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TIMING AND CONDITION-RELATED EFFECTS ON RECAPTURE PROBABILITY, MASS CHANGE AND STOPOVER LENGTH OF SPRING MIGRATING SONGBIRDS ON A SMALL MEDITERRANEAN ISLAND

EFECTOS RELACIONADOS CON LA DURACIÓN Y CONDICIÓN EN LA PROBABILIDAD DE RECAPTURA, CAMBIO DE PESO Y DURACIÓN DE LAS ESCALAS EN LA MIGRACIÓN PRIMAVERAL DE PASERIFORMES EN UNA PEQUEÑA ISLA MEDITERRÁNEA

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SUMMARY.—*Timing and condition-related effects on recapture probability, mass change and stopover length of spring migrating songbirds on a small Mediterranean island.*

We investigated, at the intra-specific level, the effects of variables such as physical condition, time, date and year of first capture, on the recapture probability, on the probability of improving physical condition during stopover and on the minimum stopover length. Over 61,000 records from 14 species have been used, composed of capture/recapture collected in a period of seven years. The probability of a bird being retrapped increased for those individuals initially trapped later in the day and with a lower physical condition. Also, the probability of improving energetic condition, during a stopover of at least two days, increased with worse energetic conditions at first capture. A longer stopover would allow improvement of the initial condition, even in the case of a small Mediterranean island with limited food resources. This might offer an opportunity for migrants to avoid situations of unbearable physical stress after the demanding crossing of the Sahara and Mediterranean.

Key words: mass gain, Mediterranean Sea, passerine, recapture probability, spring migration, stopover.

RESUMEN.—*Efectos relacionados con la duración y condición en la probabilidad de recaptura, cambio de peso y duración de las escalas en la migración primaveral de paseriformes en una pequeña isla mediterránea.*

Investigamos, a nivel intra-específico, los efectos de la condición energética, hora, fecha y año de la primera captura sobre la probabilidad de recaptura y la de mejora de la condición energética durante la parada migratoria y la duración mínima de la escala. Se utilizó una base de datos con más de 61.000 registros relativos a 14 especies migratorias, incluyendo los de captura-recaptura recogidos en un periodo de siete años diferentes. La probabilidad de que un ave sea recapturada en los días siguientes, parece aumentar en los individuos capturados a las horas más tardías del día y que poseen peores condi-

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ciones energéticas iniciales. También aumenta la probabilidad de mejorar la condición energética durante una parada de al menos dos días, debido a las peores condiciones energéticas en la primera captura. Una parada de más días permitiría mejorar las condiciones físicas iniciales, incluido el caso de una pequeña isla mediterránea con recursos tróficos limitados. Esta circunstancia podría ofrecer a las aves migratorias la oportunidad de evitar situaciones de estrés físico insoportable, después de la difícil travesía del Sahara y Mediterráneo.

Palabras clave: áreas de escala, ganancia de peso, Mediterráneo, migración primaveral, paseriformes, probabilidad de recaptura.

INTRODUCTION

Bird migration between wintering and breeding grounds is featured by alternating phases of active flight and stopover (Ellegren, 1991). During stopover birds replenish energy reserves to be used during the subsequent bouts of migration. The main elements of migration patterns are represented by length of flight bouts, stopover duration and fuel deposition rate. These elements are interrelated, as a flight bout can only be covered if the required energy reserves have previously been stored, which depends on fuel deposition rate and stopover duration (Schaub and Jenni, 2001a). During the energy-demanding and potentially risky journeys, islands may represent unique stopover opportunities for migrants during a sea crossing; this being particularly true for birds that cross the central portion of both the Sahara and Mediterranean. Migrants concentrate on these islands during their sea crossing and the large number of islands scattered throughout the Mediterranean therefore represent an ideal network of field sites for the study of migratory patterns (Spina and Pilastro, 1998). Among these small islands, Ventotene is characterised by a concentration of spring migrants arriving from the open sea during the late morning-early afternoon hours (Pilastro and Spina, 1997). Previous results suggest that most birds staging on Ventotene left North Africa during the previous night and have just completed a 16 hours non-stop flight over at least 500 km of open sea (Pilastro *et al.*, 1995). In fact, the main arrival direction of migrants is from the south-southwest, as estimated also by diurnal observations and ringing recoveries, and days with large influxes of migrants are characterised by light south to southwesterly winds (Pilastro and Spina, 1997). Data on body mass recorded on Ventotene can therefore be regarded as referring to birds that have just landed (usually within the previous 30 minutes; Jenni *et al.*, 2000) and have not yet started refuelling (Pilastro and Spina, 1997). Results from other studies (e.g. Pilastro and Spina, 1997) suggest that the majority of spring migrants stopping on Ventotene usually do not use the island as a stopover site to recover their fat reserves. However, a small proportion of individuals do stop on the island for some time (on average 2.7 % of migratory passerines). To date we do not know of other studies which took into account this fraction of migrants interrupting a sea crossing in order to stage for at least one night on a small Mediteranean island. Factors potentially involved in the departure decision are either intrinsic, such as actual fuel stores, fuel deposition rate, and the endogenous time program (time pressure), or environmental such as weather conditions at ground level, or predator risk (reviewed in Jenni and Schaub, 2003). Despite its fundamental importance, relatively little is known about which factors govern the decision to leave a stopover site (Schaub *et al.*, 2008).

Based on a large data set of capture/recapture data collected in seven different years, we aimed to test three hypotheses regarding some timing and condition related aspects of stopover:

(i) At the intra-specific level, time, date and physical conditions at first capture can influence decitions to stage for at least one night on the island. These variables might therefore significantly predict whether a bird would be retrapped or not. In particular, we expect recapture probability to increase the later the time of day and the lower the physical conditions at first capture. We also expect a significant seasonal decline of this probability when correlated with a progressive improvement of meteorological conditions which might allow a direct flight towards the Italian coasts for a higher percentage of migrants, through a reduced energetic flight cost (Yong and Moore, 1997).

(ii) The majority of birds deciding to stage for at least two days would be able to improve their condition. Furthermore, whether a bird would succeed in improving its energetic condition might be predicted by the date, year and condition at first capture. We expect also the probability of mass gain to increase for birds in poorer condition at first capture and which were originally trapped later in the season (as an effect of the progressive seasonal improvement of meteorological conditions and related food availability; Schaub and Jenni, 2001b). The probability of improving condition can also significantly vary at the inter-annual level.

(iii) The minimum stopover length (MSL) and change in energetic condition (estimated based on the variation of a condition index) would be positively correlated, hence a longer stopover would allow a larger increase of this index. Furthermore, stopover duration in birds with an MSL of at least 2 days would tend to decrease in the course of the migratory season. As environmental conditions (trophic and meteorological) become more predictable and stable during spring (Brown and Brown, 1998, 2000; Rubolini *et al.*, 2005), migrants need lower energy reserves during flight bouts, being in the meantime able to obtain higher energy recovery rates during stopover (Moore and Kerlinger, 1991; Schaub and Jenni, 2001b), so reducing stopover duration. MSL might significantly vary among years also based on the inter-annual variability in environmental conditions.

MATERIAL AND METHODS

Study area

The field work was carried out on Ventotene Island (40° 48’ N, 13° 25’ E), situated 50 km off the Tyrrhenian coast of Italy, with an area of approximately 1.23 km^2 and stretching *ca.* 3 km in a NE-SW direction, with a maximum width of less than 800 m. The vegetation is characterised by cultivations and scrub with elements of typical Mediterranean *macchia* (maquis); for further details on habitat features, see Anzalone and Caputo (1975).

Data sampling

Data were collected during the “Progetto Piccole Isole” (Small Island Project, PPI; Spina *et al.*, 1993) in seven different years (1988, 1990-1991, 1993, 1995-1996, 1999) between April 16 and May 15. Nets were operated from dawn to dusk and checked every hour, and were occasionally closed only in case of adverse weather conditions. Birds were ringed, measured (third primary length, P8, to the nearest 0.5 mm; Berthold and Friedrich, 1979; Jenni and Winkler, 1989) and weighed to the nearest 0.1 g using an electronic balance (Sartorius PT600). For retrapped birds only body mass was measured.

Species and data analysis

Data were analysed from a total of 61,008 ringed birds, belonging to the following 14 species: *Anthus trivialis* (N = 1,547), *Luscinia megarhynchos* (N = 2,157), *Phoenicurus phoenicurus* (N = 1,500), *Saxicola rubetra* (N = 4,366), *Acrocephalus schoenobaenus* (N = 1,129), *Hippolais icterina* (N = 3,664), *Sylvia cantillans* (N = 6,389), *Sylvia communis* (N = 7,017), *Sylvia borin* (N = 12,714), *Phylloscopus sibilatrix* (N = 5,063), *Phylloscopus trochilus* (N = 8,526), *Muscicapa striata* (N = 2,548), *Ficedula hypoleuca* (N = 3,293) and *Lanius senator* (N = 1,095).

Time of capture was defined as the time elapsed since local sunrise, to account for progressive change in timing of sunrise during each season (calculated using Mpj Astro 1.5.1 software). The condition index (CI) of each bird was calculated as an adjusted measure of mass based on body size (Winker, 1995), using the formula: (body mass * 100 / P8). Such estimates of condition would be biased if capture rates for different-sized birds varied during the day. However, we detected no significant relationship between morphological measurements (P8) and capture time (hours after sunrise) in any of the species analysed (P8 regressed on time, time^2, and time^3; NS after Bonferroni correction for multiple tests), indicating that birds of all size classes were captured with equal probability throughout the day. We used the length of P8 as a surrogate for body size (Salewski *et al.*, 2009). P8 has been shown to be highly correlated with wing-length (Berthold and Friedrich, 1979; Jenni and Winkler, 1989; in this study r^2 values ranging between 0.448 and 0.861), which is a measure for body size (Gosler *et al.*, 1998), but shows less inter-observer variance (Berthold and Friedrich, 1979). Salewski *et al.* (2009) showed that P8 explains a significant amount of the variation in body mass of eight long distance migrant passerines. However due to wear, P8 is expected to change over time (Arizaga *et al.*, 2006; Martin, 1996), a fact that should be considered here. In this case, P8 was chosen to estimate body size being the only available biometric measure for each ringed individual.

Minimum stopover length was estimated by subtracting the date of first capture from the one of last capture within the same field season. Thus, a one-day stopover refers to a stopover of one night and part of two days. This method differentiates between passage migrants or transients (i.e., birds that interrupt migration only during the day but presumably resumed migration the following night), and stopover migrants (i.e., birds that suspended their migration for at least one night). This method yielded a conservative estimate as we assumed that birds arrived on the day of initial capture and departed on the day of last recapture (Cherry, 1982). For convenience, birds captured after the day of initial capture were defined as “recaptures” and the others as “non-recaptures”. Following Yong and Moore (1997), individuals that were not recaptured were assumed to have departed from the study site the same day they were ringed and were hence assigned a stopover length of zero. While a minority of these birds might stay at least one night on the island avoiding the mist-nests, it is likely that most of them leave the island on the same day of their arrival. In fact, comparison of hourly trapping patterns in some Mediterranean islands at different latitudes has shown progressive northward day movements of fronts of migrants which took off during the previous night (Grattarola *et al.*, 1999; Massi *et al.*, 1995). Frequent observations on Ventotene refer to songbirds leaving the island towards north during daytime (F. Spina, *pers. obs.*). The decision by most migrants for very short stopovers and for continuing their flight during daytime might be the result of a strong selection pressure for an earlier arrival on the breeding grounds (Spina *et al.*, 1994). Stopover length could not be estimated using

Cormack-Jolly-Seber capture-recapture models, due to the extremely high proportion of transients in our sampled population (M. Schaub, *pers. comm.*).

Condition index changes (ΔCI) during stopover were estimated as the difference in index value between initial capture and last capture. Condition index change was taken as an indicator of changes in energy stores of recaptured birds. In fact, changes in body mass consist mainly of changes in fat stores and wet protein. Fat is 8.5 times more energy dense than wet protein (Jenni and Jenni-Eiermann, 1998). Therefore, changes in body mass indicate vary in energy stores only if fat and wet protein vary in parallel. This is true in most small birds investigated (Lindström and Piersma, 1993). However, we cannot exclude that an increase in body mass might be linked to water intake by a migrant, especially following dehydration after an endurance flight (Biebach, 1991; Leberg *et al.*, 1996).

The effect of time, CI and date (days numbered since 1 January) of initial capture, on the probability of an individual being recaptured in the same season, and the effect of CI, date and year on the probability of a bird having gained mass during stopover (equal to a positive (ΔCI), and only for birds with a MSL of at least 2 days), were assessed by the use of forward stepwise logistic regressions. Model significance was evaluated using likelihood-ratio tests (Norušis, 2005), and we first checked for multicolinearity between variables (Fielding and Haworth, 1995). Generalized linear model procedures (GLM, Norušis, 2005) were employed using type III sums of squares for testing statistical significance of the effects of ΔCI, initial capture date and year (fixed effect), against MSL (only for individuals with MSL of at least 2 days). GLM were applied both on data from the entire trapping period and from a sub-period obtained by deleting data from the last week of our sampling season, in order to avoid the negative effect of the end of the sampling period on stopover length; there were no substantial differences in the results obtained from the analysis of these two different data sets, hence we have considered the complete samples.The Bonferroni correction was used to account for multiple comparisons, adjusting individual P-values by the number of tests, to judge statistical significance at the 0.05 level (Legendre and Legendre, 2003). Statistics were performed using SPSS for Windows, version 13.0.

Results

Retrapped or not: effects of initial CI, time and date. A significant logistic regression model has been obtained for 12 out of 14 species (table 1). In particular the probability for a bird being retrapped seems to increase when it is trapped later in the day (50 % of species), if it has a lower initial CI (67 % of species) and if it has been trapped later in the season for the first time (33 % of species). Logistic models predict a higher retrapping probability in earlier stages of spring in only two species (17 % of species). Each species-specific model has correctly classified a percentage of cases between 94.4 % (tree pipit) and 99.3 % (spotted flycatcher).

Condition index change: effects of initial CI, date and year. In birds with an MSL of at least 2 days an average 61.8 % (± 15.6 % SD) of individuals gained mass during the stopover (or, equally, increase their CI). The significant logistic regression models obtained refer to four species (table 2). These indicate that the probability of CI increase during stopover of at least two days would increase with a lower initial CI (in all species analysed). Date has been found to be a significant predictor in only one case, indicating a higher probability of CI increase the seasonally earlier the original capture date. The year of capture does not show significant effects on the probability on CI increase. The models have correctly

TABLE 1

Effect of CI, time and date of first capture on the probability of a bird staying over at least one night in Ventotene Island. Logistic regression final models and parameter estimates (for significant models). Final models included only significant predictors. P-values after Bonferroni correction.
[Efecto del CI, hora y fecha de la primera captura en la probabilidad de que un ave permanezca al menos una noche en la isla de Ventotene. Modelos finales de regresión logística y parámetros estimados (para modelos significativos). Los modelos finales incluyen sólo los predictores significativos. Valores de la P después de la corrección de Bonferroni.]

Species	Model n	Model χ^2	df	P	Variable	B	SE	Wald χ^2	df	P
Tree pipit	1482	13.201	1	0.004	Constant	2.31	1.40	2.73	1	0.098
					Date capture	–0.04	0.01	13.20	1	0.000
Nightingale	2091	2.726	1	0.000	Constant	–5.81	0.54	114.29	1	0.000
					Time capture	0.15	0.03	19.28	1	0.000
Redstart	1448	17.178	1	0.000	Constant	4.47	2.02	4.91	1	0.027
					CI capture	–0.39	0.10	16.32	1	0.000
Whinchat	4250	54.064	1	0.000	Constant	3.21	0.96	11.21	1	0.001
					CI capture	–0.29	0.04	47.92	1	0.000
Sedge warbler	1081	14.739	1	0.000	Constant	3.97	2.29	3.00	1	0.083
					CI capture	–0.39	0.12	11.14	1	0.001
Icterine warbler	3558	22.355	1	0.000	Constant	3.97	1.76	5.06	1	0.024
					CI capture	–0.44	0.09	21.25	1	0.000
Subalpine warbler	6237	101.248	3	0.000	Constant	3.88	1.07	13.24	1	0.000
					Time capture	0.08	0.01	26.89	1	0.000
					CI capture	–0.06	0.03	4.27	1	0.039
					Date capture	–0.06	0.01	59.74	1	0.000
Whitethroat	6785	80.575	3	0.000	Constant	4.33	0.90	23.14	1	0.000
					Time capture	0.04	0.01	6.39	1	0.011
					CI capture	–0.09	0.02	19.59	1	0.000
					Date capture	–0.04	0.01	53.19	1	0.000
Garden warbler	12378	117.943	2	0.000	Constant	–1.98	0.58	11.62	1	0.001
					Time capture	0.12	0.01	80.61	1	0.000
					CI capture	–0.11	0.02	26.31	1	0.000
Wood warbler	4860	33.009	2	0.000	Constant	–11.58	1.58	53.64	1	0.000
					Time capture	0.09	0.02	13.18	1	0.000
					Date capture	0.05	0.01	18.46	1	0.000
Willow warbler	8272	54.319	2	0.000	Constant	5.31	1.46	13.12	1	0.000
					CI capture	–0.33	0.05	43.18	1	0.000
					Date capture	–0.04	0.01	13.74	1	0.000
Pied flycatcher	3201	25.074	2	0.000	Constant	–13.65	2.59	27.77	1	0.000
					Time capture	0.15	0.04	14.73	1	0.000
					Date capture	0.06	0.02	8.57	1	0.003

TABLE 2

Effect of CI, date and year of first capture on the probability of a bird increasing CI, during stopover of at least two days on Ventotene Island. Logistic regression final models and parameter estimates (for significant models). Final models included only significant predictors. P-values after Bonferroni correction.
[Efectos del CI, fecha y año de la primera captura en la probabilidad de que un ave incremente el CI, durante la parada de al menos dos días en la isla de Ventotene. Modelos finales de regresión logística y parámetros estimados (para modelos significativos). Los modelos finales incluyen sólo los predictores significativos. Valores de la P después de la corrección de Bonferroni.]

Species	Model n	Model χ^2	df	P	Variable	B	SE	Wald χ^2	df	P
Subalpine warbler	188	19.582	1	0.000	Constant	8.21	2.00	16.78	1	0.000
					CI capture	–0.40	0.10	16.04	1	0.000
Whitethroat	223	11.157	1	0.012	Constant	7.11	1.84	14.86	1	0.000
					CI capture	–0.25	0.08	10.44	1	0.001
Garden warbler	172	11.428	1	0.010	Constant	7.62	2.32	10.78	1	0.001
					CI capture	–0.30	0.09	10.31	1	0.001
Willow warbler	48	23.725	2	0.000	Constant	36.32	10.95	11.00	1	0.001
					CI capture	–1.48	0.44	11.35	1	0.001
					Date capture	–0.13	0.06	5.26	1	0.022

classified between 59.3 % (garden warbler) and 79.2 % (willow warbler) of cases.

MSL: effects of CI change, date and year. By using GLMs, significant equations have been obtained in only four species when considering birds with an MSL of at least 2 days (table 3). CI variation during stopover was positively correlated with minimum stopover length, while two species showed a negative correlation between MSL and date of first capture. In no case was the year of capture a significant predictor of MSL.

DISCUSSION

Retrapped or not: effects of initial CI, time and date. The results of logistic regressions seem to support the first prediction, at least for migrants' condition and for the time of first capture. In particular, in at least half of the species the probability of a migrant being retrapped at least on the day following first capture seems to increase if the bird has a low CI and has been trapped for the first time later in the day.

Published information about the effect of current fuel stores on departure probability are contradictory. Whereas some studies found a correlation between emigration and immigration probabilities and body mass or fat stores at first capture in some cases (Bairlein, 1985; Bairlein, 1992; Biebach *et al.*, 1986; Cherry, 1982; Dierschke and Delingat, 2001; Gannes, 2002; Loria and Moore, 1990; Moore and Kerlinger, 1987; Yong and Moore, 1997), the same or other studies found no such relationship in other cases (Dierschke and Delingat, 2001; Ellegren, 1991; Kuenzi *et al.*, 1991;

TABLE 3

Results of GLMs on MSL in relation to CI change during stopover (ΔCI), date of capture and year, for birds with a MSL of at least 2 days on Ventotene Island. Final models included only significant predictors. Only parameters of significant models were reported. P-values after Bonferroni correction.
[Resultados de los GLMs en el MSL en relación con el cambio en el CI durante la escala (ΔCI), fecha de captura y año, para aves con un MSL de 2 días en la isla de Ventotene. Los modelos finales incluyen sólo predictores significativos. Se registraron solamente los parámetros de modelos significativos. Valores de la P después de la corrección de Bonferroni.]

Species	Predictors	df	B	SE	F	P
Tree pipit	ΔCI	1	0.58	0.09	44.875	0.000
Subalpine warbler	ΔCI	1	0.30	0.11	7.964	0.005
Whitethroat	ΔCI	1	0.49	0.07	51.968	0.000
	Date capture	1	–0.20	0.03	53.521	0.000
Garden warbler	Date capture	1	–0.04	0.01	6.455	0.012

Morris, 1996; Safriel and Lavee, 1988; Salewski and Schaub, 2007). The results of our analyses seem to support the first scenario. However, we must consider that at stopover sites fat birds are known to be less active during the day than lean birds (Bairlein, 1985; Titov, 1999; Yong and Moore, 1993) and may be more risk-sensitive and behave more secretively (Moore and Simm, 1986), which can result in a lower recapture probability of fat birds (Bibby *et al.*, 1976; Salewski and Schaub, 2007; Titov, 1999).

As for the higher recapture probability for birds trapped later in the day, we can make the following assumptions. A previous study on garden warblers from Ventotene and other Central Mediterranean islands (Pilastro *et al.*, 1995), suggests that migrants land on these islands when they fly over them during daytime. As they probably have left northern Africa on average at the same time, late arriving birds have been flying for a longer time and hence show reduced reserves (Pilastro *et al.*, 1995). Birds caught later in the day may therefore have deposited less energetic reserves prior to their non-stop flight over the sea; according to flight mechanical theory (Pennycuick, 1975), optimal flight speed decreases with body mass, resulting in a later arrival. Finally, migrants captured late in the day may have been less successful in replenishing energetic reserves and continued to be active later in the day, whereas birds in better conditions should be less active and, consequently, less likely to be captured (Yong and Moore, 1997). Although it is difficult to tease apart these different explanations, pied fycatchers caught later in the day on Ventotene showed higher levels of uric acid in their plasma, indicating that these birds had to sustain their flight metabolism largely on the basis of protein catabolism, hence supporting the scenario suggested above (Jenni *et al.*, 2000).

Condition index change: effects of initial CI, date and year. As predicted, on average when the stopover is longer than one day, the majority of migrants are able to gain mass, a result not far from those reported for thrushes during their spring migration along the coasts of Louisiana (75 % - 90 %; Yong and Moore, 1997). The results of logistic regressions only partly support the second prediction. In particular, virtually only the lower initial physical conditions seem to have a significant effect in determining a subsequent CI increase during stopover. It is interesting to note that a large part of those migrants forced to stay longer, and in particular those in a poorer energetic condition, are able to improve their physical state even on a very small island with limited food resources. However, birds with a minimum stopover of at least two days increased their initial CI (or equally, their initial mass) on average by 0.80 % (± 3.23 SD) per day; this is a low value compared to known estimates (between 1 % and 6 %) for Palearctic-African migrants staging in continental sites during their spring migration (Alerstam, 1990; Maitav and Izhaki, 1994; Shirihai *et al.*, 2001; Wood, 1989). Staging on Ventotene, for migrants forced to stop for some days, would offer an opportunity to avoid situations of unbearable physical stress. This would allow migrants to reduce mortality risk after the demanding crossing of the Sahara and Mediterranean and before covering the long distance towards their breeding grounds.

MSL: effects of CI change, date and year. The third prediction is only partly supported by the results obtained. A positive tendency has been recorded in (ΔCI) increase with stopover duration. A stopover duration of at least a few days would allow an improvement in physical condition in birds deciding to interrupt their migratory flight. Available evidence suggests that energetic reserves are not restored in North Africa and hence the residual fat stores of birds landing on the island are strongly related to the energetic cost of a long journey initiated in sub-Saharan Africa (Pilastro and Spina, 1997). Birds landing on Ventotene with almost completely depleted fat reserves after crossing two large ecological barriers show a marked increase in the loss of proteins which are largely derived from flight muscles and digestive tract (Schwilch *et al.*, 2002). The possibility of improving physical condition also on a small island with reduced potential food resources opens intriguing questions about food competition, although the proportion of individuals staging longer than one day seems to be very small (on average 1.3 % ± 1.2 % SD of ringed birds).

Spring studies on other Mediterranean islands have shown similar species to have overlapping diet compositions (Marchetti *et al.*, 1996, 1998). No elements have been found supporting the idea that taxonomically close species can avoid competition at stopover sites through specialisation towards different prey size classes (Marchetti *et al.*, 1996, 1998). Among stopover migrants those belonging to some species of the genera *Sylvia* and *Phylloscopus* (subalpine warbler, whitethroat, garden warbler and blackcap) are able to gain energy rapidly through nectar consumption, even if their digestive tract, adapted for the migratory flight, is reduced and not fit for digesting large amounts of food. Many other species, however, do not seem to use this resource, even during short stopovers (Schwilch *et al.*, 2001). Stopover duration seems to decrease with season in two species only. Birds that arrive early on their breeding grounds attain higher fitness because they can occupy better territories than late arriving individuals (Salewski and Schaub, 2007; Smith and Moore, 2003).

Birds on spring migration should therefore be under selective pressure to minimise time spent on migration (Lavee and Safriel, 1989; Weber and Houston, 1997; Weber *et al.*, 1998). While stopping over, birds have to decide whether to depart after a short time and thereby minimise time spent at stopover sites, or to depart after a longer stay and thereby minimise the risk of not having enough fuel for the next flight step (Salewski and Schaub, 2007). Migrants captured later in spring are confronted with more stable and predictable environmental (both meteorological and trophic) conditions. Therefore, the optimal solution of the trade-off may be shifted towards shorter stopover under such conditions, and might be an explanation for the seasonal variations of stopover duration. With respect to the trade-off, birds might risk a crossing of the last portion of the Mediterranean Sea before it is too late for successful breeding. Therefore, for passerine migrants in poorer physical conditions, being forced to stop on the island after the demanding crossing of the Sahara and the majority of Mediterranean is an all-or nothing decision-making process (Salewski and Schaub, 2007) which may control their departure from the island to reach the Italian coasts.

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