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LOW INITIAL REFUELING RATE AT STOPOVER SITES: A METHODOLOGICAL EFFECT?

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ABSTRACT.—For various reasons, migrating birds may not refuel and gain mass immediately after they have arrived at a stopover site. That led to the concept of a search-settling time after arrival with a low or negative initial refueling rate, but its existence has not been clearly demonstrated in field studies. Body-mass changes resulting from capture–recapture data can be misleading if used for the estimation of a natural low initial refueling rate because (1) it is usually unknown whether the day of first capture is also the first day of stopover, and (2) handling at first capture may have an adverse effect on subsequent body-mass development. To circumvent those problems we increased probability of catching birds shortly after arrival by inducing landfall by tape-luring, and we estimated body-mass change without previous handling effects from concentration of two metabolites in blood plasma. In the Eurasian Reed-Warbler (*Acrocephalus scirpaceus*) studied at a stopover site in Switzerland, there was no difference in plasma-metabolite concentrations between a group of mostly newly arrived individuals and a group with few newly arrived birds. Similarly, there was no difference in those parameters between birds that had been handled before and birds at first capture. However, the analysis of capture–recapture data from two other Swiss stopover sites with longer handling times indicated that mean body mass of Eurasian Reed-Warblers and European Robins (*Erithacus rubecula*) dropped after capture and reached initial values only after one to several days. We concluded that mass loss after capture depended mainly on lost foraging time and that natural low initial refueling rate after arrival at a stopover site is not detectable under the conditions of this study. *Received 1 November 1999, accepted 14 March 2001.*

DURING THEIR MIGRATORY JOURNEY, passerines regularly need to refill their energy stores. In fact, birds spend most of the time during migration at stopover sites. Fuel deposition rate is therefore an important variable influencing stopover duration and the successful completion of the migratory journey. Several authors measured fuel deposition rates at stopover sites by calculating the difference in body mass between two capture events (e.g. Yong and Moore 1997, Schaub and Jenni 2000). Many of those investigations revealed that birds do not gain mass immediately, but may even lose body mass during the first few days after the first measurement (e.g. Nisbet et al. 1963, Hansson and Pettersson 1989). Because this delay in the onset of refueling is part of the total stopover time needed for refueling, it plays an important role in optimal migration models. In the approach used by Alerstam and Lindström (1990), a delay in the onset of refueling, called *search–settling time,* is a necessary assumption for predicting optimal stopover time. In the same way, low initial refueling rate after arrival at the stopover site is a prerequisite in their model to calculate optimal fuel load at departure. Furthermore, a prolonged stopover influences the optimal number of stopovers during the migration journey. It is therefore of great interest to verify and measure existence of possible delays in onset of refueling in resting migratory birds. For such a phenomenon, the term *initial body-mass loss after arrival* has been used (Lindström 1995). However, because the hypothetical constraints that cause initial body-mass loss may also translate into a lower, but still positive refueling rate, the term *low initial refueling rate* is used in this paper.

The evidence for the occurrence of a low initial refueling rate in small passerines is controversial and, due to methodological problems, not well documented. Field data from various species from different regions and habitats showed all three possibilities of body-mass change after first capture at a stopover site:

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many authors found a body-mass loss (e.g. Szulc-Olech 1965, Pettersson 1983, Hansson and Pettersson 1989, Mädlow 1997, Yong and Moore 1997), some found no mass change (Davis 1962), and some found a mass gain in most birds immediately after first capture (e.g. Bairlein 1987, Moore and Kerlinger 1987, Carpenter et al. 1993).

The attempt to measure mass changes immediately after arrival at the stopover site, is hampered by two problems that have not been overcome by most investigations (Lindström 1995). Firstly, body-mass changes between first and later captures do not necessarily represent body-mass changes after arrival. In habitats that are suitable for the species investigated, birds usually stop over for several days (Schaub et al. 1999, 2001; Schaub and Jenni 2001). Assuming capture probability to be independent of time since arrival, only a minority of first captures have, therefore, arrived the night before. Hence, body-mass changes after first capture are to be clearly separated from mass changes after arrival. Secondly, natural changes in body mass of recaptures have so far not been measured without adding the effect resulting from the handling during first capture. Care has to be taken not to mistake body-mass changes due to handling for natural low initial refueling rate after landing.

In order to solve these problems, we aimed at finding methods to predict the date of arrival at the stopover site and to estimate body-mass change excluding the handling effect. In order to know the date of arrival, we "created" a cohort of newly arrived birds by attracting individuals migrating over the study site through tape-luring (Schaub et al. 1999). Data of birds first caught after such nights with massive induced landfall were compared with data from birds that were first caught on other days and had most probably been resting for more than one day. Handling effects were excluded by estimating fuel-deposition rate at first capture, when birds were not yet affected by a previous capture event, from the concentrations of two metabolites in blood plasma. Plasma levels of triglycerides and β-hydroxy-butyrate have been shown to be good indicators of body-mass changes (Jenni-Eiermann and Jenni 1994; R. Schwilch unpubl. data on Eurasian Reed-Warblers).

By combining those two methods, we first investigated whether a natural low initial refueling rate (independent of a possible handling effect) was noticeable in Eurasian Reed-Warblers (*Acrocephalus scirpaceus*) arriving from their nocturnal flight at a stopover site in continental Europe during autumn migration. Tape-lured birds (mainly having arrived the night before) were expected to have plasma metabolite levels indicative of a lower refueling rate than birds caught on non-tape-luring days (with very few first arrivals). Second, we evaluated whether there is an effect of a short handling time (excluding a possible confounding effect of a natural low initial refuelling rate). Same-day retraps of non-tape-luring days were expected to have plasma metabolite levels indicating a lower refueling rate than birds caught for the first time. Third, we estimated the effect of handling on body-mass development in Eurasian Reed-Warblers and European Robins (*Erithacus rubecula*) at two other sites with longer handling times. We expected a more pronounced negative effect of a longer handling time on body mass development than at the site with short handling times.

Methods

The investigations were carried out in a small nature reserve (Wauwiler Moos; 47°10′N, 8°00′E) in Switzerland on first-year Eurasian Reed-Warblers. The Wauwiler Moos has an area of 15.8 ha, with roughly 50% covered by reeds (*Phragmites australis*), and is surrounded by intensively farmed land. Trapping was carried out in the reedbed with 147 m of mist nets arranged in two lines forming a cross. Birds were caught daily between 18 August and 22 September 1996 from early morning until midday, except for four days when catching was impossible because of bad weather. Nets were monitored continuously from dawn until midday and birds were handled immediately (banding, weighing, fat score after Kaiser 1993). They were released 0–30 m from the site of capture within <20 min after capture. From a random subsample, blood samples were taken immediately after trapping. Most Eurasian Reed-Warblers were molting a few body feathers only. After excluding the few heavily molting birds, no distinction was made between molting and nonmolting birds.

To obtain a high probability of catching freshly arrived birds, Eurasian Reed-Warbler song was played from a tape recorder during nine nights and the following mornings which caused a heavy landfall of that species. After nights of tape-luring, numbers of

Eurasian Reed-Warblers caught increased 3 to 13 times over those caught without luring. The mean probability of an individual having arrived the previous night was 50–85% after nights with tape-luring and much smaller after nights with no tape-luring (for details see Schaub et al. 1999).

To investigate the natural occurrence of a low initial refueling rate after landing, body-mass change unaffected by handling (estimated by plasma metabolite levels) was compared between a group of mostly newly arrived birds (birds captured on tape-luring days) and a group of very few newly arrived birds (birds captured on non-tape-luring days). To detect possible effects of previous handling without the possible confounding effect of natural low initial refuelling rate, we compared body-mass change (estimated by plasma metabolite levels) of birds caught for the first time on non-tape-luring days with body mass change of birds that had experienced handling the same day. Those same day retraps were caught 1–6 h after first capture.

The combined effects of handling and possibly natural low initial refueling rate was investigated by comparing the body-mass development from one capture event to the next between three arrival groups: a group with mostly newly arrived birds (birds captured on tape-luring days), a group with very few newly arrived birds (birds captured on non-tape-luring days) and a group of birds that had not freshly arrived and had already experienced more than two capture and handling events. Each individual was included in the analysis only once.

Blood samples were obtained by puncturing the brachial vein and collecting the resulting blood drops with a capillary system (Microvette CB300 Fluore, Sarstedt). The blood was centrifuged and the plasma stored under liquid nitrogen until analysis. The plasma concentration of triglycerides and β-hydroxy-butyrate was determined with standard enzymatic colorimetric tests for triglycerides including free glycerol (Merck Diagnostica) and for β-hydroxy-butyrate (Sigma Diagnostics). Because in a few birds the amount of plasma was insufficient to determine both metabolites, sample sizes differed slightly between the two metabolites. The plasma concentrations of those metabolites give an estimate of change in body mass during the day of capture (Jenni-Eiermann and Jenni 1994; R. Schwilch unpubl. data on Eurasian Reed-Warblers). Because triglyceride and β-hydroxy-butyrate levels change during the course of the day, they were analyzed in relation to time after dawn. Triglycerides, the form in which lipids are transported to the adipose tissues, increase during the day, whereas β-hydroxy-butyrate is formed during fasting and decreases rapidly with the onset of feeding (Jenni and Jenni-Eiermann 1996). Metabolite levels may also change during the time elapsed between capture and blood sampling. Birds were therefore blood-sampled as soon as possible after capture (mean 6 min, max. 17 min). Timespan between capture and blood sampling was included as a covariable in statistical analysis. Hence, the effect of the very short handling time on plasma metabolite levels was taken into account.

Because total handling time in our Wauwiler Moos study was clearly much shorter than at most other banding stations in Europe, we analyzed body-mass changes of Eurasian Reed-Warblers and European Robins trapped at two other Swiss banding stations: "Portalban," situated at the shore of Lake Neuchâtel, was run during August–October 1987–1989; for "Bolle di Magadino," situated at a river delta south of the Alps, data from the autumn migration periods of 1984 and 1985 were used. At both sites, birds were caught every day, except during heavy rain or storm. Nets were checked every hour or more frequently during very hot periods. Birds were released between 20 and 120 min after capture at a place 50 to 500 m from the nets in a wooded area. Data on the change in body mass of first-year Eurasian Reed-Warblers and European Robins (excluding individuals in juvenile plumage) were divided in two recapture groups: body-mass change between first and second capture which includes a small proportion of newly arrived birds, and body-mass change between subsequent capture events which excluded any newly arrived birds. If several capture intervals of the same bird were available, only the shortest (or, if equal, one chosen at random) was included in the analysis, so that each individual was used only once. Data were analyzed up to a capture interval of four days. The possibility that natural low initial refueling rate significantly affected change in body mass was controlled for by including "recapture group" as a variable in the analysis. For comparison, the Eurasian Reed-Warbler recaptures from the Wauwiler Moos (including tape-lured birds) were treated in the same way. Molt is known to influence fuel deposition rates (Schaub and Jenni 2000) and was included as a variable in the analysis. If sample size of molting or nonmolting birds was too small, the respective group was excluded from analysis.

The rate of change in body mass between two capture events was analyzed in a linear model that accounts for time of day at both capture events (see Schaub and Jenni 2000). Because the residuals in the models with β-hydroxy-butyrate as the dependent variable were not normally distributed, we log-transformed its concentration (ln [β-hydroxy-butyrate + 0.5]), which normalized the residuals. The residuals in the analysis of the triglyceride concentration did not deviate from a normal distribution and were therefore not transformed.

RESULTS

Eurasian Reed Warblers caught on tape-luring days did not differ significantly in body

TABLE 1. Dependence of plasma triglyceride and β-hydroxy-butyrate levels of Eurasian Reed-Warblers in Wauwiler Moos on time elapsed between capture and blood sampling (minutes), time after dawn (minutes), arrival group, and interaction terms. Arrival group distinguished between birds caught on tape-luring days (mostly new arrivals) and birds caught on non-tape-luring days (very few new arrivals).

	df	Sums of squares	*F*	*P*
		Triglycerides		
Time lag to blood sampling	1	4.72	6.92	0.010
Time after dawn	1	24.73	36.23	<0.001
Arrival group	1	0.48	0.70	0.40
Arrival group × time after dawn	1	0.72	1.05	0.31
Arrival group × time lag to blood sampling	1	0.80	1.18	0.28
Residual	97	66.20		
		β-hydroxy-butyrate		
Time lag to blood sampling	1	0.80	20.00	<0.001
Time after dawn	1	1.62	40.66	<0.001
Arrival group	1	0.13	3.28	0.07
Arrival group × time after dawn	1	0.07	1.65	0.20
Arrival group × time lag to blood sampling	1	0.09	2.19	0.14
Residual	94	3.75		

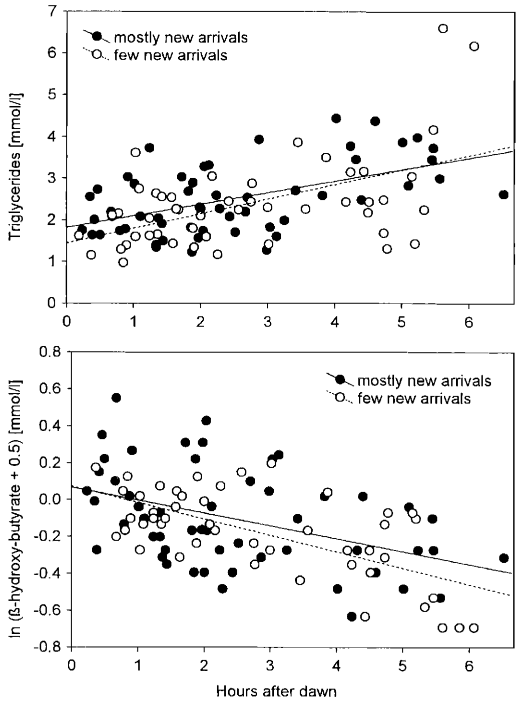

FIG. 1. Plasma triglyceride and β-hydroxy-butyrate levels in relation to time of day in Eurasian Reed-Warblers caught on tape-luring days (mostly new arrivals; dots; $n = 55$ for triglycerides and $n = 53$ for β-hydroxy-butyrate) and for conspecifics caught on non-tape-luring days (very few new arrivals; circles; $n = 48$ and 47, respectively) in Wauwiler Moos. There is no significant difference between the regression lines (see Table 1).

mass or fat score from conspecifics caught on non-tape-luring days (12.6 g ± 1.36 SD, $n = 51$ vs. 12.2 g ± 1.37, $n = 51$; $P = 0.20$; fat score: 2.92 ± 1.13 vs. 2.94 ± 1.07, $P = 0.93$).

Triglyceride concentrations increased with time after dawn and decreased with time elapsed between capture and blood sampling. Whether birds were caught on tape-luring days or not had no significant influence on triglyceride concentration, nor on its change with time of day (Table 1, Fig. 1). Plasma levels of β-hydroxy-butyrate decreased with time of day and increased with time to blood-sampling, but again there was no difference between tape-luring and non-tape-luring days (Table 1, Fig. 1). We therefore concluded that in birds not subjected to handling, there was no difference in the development of body mass (measured with plasma metabolites) between a group of birds with mostly new arrivals and a group with very few new arrivals.

Within the birds caught on non-tape-luring days, there was no difference in the two metabolite levels between birds caught for the first time and birds that had already experienced a capture event on the same day (Table 2, Fig. 2). That indicated that the short handling time in the Wauwiler Moos study had no marked effect on body-mass development estimated from metabolite levels, although a small effect was probably not possible to detect with the small sample size of previously handled birds.

TABLE 2. Dependence of plasma triglyceride and β-hydroxy-butyrate levels of Eurasian Reed-Warblers in Wauwiler Moos on time elapsed between capture and blood sampling (minutes), time after dawn (minutes), handling group, and interaction terms. Handling group distinguished between birds caught for the first time on non-tape-luring days and birds already caught before during the same days.

	df	Sums of squares	F	P
		Triglycerides		
Time lag to blood sampling	1	3.65	4.35	0.04
Time after dawn	1	24.42	29.01	<0.001
Handling group	1	0.002	0.003	0.96
Handling group × time after dawn	1	0.52	0.62	0.43
Handling group × time lag to blood sampling	1	0.81	0.97	0.33
Residual	50	41.99		
		β-hydroxy-butyrate		
Time lag to blood sampling	1	0.14	4.30	0.04
Time after dawn	1	1.01	30.59	<0.001
Handling group	1	0.05	1.51	0.23
Handling group × time after dawn	1	0.04	1.31	0.26
Handling group × time lag to blood sampling	1	0.03	0.93	0.34
Residual	49	1.62		

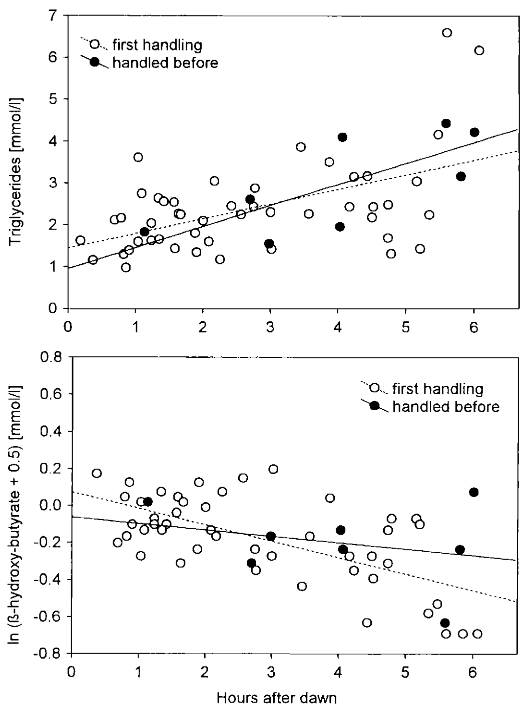

FIG. 2. Plasma triglyceride and β-hydroxy-butyrate levels in relation to time of day in Eurasian Reed-Warblers caught for the first time and on a non-tape-luring day (circles; $n = 48$ for triglycerides and $n = 47$ for β-hydroxy-butyrate) and for conspecifics that had already experienced a capture event the same day (dots; $n = 8$ and 8, respectively) in Wauwiler Moos. There is no significant difference between the regression lines (see Table 2).

When considering the change in body mass of birds recaptured the same day, the subsequent day, or two days after first capture, there was no significant difference between birds caught on tape-luring days, birds caught on non-tape-luring days, and a group of birds caught once before the capture interval considered (i.e. not newly arrived, repeated handling) (Table 3, Fig. 3). It appeared that birds recaptured the same day had on average a slightly negative body-mass balance (Fig. 3), but that effect was not significant (the zero line remains within the 95% confidence interval).

Eurasian Reed-Warblers and European Robins recaptured at banding stations Portalban and Bolle di Magadino (with longer handling times) showed no significant difference in body mass development among recapture groups (i.e. first vs. later recapture intervals), indicating that the probably very small proportion of freshly arrived birds had no significant effect (Table 4, Fig. 4). In Bolle di Magadino where both molting and not molting birds were included in the analysis, molt influenced mass change in both species, with molting birds having larger negative and smaller positive mass differences between two capture events than birds that had completed their molt. Mass changes of Eurasian Reed-Warblers from Portalban and Bolle di Magadino were also positively related to date. In both species from all sites, time of day and number of days between

TABLE 3. Dependence of the mass difference between two capture events on the difference in daytime (Δ daytime), the difference in days between the two captures (Δ day), arrival group, and interaction terms for Eurasian Reed-Warblers in the Wauwiler Moos. The variable arrival group distinguished between birds first caught on tape-luring days (mostly new arrivals), birds first caught on non-tape-luring days (very few new arrivals), and birds caught three or more times, thus certainly not freshly arrived.

	df	Sums of squares	*F*	*P*
Δ daytime	1	26.99	148.1	<0.001
Δ day	2	19.59	53.8	<0.001
Arrival group	2	0.81	2.2	0.11
Δ daytime × arrival group	2	0.85	2.3	0.10
Δ daytime × Δ day	2	0.52	1.4	0.24
Arrival group × Δ day	4	0.59	0.8	0.53
Δ daytime × Δ day × arrival group	4	0.78	1.1	0.37
Residual	120	21.87		

captures had a positive influence on mass change after capture. As revealed by negative body-mass changes (Fig. 4), capture caused a significant drop in body mass, except for the Eurasian Reed-Warbler in Wauwiler Moos, where body mass was not significantly different at day 0, but increased from the next day onwards. At Portalban, body mass in molting Eurasian Reed-Warblers remained lower than at first capture for three days and did not regain initial values until the fourth day. The nonmolting European Robins at Portalban also significantly lost mass at the day of capture, but regained initial values the next day, constantly

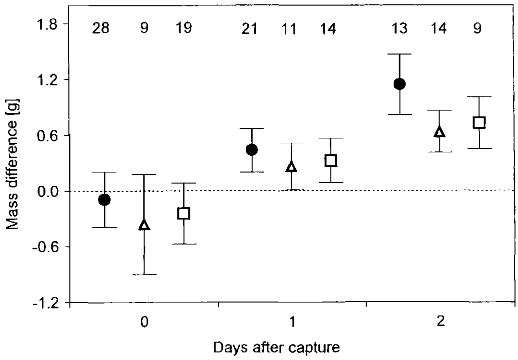

FIG. 3. Estimated differences in body mass of Eurasian Reed-Warblers recaptured in Wauwiler Moos during the same day, during the following day and during the next but one day, according to the linear model resulting from the analysis given in Table 3. Dots: tape-luring days (mostly new arrivals), triangles: non-tape-luring days (very few new arrivals), squares: no new arrivals, repeated handling. Whiskers mark 95% confidence intervals. Numbers in the graph refer to sample sizes.

increasing in mass the following days. In Bolle di Magadino, both Eurasian Reed-Warblers and European Robins lost mass at the day of capture. Birds of both species that had completed their molt regained initial body mass the following day whereas molting birds regained their initial body mass after two days.

DISCUSSION

A low initial refueling rate in birds caught at stopover sites can be explained by two types of explanations: effects of handling and natural causes (Clark 1979, Lindström 1995). Handling effects may be due to shock, stress, and to the feeding time lost while in the net; during handling, during preening after release, and during the return to an appropriate habitat. Natural causes of low initial refueling rate after arrival include illness or other abnormalities, recovery time after particularly stressful flights, and time needed to physiologically switch from endurance flight to feeding, which may include the reconstitution of the digestive tract that may have been reduced during the previous flight. Also, initial failure to locate food in an unfamiliar area, and failure to obtain food, feeding territories, or access to feeding sites due to initial social subordination can be responsible. Finally, voluntary reduction in body mass as an adaptation for prolonged stopovers has been suggested (Clark 1979, Lindström 1995).

To our knowledge, there is no investigation that could clearly separate handling effects from natural causes, and if body-mass loss after first capture was found, it was often uncrit-

TABLE 4. Dependence of the mass difference between two capture events on difference in daytime (Δ daytime), date, molt, numbers of days between the two captures (Δ day), recapture group, and interaction terms. The variable *molt* distinguished between molting birds and birds that had completed their molt. The variable *recapture group* distinguished between the first capture–recapture interval and subsequent recapture–recapture intervals. * = $P < 0.05$, *** = $P < 0.001$.

	Eurasian Reed-Warbler									European Robin					
	Wauwiler Moos			Portalban			Bolle di Magadino			Portalban			Bolle di Magadino		
Source of variation	df	ss	F	df	ss	F	df	ss	F	df	ss	F	df	ss	F
Δ daytime	1	10.97	28.51***	1	34.38	217.82***	1	40.61	124.92***	1	41.78	94.61***	1	23.40	65.08***
Date	1	0.71	1.86	1	2.14	13.58***	1	12.54	38.56***	1	1.62	3.66	1	0.35	0.98
Molt							1	6.08	18.69***				1	10.75	29.88***
Δ day	4	31.99	20.78***	4	5.16	8.18***	4	3.96	3.05*	4	114.34	64.73***	4	9.81	6.82***
Handling group	1	0.32	0.84	1	0.59	3.74	1	0.02	0.05	1	0.71	1.61	1	0.39	1.08
Δ daytime × molt							1	0.68	2.08				1	0.24	0.67
Δ daytime × Δ day	4	2.81	1.82	4	0.33	0.52	4	1.85	1.42	4	3.31	1.87	4	0.66	0.46
Δ daytime × handling group	1	0.21	0.54	1	0.06	0.36	1	0.69	2.12	1	0.08	0.18	1	0.001	0.00
Residual	121	46.56		186	29.36		150	48.76		234	103.34		102	36.68	

ically denoted to be a natural low refueling rate just after landing. An exception is the study by Hansson and Pettersson (1989) who tried to separate handling effects from natural causes of reduction in refueling rate after arrival. They examined capture and recapture data of Goldcrests (*Regulus regulus*) during autumn migration in Sweden and argued against a noticeable effect of handling on body-mass development because of differences in the decrease in body mass in different localities even though trapping and handling methods were the same. However, that does not exclude that handling was responsible for part of the mass decrease. Because they found that the initial decrease in body mass increased with the number of birds caught simultaneously, they concluded that the decrease in mass during the first day is caused by competition for limited resources. Unfortunately, no information is given on probability of first captures being birds landed shortly before capture.

In our study, we tried for the first time to apply a combination of methods to separate handling effects from natural low initial refueling rate after arrival. We assume that the tape-lured birds have a refueling rate similar to that of naturally landed birds. Over continental Europe, Eurasian Reed-Warblers migrate in short hops and only during the night (Ellegren 1993). They land during the night or at the latest in the early morning (Bruderer and Liechti 1998). It seems therefore that tape-luring attracts night migrants that would have landed at the latest a few hours later (Schaub et al. 1999). In this study, tape-lured birds did not differ in energy stores from non-tape-lured conspecifics. However, we do not know whether the behavior of tape-lured birds at the stopover site is similar to naturally landed birds.

In the case of the Eurasian Reed-Warbler in Wauwiler Moos, we found no natural low initial refueling rate after landing and no effect of handling. In Eurasian Reed-Warblers and European Robins caught at two other banding sites with longer handling times, we found a temporary effect of handling.

Effects of handling.—Eurasian Reed-Warblers in Wauwiler Moos showed only a slight and nonsignificant decrease in body mass during the day of capture, regardless of whether birds had mainly arrived the previous night or earlier (Fig. 3). Handling time in our study was

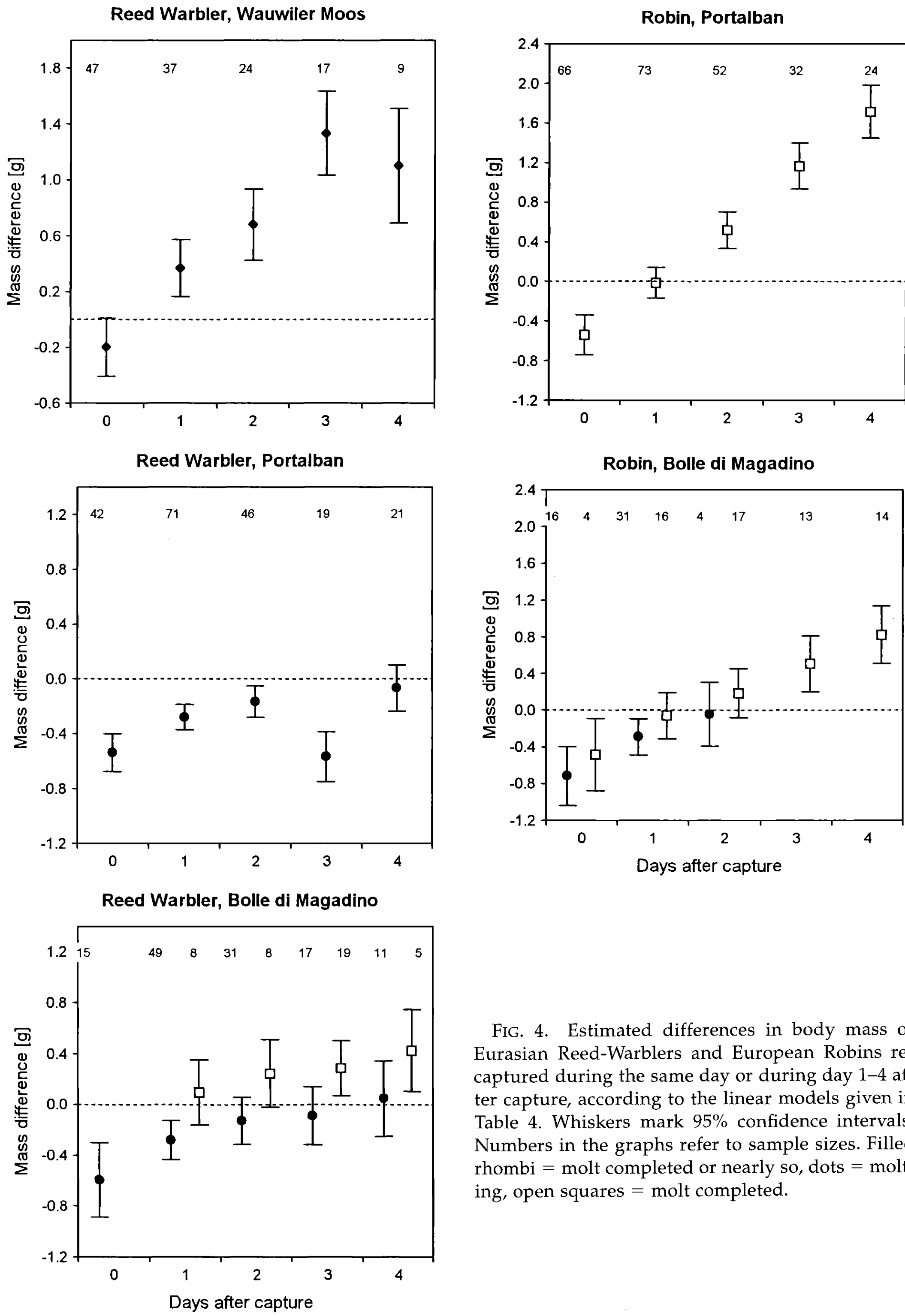

FIG. 4. Estimated differences in body mass of Eurasian Reed-Warblers and European Robins recaptured during the same day or during day 1–4 after capture, according to the linear models given in Table 4. Whiskers mark 95% confidence intervals. Numbers in the graphs refer to sample sizes. Filled rhombi = molt completed or nearly so, dots = molting, open squares = molt completed.

short (less than 20 min) and the birds were released not more than 30 m from the nets. Hence, they could resume foraging immediately. In other studies revealing no body-mass loss after first capture, mist nets were checked every 20 or 30 min and handling time was also short (Cherry 1982, Moore and Kerlinger 1987).

Recaptures from two banding stations with longer handling times showed a decrease in body mass on the day of capture that could not be assigned to natural low initial refueling rate, because only a minority of the first captures were freshly landed and because there was no difference between the first capture–recapture and subsequent recapture–recapture intervals. At Portalban and Bolle di Magadino, mist nets were usually checked every hour and the birds released up to 500 m from the nets in a wooded area. When many birds were caught at least some birds were removed from their foraging sites for up to 2 h with an additional unknown time until return to a suitable site.

Nonmolting birds regained initial body mass within a day, molting individuals within about two days or longer (Fig. 4). Assuming that all birds aimed at regaining initial body mass, molting birds seem to take longer. However, moulting birds may have experienced capture and handling as predation and, as a response, may have lowered their body mass (e.g. Lilliendahl 2000, Gosler 2001). Ellegren (1991) found that only first-year Bluethroats (*Luscinia s. svecica*) lost mass after capture, but not adults. Because we did not have sufficient data on adult birds, we could not test for age differences. Adults might be dominant over first-year birds, thus compensating body-mass loss more rapidly.

Eurasian Reed-Warblers showed a very low rate of body-mass gain in Portalban. However, in Portalban there were only few birds that had already completed molt, therefore only molting birds could be included in the analysis. Compared with the molting Eurasian Reed-Warblers in Bolle di Magadino, the refueling rate of molting conspecifics in Portalban is not exceptionally low. Within the birds that had completed molt, both species showed a lower rate of body mass gain at Bolle di Magadino than at Portalban. We suggest that those differences are caused by differences in food abundance and weather conditions during the study periods.

In summary, it seems that lost foraging opportunities during captivity and resettling in an appropriate habitat negatively affected body-mass development during the day of capture and the following day. Hence, for the sake of the birds' wellness, handling time should be minimized. However, it remains to be investigated whether lost foraging time only (time in captivity, time to go back to an appropriate habitat or to a temporary territory, time for preening) is sufficient to explain body mass development after handling or whether additional effects are involved, such as traumatic effects (Mueller and Berger 1966), emptying of the digestive tract, and increased metabolism (Lilliendahl 2000).

Occurrence of low initial refueling rate after landing.—For Eurasian Reed-Warblers in Wauwiler Moos, we were unable to detect a low initial refueling rate after landing. Considering possible reasons for a low initial refueling rate, that may not be surprising. It seems unlikely that birds intentionally reduce body mass as an adaptation for prolonged stopovers, because mean stopover duration of nonmolting Eurasian Reed-Warblers at 12 sites all over Europe is only 9.5 days (Schaub and Jenni 2001). We also had no indication of aggressive behavior of Eurasian Reed-Warblers, suggesting that social conflicts are unlikely. Failure to locate food in an unfamiliar area can also be rejected, because reedbeds are a familiar and rather uniform habitat for that species and prey density must have been high because large patches of aphids were present on reeds during the whole study period. Time needed to recover from a migratory flight may be another reason for a natural low initial refueling rate. Migrants not only deplete their fat stores during long-distance flights, but also use a certain amount of their body protein. That is reflected in reduced organs, predominantly the breast muscles and the digestive tract. Birds after long-distance flights therefore first need to restore their digestive organs before they can assimilate nutrients efficiently (Hume and Biebach 1996). In the case of Eurasian Reed-Warblers, however, that explanation is unlikely to hold, because there is good evidence that this species migrates over continental Europe in rather short hops, which is unlikely to reduce protein resources noticeably. The average length of flight bouts estimated from recoveries of birds banding in Sweden is 122 ± 17 km (Ellegren 1993), or ~3 h of flight. This agrees with results from radar observations over southern Germany that document decreasing densities of small migrants after midnight (Bruderer and Liechti 1998). In addition, tape-luring may have induced the Eurasian Reed-Warblers to land earlier than without that acoustic attraction and may have shortened flight duration.

In summary, absence of a natural low initial refueling rate in Eurasian Reed-Warblers in Wauwiler Moos is to be expected, but it also demonstrates that low initial refueling rate, which is a necessary assumption in some optimal migration models (Alerstam and Lindström 1990), is not a general phenomenon in migrating birds. Low initial refueling rate is more likely to be found in unfamiliar habitats (search and settling in an appropriate habitat), crowded habitats (competition, territory acquisition), and at places visited after long-distance flights, such as in coastal habitats or after a desert crossing (restoring the digestive tract).

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