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# Competition among European Robins *Erithacus rubecula* in the winter quarters: sex is the best predictor of priority of access to experimental food resources

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Competition for resources by individuals of different sexes, ages, body sizes or geographical origins may have varied implications, from demography to the evolution of migratory systems. European robins *Erithacus rubecula* display segregation by habitat in relation to sex, age, body size and geographic origin in the winter quarters. Here we report on an experiment to investigate the existence of asymmetries in the priority of access to food resources among unconstrained individuals in their natural environment. Feeders with mealworms were provided in an area with a high density of wintering robins and, after 15 days of provisioning, were replaced by a spring trap that was operated during a whole day. The first individuals to be caught in each trap were heavier and had higher fat and muscle scores than last-caught individuals. Based on this and on behavioural observations, we conclude that first-caught individuals had priority of access to feeders. First- and last-caught individuals did not differ in body size, wingtip shape or age ratios. However, whilst 35% of the first-caught individuals were males, only 6% of the last-caught individuals were males. This suggests that sex is an important predictor of the outcomes of competition in an area where multiple robin populations coexist in winter, while, at least on sites where no strictly sedentary individuals are present, geographic origin may be relatively unimportant.

## 1. Introduction

For migratory birds, competition during non-breeding season may determine who lives and who dies or influence the individual state and performance in subsequent nesting seasons through carry-over effects (Marra *et al*. 1998). Competition between sexes and age classes, or between individuals of different size, quality or breeding origins, may contribute to explain segregation by

habitat (Catry *et al*. 2005, Gunnarson *et al*. 2005), differential migration (Greenberg 1986, Adriaensen & Dhondt 1990, Bell 2005, Newton 2008) and demographic consequences resulting from differential mortality of particular groups. For example, many bird populations apparently have a male-biased tertiary (or adult) sex ratio, which fits with observations of generally higher male survival rates (Breitwisch 1989, Promislow *et al*. 1992, Donald 2007).

Recent studies with migratory passerines have revealed that patterns of habitat and geographical segregation of age and sex classes are common, and may actually be the norm rather than the exception (Cristol *et al*. 1999, Catry *et al*. 2005). Despite evidence that such patterns may be caused by the despotic exclusion of weaker competitors by dominant individuals (Desrochers 1989, Marra *et al*. 1993, Marra 2000), the generality of such findings is still to be established.

Competition between individuals of different populations in migratory species sharing common wintering grounds has potentially considerable implications for the regulation of these populations and to the evolution of migratory systems (Bell 2005). For example, it may be the superior competitive ability of southern (resident) populations that allows them to persist despite the annual influx into their range of wintering conspecifics (e.g., Pérez-Tris & Tellería 2002).

The European Robin *Erithacus rubecula* (hereafter Robin) is a small, differential migrant passerine in which females migrate longer distances than males (Adriaensen & Dhondt 1990). In sympatric wintering grounds, males and females show a certain degree of habitat segregation (Catry *et al.* 2004). Such segregation also applies to different age classes, and to populations of different origin (Figuerola *et al*. 2001, Tellería *et al*. 2001, Tellería & Pérez-Tris 2004, Catry 2005).

Catry *et al.* (2004) have suggested that male Robins can despotically exclude females from preferred (micro-) habitats through territorial behaviour. However, evidence for this male dominance is currently lacking, and females are known to be able to defend individual territories and even show adaptive hormone secretion thought to raise their aggression levels during the non-breeding season (Schwabl 1992). Tobias (1997) carried out removal experiments and found a trend for male Robins to show greater competitive ability for winter territories than females. However, Tobias' study was of a sedentary population, where males could have a greater motivation to become holders of territories that would later on be used for reproduction. Comparisons in the Iberian winter quarters have failed to unravel differences between territorial and floater Robins concerning age ratios and body size (Cuadrado 1997), but that study was based on small samples and did not examine sex ratios.

Studies in Southern Iberia have suggested that resident Robins are superior competitors to migrant conspecifics (which originate from Central and Northern Europe), given that they occupy the putatively best habitats, forcing migrants to colonize sub-optimal sites (Tellería *et al*. 2001, Tellería & Pérez-Tris 2004). Again, when dealing with resident individuals, this result may be interpreted in many ways. For instance, resident Robins might retain their nesting territories because they are willing to pay the price of greater investment in territorial defence or fidelity, in anticipation of future benefits during the following breeding season. This question could be further clarified by studying interactions between different populations at sites where no nesting territories exist.

In the present study, we provided supplementary resources (feeders containing food preferred by Robins) in an area with a high density of wintering Robins to investigate the existence of asymmetries in the priority of access to food among wild birds. No nesting territories existed at the study site at any time of the year (although several existed within ca. 1 km), and hence the confounding factor of competition being influenced by the differential future reproductive value of the study plots did not apply. Given the observations that males, adult birds and southern populations predominate in Iberian habitats where Robins have better body condition (Catry *et al.* 2004, Tellería & Pérez-Tris 2004), we predicted that males, adults, and birds from more southerly populations should be able to use more intensively (and perhaps monopolise) the experimental feeders as compared to females, juveniles and northern individuals.

## 2. Methods

The experiment took place during December 2007 and January 2008 at the Arrábida Natural Park (38º27'N, 09º01'W; ca. 200 m a.s.l.), in the central Portuguese coastal region, south of Lisbon. The habitat consists of dense Mediterranean shrubland growing on limestone with numerous small clearings of mostly bare ground. The vegetation is dominated by fruit-producing plants (particularly *Pistacia lentiscus*, *Phillyrea angustifolia* and *Olea europaea* var *sylvestris*) that provide Robins with abundant edible berries that form a large part of their usual diet in this type of habitat (e.g., Herrera 1998). A previous study at this same site and similar habitats has revealed a strongly female-biased sex ratio (87%; Catry *et al*. 2004).

Thirty-seven feeders were placed at least 50 m apart along undisturbed tracks. The feeders were small, plastic dish plates placed on the ground. We provided 6 grams of mealworms (= 50 individuals) per day per feeder during 15 consecutive days. Food was provided at mid-morning, when Robin activity rates appeared to be high. Mealworms could not escape from the feeders but often disappeared within 2–3 hours after being provided. Observations from a hide revealed that Robins accounted for >90% of the visits to feeders, other visitors being Dunnocks *Prunella modularis* and Sardinian Warblers *Sylvia melanocephala*.

At 28 locations, on the day before placing the feeder, a 30-m line of two-shelved mist nests were opened for three consecutive hours in windless conditions. All captured Robins were ringed, marked with a unique combination of colour rings and released on the same spot. We intended to assess the use of feeders by marked birds using a portable hide placed ca. 20 m from each feeder. This proved to be of little use, however, because many Robin visits were too short to enable us to read the colour-ring combination, and the feeders were often used by unmarked birds. Although a few colour-ringed individuals could be positively identified, systematic observations at feeders were abandoned.

On the 16$^{th}$ day after the feeding began, at ca. 10:00, the feeders were removed and a spring trap, baited with a mealworm, was placed at the same location. The first Robins were often captured within minutes after the trap had been set. Captured Robins were immediately removed for processing and the trap was re-set at the same spot. This procedure continued until ca. 16:00. We worked six trap-sites per day. Robins represented 97% ($N$ = 181) of the individual birds captured at the feeders. Other species (Dunnocks and Sardinian Warblers) were never among the first individuals to be caught at any experimental site.

Every newly-trapped bird was aged following the criteria described in Svensson (1992). Maximum wing-chord (± 0.5 mm) was measured using a wing ruler, tarsus (± 0.05 mm) was measured with callipers and body mass (± 0.05 g) was determined using a digital balance. Each primary feather (± 0.25 mm) was measured using an adapted ruler with a pin. Subcutaneous fat reserves were assessed by visual inspection using an eight-point classification (Kaiser 1993) and pectoral muscle profiles were scored with reference to the prominence of the sternal keel and muscle shape, on a four-point classification following Bairlein (1995; see also Gosler 1991).

A blood sample for molecular sexing was collected from each bird by puncturing the brachial vein. Sexing was done through the amplification by PCR (polymerase chain reaction) of a fragment of the CHD gene, using the primers P2 and P8 (Griffiths *et al*. 1998; for a review of molecular sexing in birds, see Dubiec & Zagalska-Neubauer 2006). This procedure amplifies products of different sizes in the chromosomes W and Z, which can be easily visualized after electrophoresis on an agarose gel. After processing, individual Robins were released at the capture site within 60 minutes of being caught.

We reasoned that the first birds to be trapped at a given feeder should have a high probability of being those that had priority access to the food supply and those that used it more often. Subsequent captures during the day were progressively less likely to involve dominant birds at the feeder. Preliminary analyses of body mass and condition supported this assumption (see Results). However, because dominance at the feeders was incomplete and several individuals fed from each feeder, it is doubtful that great significance could be attributed to the order of capture of each individual. Hence, we focused on comparisons involving the greatest possible contrast in capture history. We compared first-caught individuals (invariably captured soon

after the trap was set) with last-caught individuals. For the latter group, we only considered those that were captured at least three hours after the trap was initially set up, or whose capture was preceded by at least three other individuals at the same site. Molecular sexing was only performed in this subset of sampled birds. Furthermore, because we were unable to extract blood from eight individuals, sample sizes were smaller for the analyses involving sex than for those involving other individual characteristics.

Bird populations with a greater migratory tendency tend to have longer and more pointed wings, and this general trend applies to Robins, with more northerly populations differing from southern and predominantly sedentary ones (Pérez-Tris *et al*. 2000, Tellería *et al*. 2001). Hence, we calculated wingtip size and shape indices ($C_1$ = isometric size; $C_2$ = pointedness; $C_3$ = convexity) derived from size-corrected components analysis (SCCA; Lockwood *et al.* 1998), and compared their values in first- and last-caught individuals to assess if geographic origin of individuals might influence competitive relationships at the feeder sites. The use of principal components analysis scores instead of SCCA indices produced qualitatively similar results (not shown).

We made paired comparisons of first- and last-caught individuals per trap, through the use of paired *t* tests for continuous variables and through Wilcoxon signed-ranks tests for ordinal variables (fat and muscle scores). When comparing Robins that were recaptured with Robins that were never trapped again after initial ringing, we used analysis of variance (ANOVA) and Mann-Whitney *U* tests for continuous and for ordinal variables, respectively. We compared proportions using Fisher's exact tests. Throughout the paper, means are presented together with standard deviations, except if stated otherwise. All analyses were carried out using SPSS 17.0.

## 3. Results

The mean number of Robins captured per 30-m mist-net line was 4.2 ± 2.2 ($N$ = 28, range 1–9). The mean number of individual Robins captured per trap was 4.9 ± 2.1 ($N$ = 37, range 2–11). In each trap, the last individual to be caught was captured

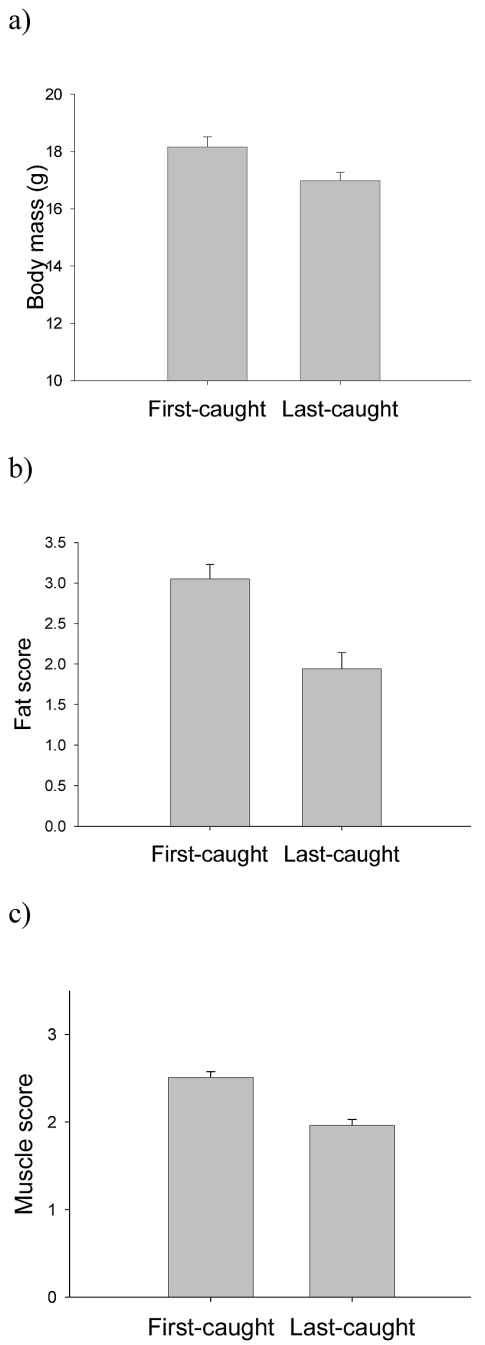


Fig. 1. Body condition of first-caught and last-caught Robins at the experimental feeding sites. (a) Body mass (paired *t* test: $t_{33}$ = 3.51, $P$ = 0.001). (b) Fat score (Wilcoxon test: $Z$ = 3.60, $P$ < 0.001). (c) Muscle score (Wilcoxon test: $Z$ = 4.02, $P$ < 0.001). Columns show mean values and error bars represent standard errors of the mean. $N$ = 34 pairs of first- and last-caught individuals per trap.

on average 275 ± 98 minutes (range: 60–420) after the first bird was captured.

First- and last-caught individuals showed marked and highly significant differences in several of the measured variables. In particular, first-caught individuals were heavier than last-caught birds, which reflected both higher fat reserves and greater muscle volume (Fig. 1). There were no significant differences between first- and last-caught birds in wing length (71.8 ± 2.1 mm and 71.3 ± 1.3 mm, $t_{32} = 1.18$, $P = 0.25$) or in tarsus length (25.4 ± 0.8 mm and 25.3 ± 0.8 mm, $t_{32} = 0.67$, $P = 0.5$), nor in any of the SSCA derived wingtip indices: $C_1$ (3.8504 ± 0.00004 and 3.8505 ± 0.00003, $t_{32} = -0.98$, $P = 0.3$), $C_2$ (1.76 ± 0.20 and 1.79 ± 0.16, $t_{32} = -0.57$, $P = 0.6$), $C_3$ (–0.10 ± 0.22 and –0.05 ± 0.20, $t_{32} = -0.95$, $P = 0.3$). These results remained consistent when age and sex effects were accounted for in a General Linear Model (results not shown).

The higher body reserves of first-caught individuals could have resulted from Robins with initially better condition (before the experiment) being those that were more successful in gaining priority of access to feeders. However, individuals caught in mist nests that were later found to be the first on the trap did not have larger body reserves (at the original capture) than Robins captured in mist-nets that were never recaptured again (Table 1).

Amongst the first-caught birds that could be aged, 39% ($N = 36$) were adults, while amongst the last-caught individuals adults represented 28% ($N = 35$); the difference in these proportions was not significant (Fisher's exact test, $P = 0.45$). In contrast, the difference in sex ratio between first (35% males, $N = 31$) and last-caught individuals (6% males, $N = 32$) was highly significant (Fisher's exact test, $P = 0.005$).

Table 1. Body mass, fat and muscle scores (mean ± SD) of Robins captured before the feeders were set up, divided into individuals recaptured using spring traps as first-caught individuals and those that were not recaptured. Mass was compared using ANOVA, and fat and muscle scores were compared using Mann-Whitney *U* test; all comparisons were non-significant ($P > 0.1$).

| Category | Mass (g) | Fat score | Muscle score |
|---|---|---|---|
| Recaptured ($N = 7$) | 16.9 ± 0.5 | 1.1 ± 0.9 | 2.4 ± 0.4 |
| Not recaptured ($N = 80$) | 16.4 ± 1.0 | 0.9 ± 0.8 | 2.3 ± 0.4 |

## 4. Discussion

European Robins are segregated by sex in their winter quarters, with females being more abundant in shrubland and males comparatively more numerous in woodland. One likely hypothesis for this segregation is that males exclude females from optimal habitats (Catry *et al*. 2004). Our study provides the first compelling evidence that male Robins indeed secure the priority of access to valuable (micro-) habitat patches when in open competition with females in the winter quarters, which may force females to abandon areas where males are more abundant. On the other hand, we found little evidence for superiority of southern over northern Robins.

### 4.1. Evidence of access priority by first-caught individuals

First-caught Robins were heavier and carried much larger fat and muscle reserves than did last-caught individuals. The most likely explanation for this pattern is our assumption that the first-caught birds were those who gained access to the supplementary feeding. Had feeders not been partly monopolized by any Robins, or stochastic factors been more important than the priority of access in determining the timing and order of capture, no major differences would have been detected in body mass and composition between first- and last-caught individuals. A difference should rather occur in the opposite direction, because Robins (and most other passerines) wintering in temperate regions tend to accumulate body reserves during the course of the short winter days (Pilastro *et al*. 1995, Herrera 1998, Thomas 2000).

The higher mass of first-caught Robins may have resulted from higher energetic intake due to supplementary feeding. Body mass of wintering passerines may indeed increase as a response to supplementary feeding (Rogers & Heath-Coss 2003). Alternatively, first-caught Robins may have been in better condition due to their higher in-

dividual quality or competitive ability even before the feeding experiment took place. However, this explanation seems less likely, as the few individuals that had also been captured before the experiment were not heavier than, and had similar reserves to, individuals caught in those same days that were never observed again. Either way, irrespective of the underlying factors, the remarkable difference in body condition between first- and last-caught Robins strongly suggests that these groups differed profoundly in their use of feeders. This was further supported by the fact that colour-ringed individuals that used feeders frequently, were usually amongst the first to be caught in spring traps (direct observations at some feeders, see Material and methods).

It is conceivable that the individual Robins that most frequently used the feeders were those that, by chance had the feeders placed in their territories. Such birds would have an advantage in further contests because they would have no "settlement costs" in the feeder area (Tobias 1997). On the other hand, despite the fact that many Robins are territorial in winter, a fraction of the population behaves as floaters, a characteristic typical for many bird species (Cuadrado 1997). Floaters would be more likely to be amongst the last-caught individuals simply because they keep moving and would therefore visit a feeder/trap only accidentally. Even if this explanation was true and there was no fair competition for the feeders between territory owners and floaters, our results still support the idea that first-caught individuals have an advantage in winter competition for resources, because territorial birds are generally thought to have a greater resource-holding potential than floaters do, and floating is seen as an inferior strategy (e.g., Rappole *et al*. 1989).

### 4.2. Sex is a good predictor of access to feeders

There was a potential for strong competition for feeders, as many individual Robins were seen to use them (see Dänhardt and Lindström 2001 for similar observations of the inability of Robins to fully monopolise feeders), and indeed the 50 daily mealworms often disappeared within 2–3 hours of being provided. Robins wintering at our study site consume large numbers of berries (authors' unpubl. data), but they prefer to ingest invertebrates whenever they are available (Berthold 1976, Cortez 2007). Hence, it is reasonable to infer that we provided a valuable resource that Robins were motivated to compete for.

Besides fat and muscle scores, sex was the only predictor of order of capture at the feeder sites, while there was no difference in size or age between first- and last-caught individuals. These results may be surprising, given that male Robins are larger than females and hence a size difference might be expected in our experiment. However, many Robin populations coexist in Iberian winter quarters (Bueno 1998, Tellería & Pérez-Tris 2004), and the morphometric variability associated with such range of geographical origins may mask sex-related patterns. Male dominance may result not so much from larger male size, but from differences in sex-specific baseline aggression levels, presumably influenced by the levels of circulating male hormones that determine aggressive behaviour (Piper 1997). In this context, it is interesting to note that habitat segregation of wintering Robins seems to be mostly influenced by sex, and not so much by age or body size (Catry *et al.* 2004).

### 4.3. Geographic origin makes little or no difference

Wingtip size or shape did not differ between first- and last-caught individuals, which indicates that the geographic origin of individuals was unimportant in determining access to feeders. This contrasts with available evidence suggesting superior competitive ability of southern Robin populations (Tellería *et al*. 2001, Tellería & Pérez-Tris 2004). Perhaps southern individuals only gain advantage over migratory ones due to previous ownership of their breeding territories. Still, because migrant individuals of more southerly origins arrive earlier to common winter quarters than their northern counterparts (Bueno 1998), such advantage should still be detected in areas where no completely sedentary individuals exist.

### 4.4. Conclusions

Our experimental setup is relatively easy to implement and could be used to further explore difficult questions such as dominance relationships in Robins (or other birds) of different origins sharing common wintering quarters (Pérez-Tris & Tellería 2002, Tellería & Pérez-Tris 2004, Newton 2008). Thus far, such studies concerning Robins have mostly dealt with birds of unknown sex, and given that this attribute seems to be of paramount importance in regulating competition between individuals, sex should not be ignored in future research. More work is needed to confirm or reject previous suggestions of asymmetries in competitive ability between Robins of different geographic origins.

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### Punarintojen keskinäinen kilpailu talvehtimisalueilla: sukupuoli ennustaa etuoikeutetun aseman ruokailuhierarkiassa

Sukupoli, ikä, fyysinen koko tai maantieteellinen alkuperä resurssikilpailussa voivat vaikuttaa populaatioihin vaihtelevasti, demografiasta muuton evoluutioon. Talvehtimisalueillaan punarinnoilla (*Erithacus rubecula*) on elinympäristöjen eriytymistä sukupuolen, iän, koon ja maantieteellisen alkuperän suhteen.

Tässä tutkimuksessa tarkasteltiin tällaisten asymmetrioiden mahdollisuutta tilanteessa, jossa muutoin rajoittamattomat yksilöt kilpailevat pääsystä ruokailemaan. Alueella, jolla on korkea punarintatiheys, tarjottiin ruokinta-automaateilla jauhopukin toukkia; 15 päivän ruokkimisen jälkeen automaatit korvattiin yhden päivän ajaksi jousipyydyksin. Ensimmäiset pyydystetyt yksilöt olivat painavampia ja omasivat korkeammat rasva- ja lihasarvot kuin viimeksi pyydystetyt.

Tämä sekä käyttäytymishavainnot viittaavat siihen, että ensin pyydystetyillä oli etuoikeus pääsyyn automaateille. Ensin ja viimeksi pyydystettyjen yksilöiden välillä ei ollut eroja ruumiin koossa, siivenkärjen muodossa eikä ikäjakaumassa. Kuitenkin ensiksi pyydystetyistä 35 % ja viimeksi pyydystetyistä 6 % oli koiraita. Tämä havainto viittaa siihen, että sukupuoli on merkittävä kilpailun lopputuloksen ennustaja talvehtimisalueella, jolla esiintyy useiden punarintapopulaatioiden yksilöitä. Sitä vastoin maantieteellinen alkuperä saattaa olla vähämerkityksinen ainakin alueilla, joilla ympäri vuoden paikallisia yksilöitä on vähän.

## References

Adriaensen, F. & Dhondt, A.A. 1990: Population dynamics and partial migration of the European Robin *Erithacus rubecula* in different habitats. — Journal of Animal Ecology 59: 1077–1090.

Bairlein, F. (ed.) 1995: Manual of field-methods. European-African songbird migration network. — Wilhelmhaven. Germany.

Bell, C.P. 2005: Inter- and intrapopulation migration patterns: ideas, evidence and research priorities. — In Birds of two worlds. The ecology and evolution of migration (eds. Greenberg, R. & Marra, P.P.): 41–52. John Hopkins University Press, Baltimore.

Berthold, P. 1976: The control and significance of animal and vegetable nutrition in omnivorous songbirds. – Ardea 64: 140–154.

Breitwisch, R. 1989: Mortality patterns, sex ratios and parental investment in monogamous birds. — In Current Ornithology 6 (ed. Power, D.): 1–50. Plenum Press, New York and London.

Bueno, J. M. 1998: Migracion e invernada de pequeños turdinos en la Peninsula Ibérica V. Petirrojo (*Erithacus rubecula*). – Ardeola 45: 193–200. (In Spanish)

Catry, P. 2005: Social composition, mass regulation and site fidelity of migrant robins *Erithacus rubecula* wintering in a marginal habitat. – Airo 15: 59–64.

Catry, P., Campos, A., Almada, V. & Cresswell, W. 2004: Winter segregation of migrant European robins *Erithacus rubecula* in relation to sex, age and size. — Journal of Avian Biology 35: 204–209.

Catry, P., Phillips, R. & Croxall, J.P. 2005: Sexual segregation in birds: patterns, processes and implications for conservation. — In Sexual segregation in vertebrates: ecology of the two sexes (eds. Ruckstuhl, K.E. & Neuhaus, P.): 351–378. Cambridge University Press, Cambridge.

Cortez, S. 2007: Aspectos de dominância social e preferências alimentares de piscos-de-peito-ruivo *Eritha-*

*cus rubecula* invernantes em Portugal. — MSc thesis, ISPA, Lisbon. (In Portuguese)

Cristol, D.A., Baker, M.B. & Carbone, C. 1999: Differential migration revisited. Latitudinal segregation by age and sex class. — In Current Ornithology vol. 15 (eds. Nolan Jr, V., Ketterson, E.D. & Thompson, C.F.): 33–87. Kluwer Academic/Plenum Publishers, New York.

Cuadrado, M. 1997: Why are migrant robins *Erithacus rubecula* territorial in winter? The importance of the anti-predation behaviour. — Ethology Ecology and Evolution 9: 77–88.

Dänhardt, J. & Lindström, Å. 2001: Optimal departure decisions of songbirds from an experimental stopover site and the significance of weather. — Animal Behaviour 62: 235–243.

Desrochers, A. 1989: Sex, dominance and microhabitat use in wintering black-capped chickadees: a field experiment. — Ecology 70: 636–645.

Donald, P.F. 2007. Adult sex ratios in wild bird populations. — Ibis 149: 671–692.

Dubiec, A. & Zagalska-Neubauer, M. 2006: Molecular techniques for sex identification in birds. — Biology Letters 43: 3–12.

Figuerola, J., Jovani, R. & Sol, D. 2001: Age-related habitat segregation by robins *Erithacus rubecula* during the winter. — Bird Study 48: 252–255.

Gosler, A.G. 1991: On the use of greater covert moult and pectoral muscle as measures of condition in passerines with data for the great tit *Parus major*. — Bird Study 31: 1–9.

Greenberg, R. 1986: Competition in migrant birds in the nonbreeding season. — In Current Ornithology 3 (ed. Johnston, R.F.): 281–307. Plenum Press, New York & London.

Griffiths, R., Double, M.C., Orr, K. & Dawson, R.J.G. 1998: A DNA test to sex most birds. — Molecular Ecology 7: 1071–1075.

Gunnarsson, T.G., Gill, J.A., Newton, J., Potts, P.M. & Sutherland, W.J. 2005: Seasonal matching of habitat quality and fitness in a migratory bird. — Proceedings of the Royal Society of London Ser. B 272: 2319–2323.

Herrera, C.M. 1998: Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: a 12-year study. — Ecological Monographs 68: 511–538.

Kaiser, A. 1993: A new multi-category classification of subcutaneous fat deposits of songbirds. — Journal of Field Ornithology 64: 246–255.

Lockwood, R., Swaddle, J.P. & Rayner, J.M.V. 1998: Avian wing tip shape reconsidered: wingtip shape indices and morphological adaptations to migration. — Journal of Avian Biology 29: 273–292.

Marra, P.P. 2000: The role of behavioral dominance in structuring patterns of habitat occupancy in a migrant bird during the nonbreeding season. — Behavioural Ecology 11: 299–308.

Marra, P.P., Hobson, K.A. & Holmes, R.T. 1998: Linking winter and summer events in a migratory bird by using stable carbon isotopes. — Science 282: 1884–1886.

Marra, P.P., Sherry, T.W. & Holmes, R.T. 1993: Territorial exclusion by a long-distance migrant warbler in Jamaica: a removal experiment with American redstarts, *Setophaga ruticilla*. — Auk 110: 565–572.

Newton, I. 2008: The migration ecology of birds. — Academic Press, Amsterdam.

Pérez-Tris, J., Carbonell, R. & Tellería, J.L. 2000: Identificación e importancia poblacional de los Petirrojos *Erithacus rubecula* locales durante la invernada en el sur de España. — Ardeola 47: 9–18. (In Spanish)

Pérez-Tris, J. & Tellería, J.L. 2002: Migratory and sedentary blackcaps in sympatric non-breeding grounds: implications for the evolution of avian migration. — Journal of Animal Ecology 71: 211–224.

Pilastro, A., Bertorelle, G. & Marin, G. 1995: Winter fattening strategies of two passerine species: environmental and social influences. — Journal of Avian Biology 26: 25–32.

Piper, W.H. 1997: Social dominance in birds: early finding and new horizons. In Current Ornithology 14 (eds. Nolan Jr., V., Ketterson, E.D. & Thompson, C.F.): 125–187. Plenum Press, New York.

Promislow, D.E.L., Montgomerie, R. & Martin, T.E. 1992: Mortality costs of sexual dimorphism in birds. — Proceedings of the Royal Society of London Ser. B 250: 143–150.

Rappole, J.H., Ramos, M.A. & Winker, K. 1989: Wintering wood thrush movements and mortality in southern Veracruz. — Auk 106: 402–410.

Rogers, C.M. & Heath-Coss, R. 2003: Effect of experimentally altered food abundance on fat reserves of wintering birds. — Journal of Animal Ecology 72: 822–830.

Schwabl, H. 1992: Winter and breeding territorial behaviour and levels of reproductive hormones of migratory European Robins. — Ornis Scandinavica 23: 271–276.

Svensson, L. 1992: Identification guide to European passerines. — Stockholm.

Tellería, J.L. & Pérez-Tris, J. 2004: Consequences of the settlement of migrant European robins *Erithacus rubecula* in wintering habitats occupied by conspecific residents. — Ibis 146: 258–268.

Tellería, J.L., Pérez-Tris, J., Ramírez, A., Fernández-Juridic, E. & Carbonell, R. 2001: Distribution of robins *Erithacus rubecula* in wintering grounds: effects of conspecific density, migratory status and age. — Ardea 89: 363–373.

Thomas, R.J. 2000: Strategic diel regulation of body mass in European Robins. — Animal Behaviour 59: 787–791.

Tobias, J. 1997: Asymmetric territorial contests in the European robin: the role of settlement costs. — Animal Behaviour 54: 9–21.