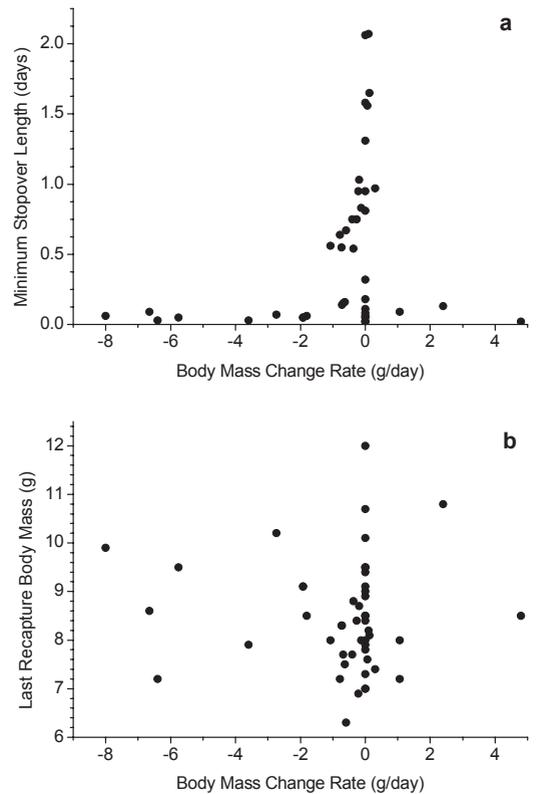


Figure 3. Stopover data of Wood Warblers that were recaptured. (a) Minimum stopover length in relation to body mass change rate and (b) last recapture body mass in relation to body mass change rate. Positive correlations may indicate that birds are maximizing speed of migration.

Rastningsdata för återfångade grönsångare: (a) Observerad rastningstid mot viktökningshastighet och (b) vikt vid sista återfångsten mot viktökningshastigheten. En positiv korrelation kan indikera att fåglarna maximerar flyttningshastigheten.

Table 3. Stopover parameters for Wood Warblers with no night or at least one night between ringing and last recapture. The parameters are: the average time between ringing and last recapture, \bar{t} ; the minimum time between ringing and last recapture, t_{\min} ; the estimated average of the actual stopover length, τ ; the estimated stopover probability, s , and its variance. The difference between estimated stopover probabilities is significant (student's $t_{45} = -3.11$, $p = 0.003$).

Rastningsparametrar för grönsångare som observerades stanna över minst en natt och de som inte observerades göra det. Tabellen visar den observerade tiden i snitt mellan märkning och sista återfångsten, \bar{t} ; den minsta observerade tiden mellan märkning och sista återfångst, t_{\min} ; den skattade faktiska rastningstiden i genomsnitt, τ ; den skattade sannolikheten att stanna per dag, s , och dess varians. Skillnaden mellan de skattade sannolikheterna för att stanna per dag är signifikant (student's $t_{45} = -3.11$, $p = 0.003$).

Nights	\bar{t} (days)	t_{\min} (days)	τ (days)	s (day ⁻¹)	var	n
0	0.068	0.021	0.047	0.045	0.0015	28
>1	1.066	0.542	0.524	0.344	0.0078	19

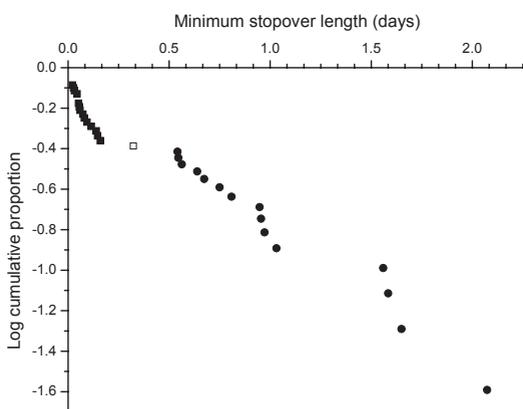


Figure 4. The distribution of minimum stopover lengths of Wood Warblers presented as the logarithm of the cumulative proportion. A linear slope indicates that birds stay with a constant stopover probability. The steeper the negative slope, the lower the stopover probability. Squares depict warblers recaptured within the same day. The slope of these birds is steep and indicates a low stopover probability (calculated without the open square data-point; see Table 3). Dots depict warblers recaptured with at least one night since ringing.

Fördelningen av observerade rastningstider hos grönsångare, här presenterade som logaritmen av den kumulativa fördelningen. En linjär kurva indikerar att fåglarna stannar med en konstant sannolikhet per tidsenhet (t ex dag). Ju brantare negativ lutning på kurvan, ju lägre är sannolikheten att stanna. Fyrkanter markerar fåglar som är återfångade sista gången inom samma dag som de ringmärktes. Prickar markerar fåglar som är återfångade med åtminstone en natt mellan ringmärkningstillfället och sista återfångsten. Lutningarna på fördelningarna för dessa två grupper återspeglas i sannolikheterna att stanna per dag som är angivna i Tabell 4 (den öppna fyrkanter är exkluderad i de analyserna).

recting for IBM; Figure 3b). This could be a self-generated correlation from variation in body mass change rate. Since minimum stopover length was not correlated with body mass change rate, high body mass change rates would on average result in high body masses at last recapture.

Two categories of stopover lengths

The estimated stop-over length of the Wood Warblers revealed two groups of birds. A plot of the logarithmic cumulative frequency distribution of recaptures versus minimum stopover length reveals two linear curves with different slopes (Figure 4). The birds known to have stayed at least one night were inclined to stay longer (daily stopover probability: 0.344) than those recaptured in the same day (daily stopover probability: 0.045; Figure 4, Table 3). On the basis of this result, the data set is divided into two categories by minimum stopover length (MSL): those with a MSL less than six hours, and those with longer. With the exception of one bird with a MSL of almost eight hours, the former group included all birds that were recaptured the last time within the same day as ringing, and the latter group all birds that had at least one night between ringing and last recapture. From now on, we will refer to these groups as the short staying group and the long staying group.

There was no difference in date of ringing between the two groups ($F_{1,46} = 0.9$, $P = 0.34$). The short staying group weighed on average more (8.9 g) at ringing than did the long staying group (8.0 g; $F_{1,46} = 8.2$, $P = 0.006$). The group with short stopover had an average last recapture weight higher

than the long staying group (8.8 g and 7.9 g; $F_{1,46} = 9.2$, $P = 0.004$). There was no difference between the groups with regard to fat score, neither that at ringing ($F_{1,46} = 1.9$, $P = 0.17$), nor at last recapture ($F_{1,46} = 0.7$, $P = 0.39$). It is likely that the difference in body mass between the two groups is to a large extent explained by a difference in body size. The short staying group had significantly longer wings (77.3 mm) than the long staying group (75.4 mm; $F_{1,46} = 11.2$, $P = 0.002$). This suggests that the long staying group predominantly consists of females, and the short staying group of males. If females stay longer than males, the short staying group is expected to include some females that were re-trapped by chance with a short time interval.

Discussion

Males of most migratory birds benefit from arriving early at their breeding grounds because early males can settle in the best territories with the highest reproductive success (Forstmeier 2002; Smith & Moore 2005). The females lack these incitements and therefore arrive later than males to the breeding grounds. In the Wood Warbler the females arrive 7–10 days after the males have established territories (Temrin 1986). It is not known if this difference in the timing of arrival is a consequence of males leaving the wintering grounds earlier than females, or if it is the result of males migrating at a faster speed than females. Males migrating earlier than females in spring is known from other passerines and also in the new world migratory system (Yong et al. 1998; Izhaki & Maitav 1998; Swanson et al. 1999; Morris et al. 2003). However, males may stay shorter on stopover sites than females as observed in spring migrating Wheatears (Dierschke et al. 2005). On the other hand, studies of spring migrating Common Yellowthroats did not reveal any difference in stopover length between the sexes (Morris et al. 2003).

In this study of Wood Warblers on spring migration at a stopover site on Capri, two groups of birds were detected on the basis of the estimated average stopover length (Table 4). One group only stayed slightly more than an hour, whereas the other group on average stayed slightly less than 13 hours. Wing lengths suggest that the shorter staying group predominantly consists of males, whereas the other group probably is dominated by females. Thus, if wing length reflects sex, the distribution of stopover times of Wood Warblers at Capri suggests that males, compared to females,

are more in a hurry to continue their migratory flight or to find richer stopover sites.

The stopover times of the Wood Warblers at Capri are very short compared to other species at other spring stopover sites. Wheatears in northern Germany stayed 1–12 days (Dierschke et al. 2005). Common Yellowthroats on spring migration stayed on average three days at their stopover site in Maine (Morris et al. 2003). Capri as a stopover site may be of low quality for the Wood Warblers, suggested by the low stopover probabilities and short estimated stopover lengths. The pattern of recaptured Wood Warblers indicate that arriving birds are landing at high elevations on the island and then move downhill to lower elevations where they stay for some time to feed (which they were seen to do). There was just one recapture indicating the opposite movement. Feeding opportunities were probably better down the slope where the vegetation was higher and denser. Birds arriving at Capri may have come from Sicily, a distance of approximately 270 km, but they may also have arrived from northern Africa. These distances usually require less than a normal fat deposit. Most of the Wood Warblers ringed at Capri had moderate to high fat scores (i.e. 3–5), suggesting that they were not in urgent need to replenish their energy stores.

The breeding range of the Wood Warblers extends from southern Italy to northern Scandinavia (Cramp 1992). Recoveries indicate that the breeding grounds of the Wood Warblers at Capri is northern and western Europe (i.e. France, UK, Germany and Sweden; Scebba 1993). The Wood Warblers at Capri could easily continue to the mainland on the fat deposits they are carrying, as the island is situated only a few kilometres from the mainland. In the studies of Wheatears at a spring stopover site (Dierschke et al. 2005), birds of the subspecies being more close to its breeding range stayed shorter times, 1–3 days, at the stopover site than did the more distant breeding subspecies (i.e. up to 12 days). Hence, there could be an additional explanation for the short stopovers of some Wood Warblers: birds which are close to their breeding grounds may move directly into their breeding territory in their next flight.

It is difficult from observations in the field and on a single stopover site to determine if migrating birds are maximising speed of migration or minimising energy consumption (Alerstam & Lindström 1990). We may observe differences between the individuals in stopover lengths and departure fuel loads, but we do not know how individuals

trade the current stopover site in relation to their expectations of future sites along the migratory route. If we assume that the individuals have the same expectations of future stopover sites along the route, time minimising species are expected to exhibit a positive correlation between fuel increase rates and stopover length, and between fuel increase rate and departure fuel loads. We only observed a positive correlation between body mass change rate and last recapture body mass, which cannot be avoided if there is variation in body mass change rate and stopover lengths are uncorrelated. The length of stopover and the large proportion of birds that do not gain body mass suggest that Capri is not an important refuelling site for Wood Warblers. Males, however, seem to make decisions to leave this poor stopover site sooner than the females, a strategy that is also expected from speed maximisers.

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Sammanfattning

Grönsångaren är en tropikflyttande art som häckar i nästan hela Europa utom längst i söder och längst upp i norr. Precis som för många andra flyttande arter anländer hanarna före honorna till häckningsplatserna. De tidigaste hanarna kan etablera sig i de bästa reviren, så därför finns det en stark selektion för att hanarna skall anlända tidigt. Visserligen finns det fördelar för honorna att också komma relativt tidigt, då tidigare kullar ger ett större reproduktivt resultat än senare kullar, men uppenbarligen har detta inte lika kraftig påverkan som en relativt tidig etablering har för hanarna. Det är inte riktigt klarlagt om hanarna lämnar vinterkvarteren tidigare än honorna, eller om skillnaden i ankomsttid mellan könen är ett resultat av att de flyttar olika snabbt. Man kan förvänta sig att bägge könen, men särskilt hanarna, försöker maximera sin flyttningshastighet. Om man antar att alla fåglar har samma förväntningar på samtliga rastplatser under flyttningen så leder det till att de fåglar som har högst fettpålagringshastighet stannar längre och lägger på sig större fettreserver än övriga.

I den här uppsatsen studerades grönsångarens rastning på Capri, under vårflyttningen 1993. Fåglarna fångades på två platser på ön, dels uppe på en bergstopp, dels cirka 100 m längre ner i sluttningen nedanför berget. Totalt ringmärktes 774 grönsångare varav 48 återfångades under rastningen. De flesta individerna (95 %) vägde mellan 7,2 g och 10,5 g. Variationen i vikt förklarades till mer än hälften av den visuella fettklassningen. Vinglängden förklarade åtta procent av variationen och tarslängden bara en procent av variationen i vikten (Tabell 1). Det var inga skillnader mellan grönsångarna ringmärkta på bergstoppen eller sluttningen, vare sig i vikt eller fettklass (Figur 1). De grönsångare som anländer till bergstoppen verkar lämna den väldigt fort då inga fåglar återfångades där. I sluttningen med dess höga och täta vegetation var det vanligt att grönsångare sågs födosöka intensivt och därför också återfångades

oftare än på toppen. Det var också vanligare att fåglarna rörde sig från bergstoppen ner i sluttningen än tvärtom.

Under flyttningsperioden övergick de fångade grönsångarna från att vara relativt långvingade till att vara mer kortvingade (Figur 2). Denna skillnad beror förmodligen på att hanar dominerar under den tidiga delen av säsongen medan honor dominerar under den senare delen. Inga andra uppmätta mått uppvisade någon trend över flyttningssäsongen (Tabell 2).

Det fanns ett samband som normalt indikerar att fåglarna maximerar flyttningshastigheten. De grönsångare som ökade mest i vikt per tidsenhet hade de högsta vikterna den sista gången de återfångades (Figur 3b). Däremot stannade de inte en längre tid än de med lägre viktökningshastighet (Figur 3a). Det senare antyder att fåglarna trots den första korrelationen inte maximerar flyttningshastigheten. Det kan vara så att en variation i hastigheten för viktökningen korrelerar med sista kontrollvikten om rastningens längd är oberoende av viktökningshastigheten. Det faktum att bara 8 av 48 återfångade grönsångare ökade i vikt är också problematiskt för analysen, och indikerar att rastningsplatsen är av låg kvalitet för grönsångarna.

Genom att ta logaritmen av den kumulativa fördelningen av de observerade rastningstiderna (tiden mellan märkning och sista återfångsten) erhåller man en rät linje där lutningen motsvarar logaritmen av sannolikheten för att stanna per dag (Figur 4). Fördelningen av de observerade rastningstiderna indikerade att vi hade två olika grupper av fåglar. En analys av vinglängderna indikerade att den ena gruppen som i snitt bara stannade lite drygt en timme, i huvudsak utgjordes av hanar (Tabell 3). Dessa stannade heller aldrig över natten. Den andra gruppen stannade i snitt knappt tretton timmar, och utgjordes till största delen av honor. Sammantaget kan man säga att Capri inte är en någon strategiskt viktig plats för grönsångare att lägga på sig energireserver för den fortsatta flyttningen. Dessutom verkar hanarna ha mer bråttom än honorna och lämnar därför Capri för att fortsätta sin flyttning med ytterligare en flygetapp, eller för att söka sig till bättre rastplatser – en strategi som är nog så viktig om man vill maximera flyttningshastigheten.