

## HOW DOES AGE AND BODY CONDITION AFFECT MIGRATORY RESTLESSNESS AND ORIENTATION IN REED WARBLERS *ACROCEPHALUS SCIRPACEUS*?

Fränzi KORNER-NIEVERGELT\*, Felix LIECHTI\*\* & Bruno BRUDERER\*\*

**SUMMARY.**—*How does age and body condition affect migratory restlessness and orientation in Reed Warblers Acrocephalus scirpaceus?* Orientation cage experiments were performed with 260 Reed Warblers on the southern coast of Spain during autumn 1996, in order to test the hypothesis that birds in good body condition should exhibit a higher amount of migratory restlessness and an activity concentrated more strongly towards one direction than birds in poor body condition. Furthermore, we tested whether body condition and age has an effect on the average preferred direction. Birds with small flight muscles decreased their migratory activity towards the end of the season, whereas birds with medium or large muscles did not. Possibly, among the birds with small muscles, there were more individuals which were going to stay over winter in Iberia. Surprisingly, birds with small fat reserves were active more often than birds with large fat reserves. Among juveniles, more birds were active than among adults. Neither age nor body condition significantly influenced orientation behaviour. We interpret the higher proportion of active individuals among juveniles and birds in poor body condition as an expression of stronger reaction to the stress situation of the experiment compared to the adults and the birds in good condition, respectively. The fact that we did not find any influence on orientation behaviour might be due to stress reactions or other unknown factors which might have outweighed potential effects of age or body condition.

**Key words:** *Acrocephalus scirpaceus*, fat reserves, flight muscle, migratory activity, migratory behaviour, orientation cage experiments.

**RESUMEN.**—*Efectos de la edad y de la condición corporal sobre la inquietud migratoria y la orientación de los Carriceros Comunes Acrocephalus scirpaceus?* Se realizaron experimentos de orientación en jaula con 260 Carriceros Comunes en la costa sur de España durante el otoño de 1996 para contrastar la hipótesis que predice que las aves con mejor condición corporal deberían presentar una mayor inquietud migratoria y una actividad más concentrada en una dirección determinada que las aves en peor condición. Además, comprobamos si la condición corporal y la edad tenían algún efecto en la dirección preferida media. Las aves con músculos de vuelo pequeños disminuyeron su actividad migratoria hacia el final de la estación, mientras que las aves con músculos medianos o grandes no la disminuyeron. Este resultado podría deberse a que las aves con músculos pequeños podrían tender a permanecer invernando en la península Ibérica. Sorprendentemente, las aves con menores reservas de grasa fueron activas más frecuentemente que las aves con mayores reservas. La proporción de aves jóvenes activas fue mayor que la de adultos activos. El comportamiento de orientación no fue afectado por la edad ni por la condición corporal. Interpretamos la mayor proporción de aves activas entre los jóvenes y los individuos con peor condición corporal como debida a una mayor sensibilidad de estas aves a las condiciones de estrés impuestas por el experimento en comparación con las aves adultas y en mejor condición. Estas condiciones de estrés, así como otros factores desconocidos, podrían haber tenido un efecto mayor sobre el comportamiento de orientación que la edad o la condición corporal.

**Key words:** *Acrocephalus scirpaceus*, actividad migratoria, comportamiento migratorio, experimentos de orientación en jaula, músculos de vuelo, reservas de grasa.

### INTRODUCTION

The decisions about when and in which direction to fly during migration are critical for the successful completion of the annual journey of a bird. Migrating birds are expected to adjust

these decisions to their physiological state. Former studies showed that lean birds stayed longer at stopover sites than fat birds to regain energy reserves (Biebach *et al.*, 1986; Loria & Moore, 1990). Release experiments with Robins *Erithacus rubecula* and Pied Flycatchers

\* Zoological Museum, University Zurich-Irchel, CH-8057 Zurich, Switzerland. e-mail fraeni@access.unizh.ch (author for correspondence)

\*\* Schweizerische Vogelwarte, CH-6204 Sempach, Switzerland. e-mail felix.liechti@vogelwarte.ch, bruno.bruderer@vogelwarte.ch

*Ficedula hypoleuca* showed that the amount of fat has an effect on the decision to migrate, lean birds being significantly less likely to embark on migration (Sandberg *et al.*, 1991). Furthermore, fat birds were significantly better oriented during orientation cage experiments than lean ones (Able, 1977). A difference in orientation behaviour between lean and fat birds is expected when they have to cross an ecological barrier, such as an open sea or a desert. It has been suggested that lean birds, when confronted with an ecological barrier, either stay where they are to replenish their energy reserves or engage in reoriented migration in order to search more profitable stopover sites (Lindström & Alerstam, 1986; Sandberg *et al.*, 1988; Åkesson *et al.*, 1996; Sandberg & Moore, 1996; Bruderer & Liechti, 1998).

In this study we examined the migratory activity and orientation of Reed Warblers *Acrocephalus scirpaceus* in registration cages on an East-West running coastline in southern Spain during autumn. We expected that, among the Reed Warblers in good condition, more individuals would exhibit migratory restlessness. Furthermore, birds in good condition are expected to show a higher concentration of their activity towards one direction, and they are expected to exhibit more southerly (towards the open sea) directional preferences than lean birds which were expected to prefer westward directions along the coastline.

## METHODS

### *Experimental birds, study site, experimental set-up and procedure*

The Reed Warbler is a long-distance migrant, wintering south of the Sahara (Cramp, 1992). Most of the European birds initiate their autumn migration towards SW, flying over the Iberian Peninsula to Africa. According to ringing recoveries, the Bay of Biscay is crossed occasionally and the Mediterranean more or less regularly (Zink, 1973). The birds weigh 9–10 g during the breeding season, but can reach up to 20 g during migration (Glutz & Bauer, 1991; Cramp, 1992). For the experiments, we selected 260 birds weighing at least 10 g. 52% of them were adults.

The study area was situated on the southern coast of Spain, 25 km E of Málaga (36° 25' N;

6° 50' E; Fig. 1). The landscape is hilly with sparse, dry bush vegetation and a few olive trees. Lush vegetation is restricted to a narrow zone along the coast in artificially irrigated fields and to an estuary situated 2 km to the E from the study area (Nievergelt *et al.*, 1999).

Reed Warblers were caught in mist-nets put up in fields of sugar cane *Saccharum* sp., Maïs *Zea mais* and in reeds (mostly *Arundo donax*) in the mornings from 4 August 1996 to 19 October 1996. The birds were ringed and weighed, and then transported in cloth-bags over 1.5–3 km to the field station. Here, the birds were aged (following Svensson, 1992, only juveniles and adults were discriminated), and fat and muscle scores were taken according to Bairlein *et al.* (1995). Fat scores from 0–4 were considered as low fat reserves, fat scores 5–8 as high fat reserves. For the flight muscle, scores 1–2 were designated as small, and score 3 as large. Each bird was fed with a mealworm *Tenebrio* sp. and water. During the day, the birds were kept outdoors individually in transparent cloth-cages about 300 m away from the study area in the shade of olive trees. They could see the natural surroundings but were not affected by the people at the station. In the cages the birds had free access to mealworms, berries and water.

The birds were tested in registration cages the following night during the first hour after sunset, which is known as the time when nocturnal migrants normally start their migratory flights. Each of the 260 Reed Warblers was tested only once in an Emlen-funnel (Emlen & Emlen, 1966) lined with type-writer correcting paper that recorded the scratches made by active birds (Nievergelt & Liechti, 2000).

### *Data analyses*

The total number of scratches (**n**) was used as a measurement of activity. Individuals that left less than 40 scratches were considered as inactive. The direction preferred by each individual and individual concentration of directions were calculated by vector addition from the number of scratches in each 15°-sector. The length of the mean vector (**r**) was corrected for the number of scratches (**r** divided by the expected value of the linear regression of **r** on **n**), and was used as a measurement for the



FIG. 1.—Geographic situation of the study area on the southern coast of Spain. The inside graph indicates the distribution of flight directions of free-flying birds observed by radar at the study site (black dot). Only the tracks of small songbirds identified by their wing beat frequency (16-20 Hz; see Bruderer *et al.*, 1995), were considered. The average direction of these flight directions was taken as an estimate of the natural migration direction of Reed Warblers. Coastlines, rivers, reservoirs and mountain areas above 1000 m a.s.l. are also shown in the map.

*[Localización del área de estudio en la costa sur de España. El gráfico incluido indica la distribución de direcciones de vuelo de aves en libertad observadas mediante radar desde la zona de estudio (punto negro). Sólo se consideraron las direcciones de pequeños passeriformes, identificados por su frecuencia de batido de las alas (16-20 Hz; véase Bruderer et al., 1995). La dirección media de esta distribución se consideró como una estima de la dirección natural de migración de los Carriceros Comunes. El mapa señala además las líneas de costa, los ríos, los embalses y las zonas de montaña por encima de los 1000 m s.n.m.]*

individual concentration of the scratches around the preferred direction (Batschelet, 1981). Whether the scratches of an individual were significantly oriented was tested with the Rayleigh test (Batschelet, 1981). Individuals which did not show any significant preferred direction were considered as not oriented. The natural migration direction was calculated as the mean flight direction of free-flying small birds (wing beat frequency > 16) observed by radar at the same time (Bruderer *et al.*, 1995; Fig. 1).

The influence of age, fat score, muscle score, date and cloud cover on activity (total number of scratches), on the concentration of orientation (corrected  $r$ ), and on the deviation of the preferred direction from the natural migration direction was analysed using general linear models, type III ANOVAs performed with SPSS 8.0 software. Age (3, 4), muscle score (0-3) and cloud cover (0, 1) were treated as fixed factors, and date and fat score (0-8) as covariates. We entered all main effects and all two-way interactions into the model. The number of

scratches were square-root transformed before the analysis. The proportions of active individuals in the different condition groups were compared by a log-linear analysis. Differences in the proportion of active birds between juveniles and adults were tested by means of  $\chi^2$  tests. The distribution of the preferred directions from different groups of birds were compared using the Mardia-Watson-Wheeler test (Batschelet, 1981).

RESULTS

Activity

The linear model only explained 13.7% (adjusted  $R^2 = 0.137$ ) of the variation in activity. Date ( $P = 0.016$ ) and the interaction term muscle score  $\times$  date ( $P = 0.049$ ) contributed significantly to the model. However, date is not bio-

logical meaningful, since with the progress of the season, we counted more and more groups of scratches than individual scratches, so that the number of scratches (activity) decreases towards the end of the season due to a change in the counting method. Nevertheless, the decrease in activity towards the end of the season was more pronounced for individuals with small muscles than for those with large muscles. The linear regression of number of scratches on date gives a slope of  $\beta = -0.24$  ( $P = 0.055$ ) for birds with muscle score 1 and  $\beta = 0$  ( $P > 0.1$ ) for the other two groups.

In order to analyse the frequencies in the three-way contingency table (Fig. 2), using fat (lean vs. fat), muscle (small vs. large) and activity/orientation (inactive, active-not oriented, active oriented) we performed a log-linear analysis. The model that best fitted the data (maximum likelihood  $\chi^2 = 5.59$ ,  $df = 4$ ,  $P = 0.23$ ) included two interactions, (1) fat  $\times$

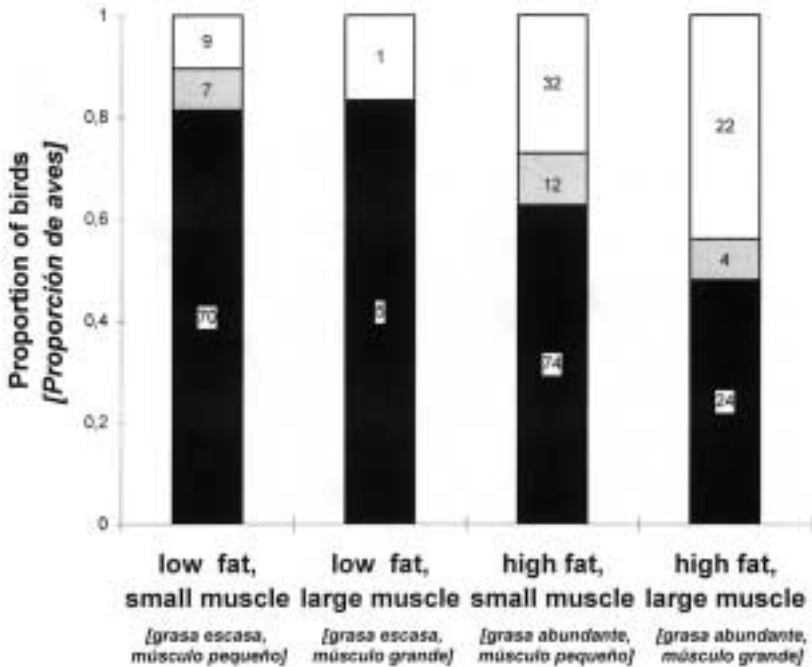


FIG. 2.—Proportion of active (oriented and disoriented) and inactive birds in each body condition group. Black: active and oriented; grey: active and disoriented; open: inactive. Figures within the bars indicate the number of birds in each category.

[Proporción de aves activas (orientadas y no orientadas) e inactivas en cada grupo de condición corporal. Barras negras: activos y orientados; barras grises: activos y no orientados; barras vacías: inactivos. Los números dentro de las barras indican en número de individuos de cada categoría.]

muscle ( $\chi^2 = 21.99$ ,  $df = 1$ ,  $P < 0.0001$ ), and (2) fat  $\times$  activity/orientation ( $\chi^2 = 17.39$ ,  $df = 2$ ,  $P = 0.0002$ ). The first interaction term showed that lean birds with large muscles were very rare, and the second interaction term showed that lean birds were more often active and oriented than fat birds, which are often inactive (Fig. 2). The other two-way interactions were not significant ( $P > 0.09$ ). More juveniles were active (84%) than adults (68%,  $\chi^2 = 9.2$ ,  $df = 1$ ,  $P < 0.05$ ; table 1).

### Concentration

The linear model could explain only 0.5% of the variability (adjusted  $R^2 = 0.005$ ) and no term contributed significantly to the model (all  $P > 0.05$ ). We could not find any influence of either age, muscle score, fat score, date or cloud cover on the individual concentration of activity. Consequently, no significant differences could be found for the proportions of oriented and not oriented birds among the active birds between the groups of different body condition ( $\chi^2 = 1.1$ ,  $df = 2$ ,  $P > 0.05$ ; Fig. 2).

### Preferred directions

In order to include the directional preference as the dependent variable in the general linear model, we had to linearise this circular variable.

We addressed this by using the square-root transformation of the absolute deviation of the preferred direction of each individual from the natural migration direction (208°; Fig. 1). Only 0.7% of the variation was explained by the linear model. Again, no effect was found of either age, muscle score, fat score, date or cloud cover. This was also supported by the comparison of the distribution of individual preferred directions between age classes ( $W \equiv \chi^2 = 0.82$ ,  $df = 2$ ,  $P > 0.05$ ; Mardia-Watson-Wheeler test). Individual preferred directions differed among the groups defined by body condition ( $W \equiv \chi^2 = 17.44$ ,  $df = 6$ ,  $P \approx 0.02$ ; Fig. 3). This significance was caused by the high fat/small muscle group, that showed a considerable proportion of south-easterly directions. No relationship could be detected between activity (number of scratches) and deviation of individual preferred direction from the mean migratory direction ( $R^2 = 0.0116$ ,  $P > 0.05$ ).

### DISCUSSION

Among migrating birds tested in orientation cages during the first hour after sunset a higher proportion of juvenile individuals were active as compared to adults, and of birds with low fat reserves as compared to birds with high fat reserves. Birds with small muscle sizes decreased their activity with the progress of the season, whereas birds with large muscle sizes did not.

TABLE 1

Number of tests ( $n$ ), number and proportion of active birds (>40 registrations per hour) according to age class (ad.: adults; juv.: juveniles) and to four body condition classes based on fat and muscle scores (see text for details).

[Número de experimentos ( $n$ ), y número y proporción de aves activas (más de 40 registros de actividad por hora) según clases de edad (ad.: adultos; juv.: jóvenes) y categorías de condición corporal basadas en índices de reservas grasas y de tamaño del músculo pectoral (véase el texto para más detalles).]

	Low fat, small muscle [Grasa escasa, músculo pequeño]		Low fat, large muscle [Grasa escasa, músculo grande]		High fat, small muscle [Grasa abundante, músculo pequeño]		High fat, large muscle [Grasa abundante, músculo grande]		Total [Total]	
	$n$	Active [Activos]	$n$	Active [Activos]	$n$	Active [Activos]	$n$	Active [Activos]	$n$	Active [Activos]
ad.	40	32 (80%)	3	2 (67%)	72	49 (68%)	21	9 (43%)	136	92 (68%)
juv.	46	45 (98%)	3	3(100%)	46	37 (80%)	29	19 (66%)	124	104 (84%)
total	86	77 (90%)	6	5 (83%)	118	86 (73%)	50	28 (56%)	260	196 (75%)

Additionally, we found that lean Reed Warblers with large muscles are rare on the southern coast of Spain during autumn.

No effect of age was found on the orientation behaviour measured by individual concentration of registrations towards one direction, by deviations of the individual preferred direction from the natural migration direction, and by the preferred directions themselves. Little effect of body condition on the average preferred direction was found, and no significant effects on the other two measurements of orientation behaviour.

### Activity

At the beginning of our study, we were only interested in the directional preferences of the birds and in whether a bird was active or not (i.e., it produced more or less than 40 scratches). Since the exact census of the scratches on the typewriter correction paper is very time consuming, we counted groups of scratches instead of individual scratches for those birds that had more than 40 scratches, after having tested that this change in method did not influence the estimate of the preferred direction of each individual bird. As a result, the number of scratches decreased with the progress of the season due to a change in the counting method. Therefore, all three slopes in the regressions of the number of scratches on date for each muscle score must be corrected slightly towards positive values. But this correction was so small ( $\beta = 0.05$ ) when compared with the differences in the slopes for birds with muscle score 1 and for the other groups ( $\beta(1) = -0.24$ ), that it did not affect the result from the interaction term muscle  $\times$  date. Birds with small muscles decreased their activity with the advance of the season, whereas birds with medium to large muscles sizes did not. A few Reed Warblers regularly overwinter in Iberia (Cramp, 1992), so that it could be that, at the end of the season, among the birds with small muscle sizes there were more individuals that were going to stay in Iberia, and therefore showed less migratory activity, than among the ones with large muscles.

The lower proportions of active individuals in adults as well as in birds with large fat reserves and large muscles were not expected. Ellegren (1993) found that adult Reed and Sedge

Warblers *A. schoenobaenus* migrate faster than juveniles. We therefore could expect adults to show higher activity in registration cages. However, among the juveniles more individuals were active than among adults. Possible explanations for the higher proportion of active birds among juveniles may be that the more experienced adults may be better at distinguishing between profitable (free ranging) and non-profitable (experimental) situations. Adults might start later at night than juveniles, or, most likely, other unknown indirect influences are important.

Biebach *et al.* (1986) as well as Loria & Moore (1990) showed that lean birds stayed longer at stopovers than fat individuals in order to replenish their fat reserves. Correspondingly, lean birds exhibited only diurnal activity in registration cages, whereas fat birds were also nocturnally active (Bairlein, 1985; 1987). Furthermore, fat birds showed a higher amount of migratory restlessness in registration cages (Evans, 1968; Berthold, 1976; 1988; Moore & Kerlinger, 1987; Sandberg & Moore, 1996), and injection of fat into lean migratory birds increased their activity during the migratory season, but in other periods or in sedentary species this effect did not occur (Dolnik & Blyumental, 1967). In the laboratory, migratory activity in Spotted Flycatchers *Muscicapa striata* could be suppressed by low fat reserves combined with food provision (Biebach, 1985). Similar suppression of migratory activity was found in Garden Warblers *Sylvia borin* (Gwinner *et al.*, 1985). The combination of the two factors, depleted fat reserves and the possibility to feed, was actually given for the low fat birds in our experiments. However, they showed higher activity than the fat ones. Surprisingly, we hardly found any corresponding results in the literature. Muheim (1996) observed a negative correlation of body mass and migratory activity in Chaffinches *Fringilla coelebs* caught during active migration on an Alpine pass and tested immediately after capture. Also, during the experiments of Wiltschko & Schmidt (1974) on the southern coast of Spain, fat Garden Warblers showed hardly any activity (Wiltschko, *pers. com.*). We may speculate that freshly caught birds could react differently than birds kept in captivity for a few days, but, although some authors performed experiments over several preceding days, it has never been investi-

gated whether the behaviour in the registration cages changed over time. Our personal impression is that lean birds (compared to the fat and strong ones) and juveniles (compared to adults) showed stronger reactions to the stress situations during the experiment we performed. These stronger reactions were expressed as higher activities. The amount of scratches in an orientation cage experiment should, therefore, not be interpreted as amount of migratory restlessness, at least not when the birds are tested during the day of capture.

Lean birds with large muscles were very rare as compared to birds with other combinations of muscle size and fat reserves (low fat/small muscle, high fat/small muscle, high fat/large muscle). We conclude, therefore, that Reed

Warblers build up fat before muscle during autumn migration.

### Orientation

The lack of a significant influence of age on orientation behaviour suggests that the orientation ability based on the magnetic field and the stars did not differ between juveniles and adults. If birds were able to perceive the topography in the Emlen-funnel, adults would be better oriented than juveniles, since adults can use topography as a further clue for orientation. This was not possible in our case.

Interestingly, fat birds with small muscles showed a more southerly average direction than the other three groups (Fig. 3). However, this

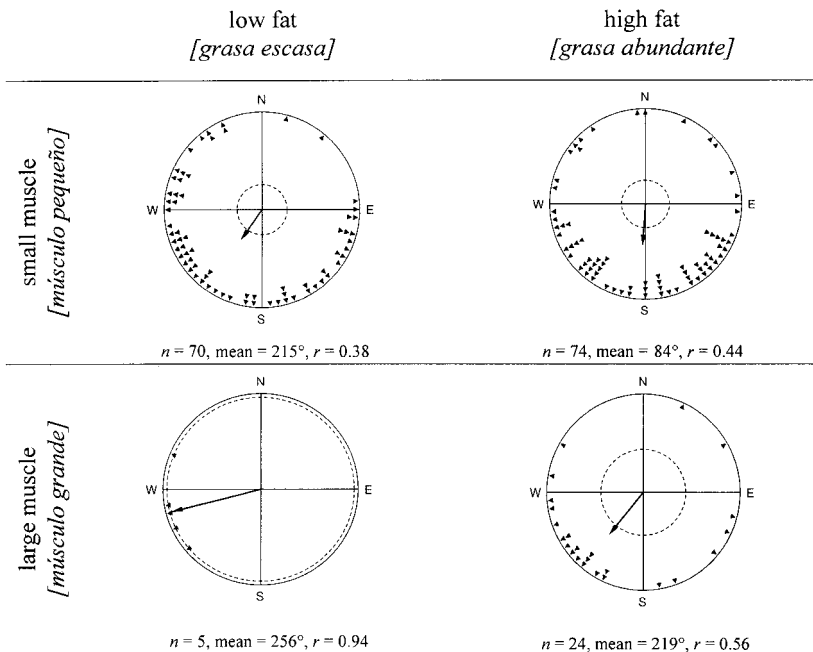


FIG. 3.—Orientation behaviour of Reed Warblers in Emlen-funnel experiments on the southern coast of Spain during autumn 1996. The experiments are grouped according to the bird's fat score and size of the pectoral muscle (see text for details). Triangles: individual means of active and significantly oriented birds; arrows: mean vectors of each sample; r: lengths of the mean vectors; inner circle: 1% limit of significance according to the Rayleigh test.

[Comportamiento de orientación de Carriceros Comunes en experimentos con jaulas en chimenea de Emlen realizados en la costa sur de España durante el otoño de 1996. Los experimentos se agrupan de acuerdo con los índices de reservas grasas y de tamaño del músculo pectoral de los individuos (véase el texto para más detalles). Triángulos: medias individuales para aves activas y significativamente orientadas; flechas: vectores medios para cada muestra; r: longitud de los vectores medios; círculo interno: límite de confinaza del 1% según la prueba de Rayleigh.]

result is not easy to interpret. Surprisingly, many high fat/small muscle birds preferred directions towards South-East, a direction seldom observed by radar on free flying birds. It is not clear at this stage whether the observed preference for South-East directions was an experimental artefact or a biological phenomenon.

Other authors have found meaningful effects of body condition on directional preference in migratory birds. Sandberg (1994) tested Robins in registration cages during migration in southern Sweden and found that lean Robins were significantly more likely to engage in reverse migration than fat ones. Sandberg & Moore's (1996) Red-eyed Vireos *Vireo olivaceus* preferred directions (measured in orientation cages) across the Gulf of Mexico when fat, while lean birds preferred directions along the coastline or towards the mainland. The same authors released birds after testing them in orientation cages. Results of vanishing bearings of the free flying birds were in agreement with the former orientation cage experiment. We performed similar release tests, but all birds headed either along the coast, flew inland where lights of houses were visible or landed nearby when released aloft from a captive balloon (*unpubl. data*). We interpreted all these behaviours as clear escape reactions. It is possible that the stress reaction of Reed Warblers in our experiments (see above) could have masked the effect of body condition and age on orientation behaviour. Sandberg (1994) tested his Robins not before they were acclimatised to captivity and fed properly, which was about 1 or 2 days after capture, while we tested Reed Warblers on the day of capture (10-14 h after capture). However, the Red-eyed Vireos of Sandberg & Moore's (1996) study were also tested not later than 10 hours after capture, and they showed a strong effect of body condition on orientation behaviour. The sea crossing along the trans-Gulf route is much longer (>1000 km) than the sea crossing from Spain to Morocco (170 km), and perhaps the selection for differential behaviours depending on body condition could be stronger at the Gulf of Mexico than at the Mediterranean. Even quite lean birds might be able to cover the distance of about 200 km to profitable refuelling sites in Morocco (Schaub, 2000). Parallel radar observations of free-flying nocturnal migrants showed a clear shift of mean flight direction towards the coastline in the

course of the night (Nievergelt *et al.*, 1999). According to the results presented here, this directional shift might not be due to decreasing fat reserves with the ongoing flight stage, as suggested by Nievergelt *et al.* (1999). Instead, nocturnal migrants may gradually increase the avoidance of sea crossing with the ongoing night to ensure the availability of a resting site at the end of the flight stage. On the other hand, it could be that we did not find any differential orientation behaviour due to stress reaction of the birds.

ACKNOWLEDGEMENTS.—This study was part of the Mediterranean project on bird migration of the Swiss Ornithological Institute, which was supported by the Swiss National Science Foundation (Grant No. 0031-432 42.95), the Silva-Casa Foundation, the Swiss Ornithological Institute and the Zoological Museum, University of Zurich. We are indebted to a number of volunteers helping us during the field work. Dr. H.-R. Roth kindly provided statistical advice. Thanks to Dr. M. Díaz, P. Korner and Javier Pérez-Tris for revising the manuscript. For the translations into Spanish we are grateful to the editorial board of *Ardeola*.

#### BIBLIOGRAPHY

- ABLE, K. P. 1977. The orientation of passerine nocturnal migrants following offshore drift. *Auk*, 94: 329-330.
- ÅKESSON, S., KARLSSON, L., WALINDER, G. & ALERSTAM, T. 1996. Bimodal orientation and the occurrence of temporarily reverse bird migration during autumn in south Scandinavia. *Behavioural Ecology and Sociobiology*, 38: 293-302.
- BAIRLEIN, F. 1985. Body weights and fat deposition of Palearctic passerine migrants in the central Sahara. *Oecologia*, 66: 141-146.
- BAIRLEIN, F. 1987. The migratory strategy of the Garden warbler: a survey of field and laboratory data. *Ring and Migration*, 8: 59-72.
- BAIRLEIN, F., JENNI, L., KAISER, A., KARLSSON, L., NOORDWIJK, A. VAN, PEACH, W., PILASTRO, A., SPINA, F. & WALINDER G. 1995. *Manual of Field Methods*. European Science Foundation. Wilhelmshaven, Germany.
- BATSCHLET, E. 1981. *Circular Statistics in Biology*. Academic Press. London.
- BERTHOLD, P. 1976. Über den Einfluss der Fettd deposition auf die Zugruhe bei der Gartengrasmücke *Sylvia borin*. *Die Vogelwarte*, 28: 263-266.
- BERTHOLD, P. 1988. The control of migration in European warblers. In, H. Ouellet (Ed.): *Proceedings of the XIXth International Ornithological Con-*



- gress, pp. 22-29. University of Ottawa Press. Ottawa.
- BIEBACH, H. 1985. Sahara stopover in migratory flycatchers: fat and food affect the time program. *Experientia*, 41: 695-697.
- BIEBACH, H., FRIEDRICH, W. & HEINE G 1986. Interaction of body mass, fat, foraging and stopover period in trans-Saharan migrating passerine birds. *Oecologia*, 69: 370-379.
- BRUDERER, B. & LIECHTI, F. 1998. Flight behaviour of nocturnally migrating birds in coastal areas - crossing or coasting. *Journal of Avian Biology*, 29: 499-507.
- CRAMP, S. 1992. *The Birds of the western Palearctic, Vol. VI. Warblers*. Oxford University Press. Oxford.
- DOLNIK, V.R. & BLYUMENTAL, T. I. 1967. Autumnal premigratory and migratory periods in the chaffinch *Fringilla coelebs coelebs* and some other temperate-zone passerine birds. *Condor*, 69: 435-468.
- ELLEGREN, H. 1993. Speed of migration and migratory flight lengths of passerine birds ringed during autumn migration in Sweden. *Ornis Scandinavica*, 24: 220-228.
- EMLÉN, S. T. & EMLÉN, J. T. 1966. A technique for recording migratory orientation of captive birds. *Auk*, 83: 361-367.
- EVANS, P. R. 1968. Reorientation of passerine night migrants after displacement by the wind. *British Birds*, 61: 281-303.
- GLUTZ VON BLOTZHEIM, U. N. & BAUER, K. M. 1991. *Handbuch der Vögel Mitteleuropas. Vol. 12/1. (Passeriformes (Teil 3); Teil I: Sylviidae.)*. AULA-Verlag. Wiesbaden.
- GWINNER, E., BIEBACH, H. & KRIES, I. V. 1985. Food availability affects migratory restlessness in caged garden warblers *Sylvia borin*. *Naturwissenschaften*, 72: 51-52.
- LINDSTRÖM, Å. & ALERSTAM, T. 1986. The adaptive significance of reoriented migration of chaffinches *Fringilla coelebs* and *F. montifringilla* during autumn in southern Sweden. *Behavioural Ecology and Sociobiology*, 19: 417-424.
- LORIA, D. E. & MOORE, F. R. 1990. Energy demands of migration on red-eyed vireos *Vireo olivaceus*. *Behavioural Ecology*, 1: 24-35.
- MOORE, F. & KERLINGER, P. 1987. Stopover and fat deposition by North American wood-warblers (Parulinae) following spring migration over the Gulf of Mexico. *Oecologia*, 74: 47-54.
- MUHEIM, R. 1996. *Orientation of night- and day-migrating passerines at the Alpine pass Col de Bretolet*. Diploma Thesis. Zoological Institute, University of Zurich. Zurich.
- NIEVERGELT, F., LIECHTI, F. & BRUDERER, B. 1999. Migratory directions of free-flying birds versus orientation in registration cages. *Journal of Experimental Biology*, 202: 2225-2231.
- NIEVERGELT, F. & LIECHTI, F. 2000. Methodische Aspekte zur Untersuchung der Zugaktivität im Emlen-Trichter. *Journal für Ornithologie*, 141: 180-190.
- SANDBERG, R. 1994. Interaction of body condition and magnetic orientation in autumn migrating robins *Erithacus rubecula*. *Animal Behaviour*, 47: 679-686.
- SANDBERG, R. & MOORE, F. R. 1996. Migratory orientation of red-eyed vireos *Vireo olivaceus* in relation to energetic condition and ecological context. *Behavioural Ecology and Sociobiology*, 39: 1-10.
- SANDBERG, R., PETTERSSON, J. & ALERSTAM, T. 1988. Why do migrating robins *Erithacus rubecula* captured at two nearby stop-over sites orient differently? *Animal Behaviour*, 36: 865-876.
- SANDBERG, R., PETTERSSON, J. & PERSSON, K. 1991. Migratory orientation of free-flying Robins *Erithacus rubecula* and Pied Flycatchers *Ficedula hypoleuca*: Release experiments. *Ornis Scandinavica*, 22: 1-11.
- SCHAUB, M. & JENNI, L. 2000. Fuel deposition of three passerine bird species along the migration route. *Oecologia* 122: 306-317.
- SVENSSON, L. 1992. *Identification guide to European passerines*. British Trust for Ornithology. Norfolk.
- WILTSCHKO, W. & SCHMIDT, K. H. 1974. Direcciones preferenciales de migrantes nocturnos (Passeres) por Almería. *Ardeola*, 20: 127-140.
- ZINK, G. 1973. *Der Zug europäischer Singvögel*. Vogelzug-Verlag. Möggingen.

[Recibido: 3-4-01]  
[Aceptado: 15-2-02]

