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Two worlds apart: do dramatic differences in wintering European robin populations result from despotism or from habitat specialisation?

Em mundos separados: serão as diferenças dramáticas entre populações de piscos-de-peito-ruivo invernantes resultado de despotismo ou de especializações?

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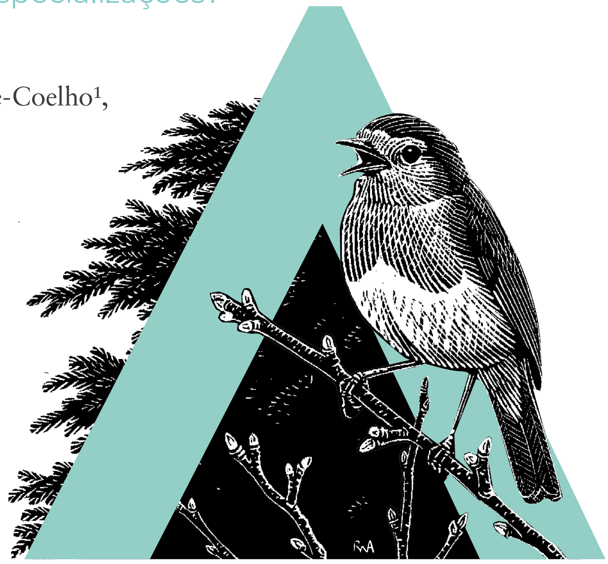

ABSTRACT

The differential distribution of conspecific animals among habitats may be influenced by habitat specializations or by asymmetric competitive interactions. We studied migrant robins *Erithacus rubecula* wintering in two contrasting Iberian habitats: Mediterranean shrubland and open cork-oak woodland. Females largely dominated (74% of individuals) in shrubland, while males (73%) did so in woodland. After accounting for sex and age effects, there were clear differences in body size and shape between habitats (individuals in shrubland were smaller and had a short wing relative to tail), but similar hydrogen isotope ratios in feathers at the two sites suggest no overall differences in migratory origin. Population density was 6 times higher in shrubland and exploitation competition for food was also more intense in this habitat, as revealed by an experiment with feeders. Fleshy fruit food was abundant on shrubland only, but its availability sharply declined during autumn, with virtually none left in winter. Invertebrates were more abundant throughout autumn and winter in woodland. Dangerous avian predators were only recorded in shrubland. An absence of dietary differences (revealed by isotopes in whole blood) between males and females (or of birds of different size) within habitats argues against the hypothesis that there are size or sex-specific specialisations. Similarly, the fact that fat scores were higher in shrubland and muscle scores higher in woodland, but without differences between sexes within habitats, argues against the idea of specialisation. Overall, results suggest that subdominant robins (females and small individuals) are forced to crowd at the shrubland habitats, where increased intraspecific competition, shortage of preferred animal food and possibly increased predation risk represent considerable disadvantages, which is reflected by their reduced protein reserves and the choice to accumulate large strategic fat reserves, perhaps as an insurance against starvation risk.

Keywords: Competition, *Erithacus rubecula*, Habitat-segregation.

RESUMO

A distribuição diferencial de animais de uma espécie entre habitats pode ser resultado de especializações ou de assimetrias nas interações competitivas. Estudámos piscos-de-peito-ruivo *Erithacus rubecula* migradores durante o inverno em dois habitats ibéricos contrastantes: matos mediterrânicos e montados de sobro abertos. As fêmeas representaram74% dos indivíduos capturados nos matos, enquanto nos montados os machos representaram 73%. Depois de corrigir para os efeitos do sexo e da idade, houve diferenças claras no tamanho e forma do corpo entre habitats (os indivíduos em matos eram mais pequenos e tinham uma asa curta em relação à cauda), mas os rácios de isótopos de hidrogénio nas penas nos dois locais não sugerem diferenças globais na origem migratória. A densidade populacional foi 6 vezes mais elevada em matos e a competição foi também mais intensa neste habitat, como revelou uma experiência com alimentadores. As bagas revelaram-se abundantes nos matos apenas, mas a sua disponibilidade diminuiu acentuadamente durante o outono, não restando praticamente nenhuma no inverno. Os invertebrados foram mais abundantes no montado. Os predadores de aves perigosas só foram registados em matos. A ausência de diferenças na dieta (reveladas por análise de isótopos do sangue) entre machos e fêmeas (ou entre aves de tamanhos diferentes) dentro de cada habitat contraria a hipótese de que existiriam especializações dos diferentes sexos ou ligadas ao tamanho corporal. Da mesma forma, o facto de as reservas de gordura serem maiores nos matos e os índices do músculo no montado, mas sem diferenças entre os sexos dentro dos habitats, contraria a ideia de especialização. Globalmente, os resultados sugerem que os piscos subdominantes (fêmeas e pequenos indivíduos) são forçados a aglomerar-se nos habitats de matos, onde o aumento da competição intraespecífica, a escassez de comida animal e possivelmente o aumento do risco de predação representam desvantagens consideráveis, o que se reflete na redução das reservas proteicas e na escolha de acumular grandes reservas estratégicas de gordura, talvez como um seguro contra o risco de inanição.

Palavras-chave: Competição, *Erithacus rubecula*, Segregação de habitat.

Introduction

Many migratory species show various levels of segregation of different classes (such as age or sex groups) amongst wintering habitats (Catry et al. 2005). Two main hypotheses attempt to explain segregation. The dominance hypothesis suggests that dominant classes effectively exclude (through territorial behaviour or other forms of interference) subdominant groups from the best habitats, hence competition is the main driving force (Gauthreaux 1978, Greenberg 1986). The specialization hypothesis states that segregation results from class-specific preferences and adaptations to different habitats (Selander 1966, Catry et al. 2005).

Few studies have provided solid evidence for either of the two main competing hypotheses accounting for segregation (but see, for example, Ardia & Bildstein 1997, Durell 2000, Latta & Faaborg 2002, Phillips et al. 2004, Cooper et al. 2021). Amongst the most detailed and influential is the study on wintering American Redstarts *Setophaga ruticilla* in Jamaica, where habitat segregation of sexes has been unequivocally attributed to the dominance hypothesis. Males predominate in mangroves, and females in scrub habitat. Patterns of settlement, territorial and agonistic interactions, removal experiments, and differences in body condition and hormone levels all suggest that males exclude females from the best mangrove habitats (Marra et al. 1993, Marra & Holberton 1998, Marra 2000). In contrast, studies of another territorial neotropical passerine migrant, the Hooded Warbler *Wilsonia citrina*, including removal experiments and investigations into the innate habitat preferences of different sexes, suggest that males and females select habitats differently, presumably as a result of sex-specific specialisations (Morton et al. 1987, 1993, Morton 1990).

In the European Robin *Erithacus rubecula*, a small migratory passerine, several studies have documented the segregation of individuals of different ages, sexes, body sizes and geographical origins amongst wintering habitats (Figuerola et al. 2001, Tellería et al. 2001, Tellería & Pérez-Tris 2004, Catry et al. 2004, De la Hera et al. 2018). Robins often are strongly territorial, even in winter, and territoriality is an obvious mechanism by which dominant classes could exclude subordinates from preferred patches. Experimental work, for example, suggests that male robins are dominant over females when competing for experimental food sources (Campos et al. 2011).

Catry et al. (2004) suggested that, in wintering Iberian grounds, male robins prefer comparatively open habitats because this is where they can easily exert their dominance and evict intruders from chosen territories, which means they can monopolise sufficient resources to allow overwinter survival and preparation for timely spring migration. According to this hypothesis, areas with dense vegetation would allow subordinates to better escape harassment and eviction, and hence would harbour robin populations not only denser, but also with a greater proportion of subdominant individuals.

However, alternative potential explanations for the reported segregation patterns exist. Herrera (1978), for example, suggested that individual robin morphology may influence their dietary choices, and given that different habitats contain disparate robin food sources (such as invertebrates, berries and acorns) it is plausible that segregation might result from specialization (e.g. Durell 2000). Indeed, robins of different migratory origins show contrasting diets in shared winter-quarters (Catry et al. 2016).

To further assess the possible causes and consequences of habitat segregation in this model species, we chose to study robins at an open woodland with virtually no undergrowth and also in an area of dense Mediterranean shrubland. Wintering robins in Iberia have never been systematically sampled in areas with no undergrowth and we predicted that, unlike all previous studies, we would find a strong male-bias in this habitat, providing a suitable contrast with dense shrubland where females largely dominate (Catry et al. 2004). The study was carried out at sites where no robins nested (at the time of this research), to avoid the confounding factor of robin distribution being influenced not only by the survival value provided by the chosen habitats, but also by potential future reproductive value of winter home-ranges latter converted into nesting territories.

According to the dominance hypothesis (in its robin-related context, as outlined above), we predicted that (1) shrubland, due to its abundant cover and impossibility of efficient territory defence, would have higher densities of robins; (2) dominant classes (males, adults, large individuals) would all be over-represented in the same habitat type (woodland), (3) woodland would have a greater availability of invertebrates, the preferred robin food (Berthold 1976), (4) competitive pressure (or exploitation competition) would be higher on shrubland, (5) protein reserves (as measured by muscle-scores) would be higher on woodland, (6) strategic fat reserves would differ between habitats. If specialization was the predominant operating mechanism underlying population structuring, we predict that (7) classes segregated by habitat would show distinct dietary preferences (given that the availability of major food-types profoundly differ between habitats). Furthermore, unlike predictions 5 and 6, the specialization hypothesis predicts (8) no major overall differences in an indicator of physiological condition (muscle scores) between habitats and (9) a habitat-specific relationship between sex and body reserves (e.g. an interaction of sex and habitat), resulting from the fact that each sex would be better adapted to the habitat where it is most abundant, and hence suffer different constraints and different starvation risks.

Methods

The study was carried out in coastal central Portugal, in the winter of 2008/09. The "Arrábida" study site is an area at Serra da Arrábida (38º27'N, 9º 01' W, at ca 200 m a.s.l.), on a limestone plateau covered with well developed shrubland with numerous small clearings of almost bare ground. This site is dominated by fruit producing plants (see results) that represent an important food source for robins. The "Charneca" study site is located near Alcochete (at 38º 49'N, 8º 49' W, 25m a.s.l.) in open cork oak *Quercus suber* woodland. At this site the shrub layer is very sparse and the ground is mostly covered by short grass and is used by grazing cattle. The two study sites (separated by 45 km) are inserted in large blocks of continuous habitat and enjoy a similar climate.

Robin census

In a distance sampling design, transects with 3 bands and a width of 10m (Bibby et al. 1992) were carried out at Arrábida (2760 m of transect on each survey) and at Charneca (2425 m) on clear windless mornings, in mid-October and in late November (later in the season robins are already settled and largely silent and harder to observe), to gather information on the density of the species in each habitat.

Bird sampling

At each site, robins were captured by using spring-traps baited with mealworms, from mid-morning to mid-afternoon, in November, December and January. Fieldwork was organised so that each trapping session was always done at both sites (visited in consecutive days with similar weather conditions) in order to minimise the effects of possible confounding factors, such as short-term weather fluctuations and changes in daylight duration and seasonality.

Every newly trapped bird was aged following the criteria described in Svensson (1992). Maximum wing-chord was measured using a wing ruler and body mass was taken using a digital balance. Tail length was measured using an adapted ruler with a pin and tarsus length was measured with callipers. Subcutaneous fat reserves were assessed by visual inspection using a 9-point scale (Kaiser 1993) and pectoral muscle profiles (Gosler 1991) were scored using a 4-point scale from Bairlein (1995). All measurements were by the same observer. Approximately 60 µl of blood were obtained by puncturing the *vena ulnaris*. A drop was preserved in ethanol for molecular sexing and the remaining was frozen until further processing.

Food availability - Invertebrates

Robins mostly prey on invertebrates exposed on the surface of the bare ground, leaf litter or short grass. In Mediterranean areas, a wide spectrum of invertebrate prey may be taken, with ants being particularly important in some habitats (Herrera 1977, Debusse & Isenmann 1985). To compare the availability of potential invertebrate prey between habitats, we used the approach detailed by Strong & Sherry (2000) with slight modifications. Plots measuring 40 × 40 cm were randomly placed in each study area and invertebrates seen during a 60 second scan were recorded; the body length (excluding legs and antennas) of each individual seen was estimated (always by the same observer) using 1 mm size categories. Counts were made in mid-December (early winter) and late January/early February (late winter). Counts always took place between 1000h and 1500h, on days with no wind and under clear skies.

Voucher specimens were collected in both study areas and measured with digital callipers (to the nearest 0.1 mm). They were then oven-dried and weighed to the nearest 0.1 mg. Mass-length equations were fitted to each of the groups present: Formicidae, Non-ant Hymenoptera, Coleoptera, Diptera, etc. Several models were fitted, and the power model ($Mass = a \times Length^b$) was retained given its higher R^2 (see also Strong & Sherry 2000, González et al. 2002). Visual estimates of invertebrate sizes made in plot-counts were then converted into dry biomass using predicted values from the fitted equations. To do this, the mid-point of each estimation size category was used (e.g. 1.5 mm for 1.00-1.99 mm). Invertebrates unlikely to be robin prey, such as bright red soil mites (Acarina) and springtails (Collembola; Herrera 1977, Debusse & Isenmann 1985, Cramp 1988) were excluded from these calculations.

Food availability - Berries

The abundance of fleshy fruits in each habitat in November was calculated by randomly placing 32 quadrats (3 m² each) at each site and counting all the berries in that area. To get a finer idea of the seasonal evolution of berry availability, individual branches (of different individual plants; 7-15 branches per species) of berry-producing plants were marked and the number of ripe berries counted once per month from November until February.

Food availability - Acorns

General acorn availability (of *Quercus coccifera* at Arrábida and *Quercus suber* at Charneca) on the ground was assessed by counting acorns in randomly placed 40 × 40 cm quadrats in both study areas in January. Every acorn was cut open to check if it was fresh or rotten. Only fresh acorns were considered. Robins cannot feed from whole acorns and need them to be torn by acorn predators (such as mice) or other mechanical action (such a trampling). Because we have no way of estimating the true acorn availability for robins, we kept acorn measurements very simple and did not consider seasonal variation, even though it was obvious that acorn abundance steeply declined as the season progressed.

Competition pressure

In late November and late January, experiments were carried out to obtain a measure of exploitation competition for favoured robin prey. Free-living robins will readily accept live mealworms *Tenebrio molitor*, and cafeteria experiments clearly indicate they prefer mealworms to berries or acorns (own unpubl. data). Feeding stations were spread out (35 m between stations) along tracks in each of the study habitats. Each station consisted of a plastic dish, at the centre of which a single mealworm was tied to the top of a little wire. The wriggling of the worm, and the movement of its shadow on the dish (which provided a standardised background, to control for differences between habitats) made the bait readily visible. Experiments were only carried out on sunny and windless days, around noon. Each station was left for 90 minutes, after which the outcome was recorded (bait taken or not taken). Experiments were not carried out at sites where robins had been previously spring-trapped.

Predators

No systematic predator surveys were carried out, but all observations of raptors potentially capable of catching robins were noted during other fieldwork.

Stable isotopes

Nitrogen (δ^{15}N) isotope values in bird tissues may allow a clear distinction between individuals with a predominantly frugivorous diet from individuals higher up in the food chain. δ^{13}C values may prove useful distinguishing between different plant foods (e.g. Inger & Bearhop 2008). We determined δ^{13}C and δ^{15}N in whole blood for an indication of diet composition. Turnover half-life of whole blood for birds the size of a robin is approximately 5 days (Hobson & Wassenaar 2008), which means that our measurements will mostly refer to diet assimilated 1-2 weeks before sampling.

Stable hydrogen isotope ratios (δ^2H), can also provide information on the origins of individuals (Bearhop et al. 2005, Hobson & Wassenaar 2008), particularly if sampled on inert tissues grown during the breeding season (such as particular feathers). Detailed studies at continental level documented a clinal variation in δ^2H in precipitation and δ^2H in locally grown feathers of wild birds across Europe along a SW to NE axis (Hobson et al. 2004). This applies to robins (Catry et al. 2016) and here we use δ^2H as a broad indication of the geographical origin of our study birds that likely included a mixture of birds from a very wide range of latitudes (Bueno 1998).

Feathers were washed, dried, finely cut, and then weighed (0.1 mg) into small silver capsules, and analysed for hydrogen isotope ratios (δ^2H) using continuous flow isotope ratio mass spectrometry (CF-IRMS), using a high temperature reduction system (TC/EA) interfaced with a Thermo-Fisher-Scientific Delta V Plus IRMS. One of the pitfalls of hydrogen isotope analysis of keratinous materials is that around 20% of the hydrogen in keratin readily exchanges with ambient water vapour. We used the "comparative equilibration" (Wassenaar and Hobson, 2003) approach to correct the data, such that the δ^2H data here represent the indigenous, unexchangeable hydrogen. As such, all samples and standards are stored close to the IRMS, and samples given at least ten days to equilibrate with laboratory air. The standards used for this approach are CFS, BWB-II and ISB. A fourth keratin standard not used in the calibration, WG, routinely has a standard deviation of around 2 ‰. Blood was oven-dried and the resulting powder was weighed into tin capsules and then also analysed for nitrogen (δ^2N) and carbon (δ^2C) isotope ratios.

Molecular sexing

Sexing from blood samples 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).

Data analyses

To extract independent measures of body size and shape from measurements of wing-length, tail-length and tarsus-length we used Principal Component Analysis (Table 1). PC1 scores were used as a measure of body size and PC2 and PC3 scores as measures of body shape.

Because no robin had a 0 muscle score and only 4% of the individuals measured had score 1, we pooled scores 1 and 2 to obtain a 2-score scale. This variable was analysed with GzLM with a binomial error distribution and logit link function.

We attempted to analyse fat scores as a function of other variables through ordinal logistic regression, but different models always failed the test of parallel lines, indicating a serious violation of the assumptions (Norušis, 2008). Given the fact that fat scores in our samples were approximately normally distributed and that their relationship with body mass shows only a slight deviation from linearity, we opted to fit models for this variable with a Gaussian error distribution and identical link function (as it is often done; e.g. Pérez-Tris and

Table 1 - Scores of a Principal Component Analysis from measurements of tarsus, wing-chord and tail-length of robins (n=121).

Tabela 1 - Scores de uma Análise de Componentes Principais a partir de medições do tarso, da asa e do comprimento de cauda de piscos-de-peito-ruivo (n=121).

	PC1	PC2	PC3
Tarsus	0.452	0.892	0.001
Tail	0.892	-0.225	-0.391
Wing	0.892	-0.227	0.391
% Variance explained	60	30	10

Tellería, 2002). We believe this approach to be useful, given that results are clear cut. All analyses were carried out using SPSS 17.0.

Variables with distributions strongly violating assumptions of normality were analyzed using non-parametric statistics, such as Mann-Whitney U test to compare abundance of invertebrates and acorns between sites. Other continuous variables were analysed using general linear models (GLM), with Gaussian error distribution and identical link function, with age (2-classes), sex, site and month as fixed factors, plus δ^2H, PC1, PC2 and PC3 as covariates, where necessary. Models with all variables were run first and non-significant variables progressively removed, but tested again each time a new variable was removed, to confirm their non-significance. This was done backwards and forward until only significant variables remained in the models.

Results

Density and social composition

Estimated robin density at Arrábida was 21.7 birds/ha in October and 11.0 birds/ha in November, ca. 6 times higher than at Charneca, where the corresponding figures were 3.7 and 1.7 birds/ha. Although we could not reliably census robins later in the season, it was patently obvious from visual and auditory contacts, as well as from capture rates in traps, that robins remained much more abundant at Arrábida throughout the winter.

The sex ratio of robins wintering at each site differed, with 26% (N = 76) of the individuals captured at Arrábida being male and the corresponding value at Charneca being 73% (N = 45; Fisher's Exact Test $P < 0.001$). Overall, the age structure of robin populations wintering at each site did not differ significantly (Fisher's Exact Test $P = 0.18$), although there was a tendency for more adult birds to be found at Charneca (44.7%, N = 47) than at Arrábida (32%, N = 79). A loglinear analysis did not reveal a significant interaction between age, sex and site (likelihood ratio change for deleting the 3-way interaction: $\chi^2_1 = 2.65$, $P = 0.103$).

Adult and juvenile robins did not differ in PC scores along any of the principal component axes, but both sex and site influenced at least some of the PC axes, and so were included together in the following general linear models (GLM). When controlling for possible site effects, males and females differed in PC1 ($F_{1,113} = 22.7$, $P < 0.001$) and PC2 ($F_{1,113} = 6.0$, $P = 0.016$), but not in PC3 ($F_{1,113} = 0.71$, $P = 0.37$).

Robins from Arrábida and Charneca differed considerably in size and shape as revealed by comparisons of PC scores (Table 2). As there was a significant interaction between sex and site in PC1 scores ($F_{1,113} = 8.8$, $P = 0.004$), we present results for each sex separately in Table 2.

Age (but not sex) influenced δ²H in feathers ($F_{1,120} = 5.7$, $P = 0.019$), but there was no significant difference between sites (Table 2).

Food availability

Invertebrates – there were no differences in overall invertebrate biomass, in ant biomass or in non-ant invertebrate biomass between early and late winter (tested by Mann-Whitney U Tests), and so we pooled the two periods in the following tests and figure. The Charneca site had significantly higher overall invertebrate biomass (Fig. 1), and higher biomass of all the main individual potential prey groups: ants (Mann-Whitney U Test, $P < 0.001$), non-ant Hymenoptera ($P = 0.05$), Diptera ($P = 0.02$), Hemiptera ($P < 0.001$) and Aranae ($P = 0.02$) with the exception of Coleoptera, which showed no difference between habitats ($P = 0.9$).

Figure 1- Box-plot comparing total invertebrate biomass in sampling plots in the two study habitats. The difference between study sites was highly significant (Mann-Whitney U = 1814, P < 0.001).

Figura 1 - Box-plot comparando a biomassa total de invertebrados em quadrados de amostragem nos dois habitats de estudo. A diferença entre os locais de estudo foi altamente significativa (Mann-Whitney U = 1814, P < 0,001).

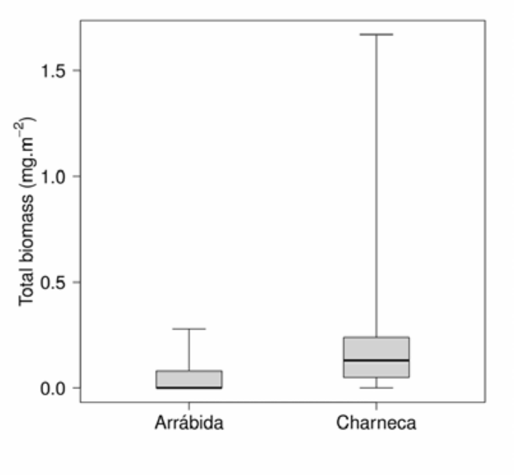

Table 2 - Means (±SD) and comparisons of PC1 (indicating body size), of PC2 and PC3 scores (indicating body shape) and of δ2H in feathers (indicating broad geographical origin) of wintering robins at Arrábida (N = 73) and Charneca (N = 44).

Tabela 2 - Médias (±SD) e comparações de PC1 (indicando o tamanho do corpo), de PC2 e PC3 (indicando a forma do corpo) e de δ2H em penas (indicando a origem geográfica) de piscos-de-peito-ruivo de inverno na Arrábida (N = 73) e na Charneca (N = 44).

	Arrábida	Charneca	Stat. Comparison
PC1 Scores	-0.30 ± 0.84	0.49 ± 1.05	$F_{1,113}$ = 4.19, **P = 0.04**[a]
Males	-0.52 ± 0.85 (N=20)	0.84 ± 0.86 (N=32)	$F_{1,51}$ = 13.4, **P = 0.001**
Females	-0.37 ± 0.81 (N=53)	0.33 ± 0.94 (N=12)	$F_{1,64}$ = 0.40, P = 0.53
PC2 Scores	0.15 ± 0.97	-0.25 ± 1.02	$F_{1,113}$ = 1.15, P = 0.29[a]
PC3 Scores	-0.28 ± 0.97	0.45 ± 0.89	$F_{1,113}$ = 11.1, **P = 0.001**[a]
δ²H	-86.1 ± 12.6	-87.4 ± 9.6	$F_{1,118}$ = 0.58, P = 0.45[b]

[a] *Comparisons in full GLM models accounting for sex effects*

[b] *Comparisons in full GLM model accounting for age effects*

Acorns and fleshy fruits

The number of fresh acorns per 40 × 40 cm quadrat was 0.26 ± 1.07 (N = 70) at Arrábida and 0.48 ± 3.012 (N = 77) at Charneca (Mann-Whitney U = 2624.5, P = 0.8). In autumn, there was a large diversity and high abundance of berries that constitute robin foods at Arrábida, but fleshy fruits were virtually absent at Charneca (Table 3). The availability of ripe fruit declined steeply as winter progressed, with little fruit left in January and none in February (Fig. 2).

Competition experiments

The rate of disappearance of mealworms from feeding stations was much higher at Arrábida than at Charneca (Table 4). Field observations and trapping with similarly baited spring traps indicate that at Arrábida virtually all experimental stations where the

Figure 2- Seasonal decline in ripe fruit abundance at Arrábida (November 2008 – February 2009) as assessed by monitoring berries on marked branches. Values presented as percentage of number recorded in November.

Figura 2 - Declínio sazonal da abundância de bagas maduras na Arrábida, avaliado através da monitorização em ramos marcados. Valores apresentados como percentagem do número registado em Novembro.

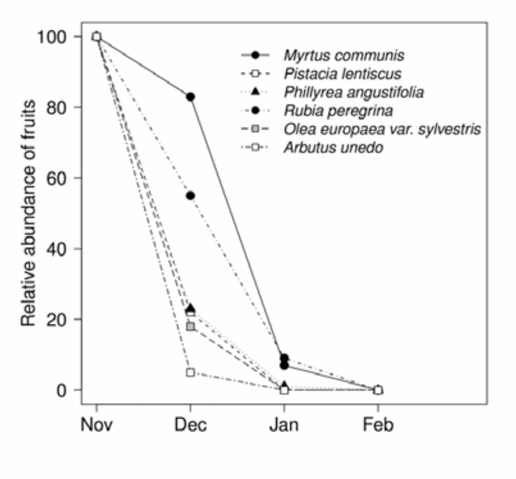

Table 3 - Densities of ripe fleshy fruits (mean ± SE per m^2) in November at the two study sites as assessed in 3 m^2 plots (N = 32 plots at each site). The symbol + indicates that the plant species was present with berries in the area, but at a very low density (not occurring in randomly placed plots).

Tabela 3 - Densidades de bagas maduras (média ± SE por m^2) em novembro nos dois locais de estudo, conforme avaliado em quadrados de 3 m^2 (N = 32 quadrados em cada local). O símbolo + indica que a espécie vegetal estava presente com bagas na área, mas com uma densidade muito baixa (não ocorrendo em quadrados colocados aleatoriamente).

	Arrábida	Charneca
Myrtus communis	16.4 ± 6.5	+
Pistacia lentiscus	5.3 ± 2.3	Absent
Phillyrea angustifolia	3.3 ± 2.2	Absent
Rubia peregrina	2.9 ± 1.6	Absent
Olea europaea var. sylvestris	0.1 ± 0.1	Absent
Arbutus unedo	0.1 ± 0.1	Absent
Smilax aspera	+	Absent
Viburnum tinus	+	Absent

bait was taken must have been used by robins, while at Charneca stonechats *Saxicola torquatus* must also have been responsible for the disappearance of a proportion of the mealworms.

Isotopes in blood (diet)

Nitrogen isotopes ($\delta^{15}N$) in whole blood differed between study sites and between months, but when accounting for these two factors, showed no differences between males and females (Table 5). A similar situation occurred with carbon isotopes ($\delta^{13}C$), but with site as the single significant predictor (Table 6). None of the PC axes were significant as correlates of $\delta^{15}N$ or $\delta^{13}C$, and so were excluded from the above models.

Predators

The only specialist/efficient passerine predators (potentially regularly consuming robins) seen during fieldwork were at Arrábida: 4 observations of sparrowhawks *Accipiter nisus* and 3 of hen harriers *Circus cyaneus*.

Body condition

There were pronounced differences in the body reserves of robins wintering at the two study sites. We tested models with all combinations of the following categorical predictors: site, month, age, sex, plus δ^2H, PC1, PC2 and PC3 as covariates. Only site ($F_{1,118} = 28.3$, $P < 0.001$) and month ($F_{3,118} = 8.0$, $P < 0.001$) were significant predictors of fat reserves, with no significant interaction. Fat scores were higher at Arrábida (2.05 ± 1.02, N = 79) than at Charneca (0.81 ± 0.88, N = 47) and increased from November to reach a peak in January. To test the interaction between site and sex, we forced sex into the models, resulting in a non-significant interaction (site × sex $F_{1,106} = 0.85$, $P = 0.36$).

There was a lower frequency of maximum muscle scores at Arrábida (34% of 79 individuals) than at Charneca (74%, N = 47, Wald = 16.1, $P < 0.001$), with a significant effect of month (Wald = 9.6, $P = 0.023$) resulting from higher scores in December. Despite the absence of an overall sex effect, we tested for possible opposite trends for muscle in relation to sex: a loglinear analysis did not reveal a significant interaction between site, sex and muscle score (likelihood ratio change for deleting the 3-way interaction: $\chi^2_1 = 2.08$, $P = 0.15$).

As a result of opposing, but not synchronously opposed, trends in fat and muscle scores, body mass did not consistently differ between the two study sites, with location showing a strong interaction with month (Table 7, Fig. 3).

Figure 3- Body mass (mean ± SE) of robins sampled at two locations and in different months. Note that mass is not corrected for size, which means that differences in body reserves between sites in December and January are larger than suggested by the graph (robins at Arrábida have a smaller body size). See Table 7 for statistics.

Figura 3 - Massa corporal (média ± SE) de piscos amostrados em dois locais e em meses diferentes. Note-se que a massa não é corrigida para o tamanho, o que significa que as diferenças nas reservas corporais entre locais, em Dezembro e Janeiro, são maiores do que o sugerido pelo gráfico (os piscos na Arrábida têm um tamanho corporal mais pequeno). Ver Tabela 7 para estatísticas.

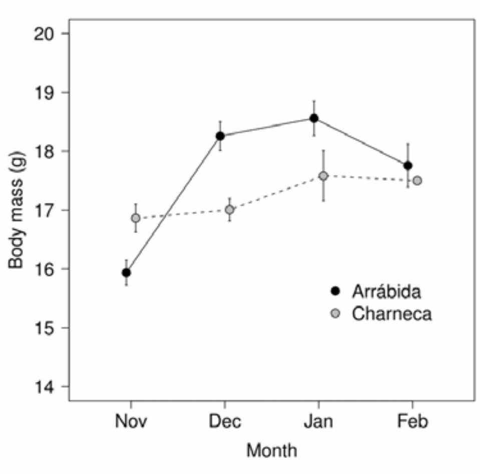

Table 4 - Percentage of experimental stations (with sample sizes in brackets) from which mealworms disappeared after 90-minute trials at each habitat in early and late winter.

Tabela 4 - Percentagem de estações experimentais (com tamanhos de amostra entre parênteses) das quais desapareceram lagartas após experiências de 90 minutos em cada habitat no início e no final do Inverno.

	November	January
Arrábida	79% (34)	95% (40)
Charneca	39% (28)	35% (40)
Fisher's Exact Test	P = 0.002	P < 0.001

Table 5 - GLM with significant predictors of robin $\delta^{15}N$ in whole blood (model adjusted $r^2 = 0.53$).

Tabela 5 - GLM com preditores significativos de $\delta^{15}N$ em sangue de piscos (modelo ajustado $r^2 = 0.53$).

	Df	Mean Square	F	P
Site	1	31.54	48.81	< 0.001
Month	3	9.77	15.12	< 0.001
Sex	1	0.18	0.28	0.60
Error	73			

Table 6 - GLM with significant predictors of robin $\delta^{13}C$ in whole blood (model adjusted $r^2 = 0.42$).

Tabela 6 - GLM com preditores significativos de $\delta^{13}C$ em sangue de piscos (modelo ajustado $r^2 = 0.42$).

	Df	Mean Square	F	P
Site	1	10.29	39.82	< 0.001
Sex	1	0.102	0.40	0.53
Error	75			

Table 7 - GLM with significant predictors of robin body mass. Note that sex is not included in the model as it was non-significant once body size (PC1 scores) was accounted for (model adjusted $r^2 = 0.45$).

Tabela 7 - GLM com preditores significativos de massa corporal de piscos. Note-se que o sexo não está incluído no modelo, uma vez que não era significativo depois de ser levado em conta o efeito do tamanho corporal (scores PC1) (modelo ajustado $r^2 = 0.45$).

	Df	Mean Square	F	P
PC1 scores	1	17.04	15.12	< 0.001
Site	1	7.05	6.26	0.014
Month	3	18.73	16.63	< 0.001
Site × month	3	6.14	5.45	0.002
Error	111			

Discussion

This study documents dramatic contrasts in parameters related to demography, social composition and physiological state of a wintering migratory passerine using two distinct habitats in Iberia. Wintering European Robin populations differed in population density, sex-ratios, body size, body shape, overall body mass, fat reserves and protein reserves. Such differences reflect contrasting environments, with different cover, types of food-sources, seasonal trends in food availability and predator presence.

The predominance of females and small individual robins in shrub-dominated habitats has been described before, and previous studies (Tellería et al. 2001, Tellería & Pérez-Tris 2004, Catry et al. 2004) also showed that juveniles are more frequent in these habitats (a non-significant trend was also apparent in our dataset). As argued before (prediction 2; Catry et al. 2004), the co-occurrence of females, juveniles and small individuals in the same habitat is suggestive of exclusion by dominant individuals (males, adults, large birds). Male dominance is well established in robins (Campos et al. 2011), as well as its widespread territorial behaviour in the winter quarters (Schwabl 1992).

There were slight, but highly significant, differences in body shape of robins present at the two study sites, with more long-winged and short-tailed robins in the open woodland habitat. Long wings and short tails are morphological characteristics associated with long-distance migration (Leisler & Winkler 2003), but the above finding is unlikely to be related to a different make up of wintering communities in relation to broad geographical areas of origin, given that hydrogen isotope ratios in feathers did not differ between sites. Ecomorphological studies do suggest that birds living in more open habitats usually have relatively longer wings and shorter tails (Leisler & Winkler 1985), and so this supports the view that there may be, to some degree, a specialization of robins of different body shapes in their choice of habitat. Alternatively, individuals with the “right” body shape might be more successful at competing for territories in an open habitat.

Male and female robins differ in body size. Females are smaller and smaller individuals are more often found in female-dominated habitats which is is also consistent with a scenario where shrubland is selected by small individuals because small body size is more suited to this habitat. Other evidence, however, contradicts this explanation (see below). Males and females also differ in body shape (in PC2 scores, but not in PC3). Interestingly, however, after accounting for sex effects, there were no differences in the wintering populations of the two sites along the PC2 axis, but rather along the PC3. This is evidence against the specialisation of sexes. Females do not have a body shape that is more similar to the shape of the birds that chose (or were forced) to live in shrubland.

Robins clearly prefer animal food to fruits and berries and when fed on an exclusively vegetarian diet soon lose weight and die (Berthold 1976). The readiness with which our experimental animal prey was taken, in an environment with super-abundant fruit foods, is also testimony of such preference. Overall invertebrate biomass, as well as abundance of different prey types, was considerably higher at the woodland site. Hence, preferred food was more abundant at the site with lower population density. Not surprisingly in this context, depletion of experimental food sources (mealworms) occurred much more rapidly in shrubland, hinting at a strong exploitation competition in this habitat. Since robins consume large quantities of diverse berries in Iberia (Herrera 1998), fewer invertebrates at Arrábida might not matter much. However, our results show that berry abundance sharply declines during the cold season, and fruits are virtually non-existent by mid to late winter. Furthermore, acorns were rotten by this time of the season. Hence, robins at Arrábida likely faced a significant food shortage.

Many studies have found subordinate or less experienced birds, or individuals facing more challenging contexts, to carry larger fat reserves in winter (e.g. Krams et al. 2010), while the same does not seem to apply to protein reserves, which may be a better indicator of good physiological condition than fat (Gosler 1991, 1996, Latta 2003). The shortage of animal food at Arrábida is the most likely explanation for the low muscle-scores recorded there (fruits have a very low protein content). Pectoral muscles are the most important avian protein-storing organs, their volume being a good indicator of overall protein reserves (Gosler 1991, Bauchinger et al. 2011 and references therein).

Could the higher pectoral muscle scores at Charneca simply reflect a greater predation risk at this site (van den Hout et al. 2006)? We believe this to be relatively unlikely, given that during fieldwork specialist passerine predators were regularly seen hunting at Arrábida, but not at Charneca. It could be argued that the small fat reserves at Charneca might also point to the possibility of greater predation risk at this latter site, but in fact, the relationships between starvation risk, predation pressure and fat reserves are complex (Ekman 2004, MacLeod et al. 2007) and hard to predict in our study system with the available information.

What is clear is that robins had a very dissimilar body mass and composition (in terms of fat relative to muscle) at the two study sites, reflecting distinct environmental circumstances and constraints. If each sex was best adapted to the habitat where it was most numerous, we would predict males and females would show contrasting trends in fat and protein reserves in different habitats. For example, muscle scores of females could be lower in woodland, but higher on shrubland, when compared to males (Catry et al. 2007). In fact, neither fat scores nor muscle scores were affected by an interaction term defined by sex and site, which argues against the specialization hypothesis.

If males have an advantage over females, why was it that, after accounting for site differences, sex was not a predictor of fat or protein reserves? For example, in shrubland, male robins have been shown to have priority of access to experimental food sources (Campos et al. 2011) and their dominance presumably could allow them to monopolise natural resources through territorial behaviour. One possible explanation is that, because of the high rates of territorial intrusion in shrubland and the difficulty in detecting and rapidly evicting intruders due to the dense shrub, territorial males end up wasting energies in constant territorial defence. This would be a situation akin to that described for the Seychelles Magpie Robin, *Copsychus sechellarum*, where better quality territories do not produce more offspring (López-Sepulcre et al. 2010). As shown by those authors, under certain conditions, a despotic system can still produce an equal-returns situation due to interference and conflict (López-Sepulcre et al. 2010). More research is needed to test this specific hypothesis.

Despite their preference for invertebrates, European Robins are extensively frugivorous outside the breeding season (Herrera 1998). In early Autumn, Arrábida provided an extremely high density of fruit foods, although those rapidly declined until disappearing by late winter. Food sources (invertebrates) were more stable at Charneca, but due to the clearing of undergrowth of the cork-oak woodland by human management, the area was practically devoid of berry-producing plants, unlike most Mediterranean natural habitats in autumn, when migrant robins arrive. Hence, robins could have been lured into an ecological trap (in its broader sense - favouring a less valuable habitat, due to recent changes in habitat quality rankings), and failing to recognize a higher quality site (Gilroy & Sutherland 2007). This could perhaps account for large differences in population density of robins at the two sites, but it is hard to see why it would give rise to such extreme differences in social composition. Hence, even if perceptual errors by arriving migrants do take place, they are likely to play a minor role in the overall pattern here described.

Conclusions

All six predictions of the competition hypothesis (but none of the three predictions from the alternative model) were upheld by the robin data, although prediction 2 in an incomplete way. Some of the most compelling evidence for the dominance hypothesis in other systems results from removal experiments (Ardia & Bildstein 1997, Marra 2000). However, even if successfully performed, removal experiments are unlikely to be fully clarifying in situations like the present one, where continuous blocks of relatively homogenous habitats exist, because birds settled in poor quality areas may have difficulty in sampling high quality patches in locations removed from their initial area of settlement. Because phenomena in ecology are often scale-dependent, studying areas of habitat confluence and heterogeneity (where removal experiments are usually carried out), highlighting as it may be, also presents limitations. We believe that our isotopic evidence for no sex-specific dietary preferences, as well as for no habitat-specific differences in body reserves between males and females, provide novel (and some of the best) evidence that habitat segregation in an Old-world passerine migrant is unlikely to be a result of different specialisations by males and females.

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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.

Ardia, D.R. & Bildstein, K.L. 1997. Sex-related differences in habitat selection in wintering American kestrels, *Falco sparverius*. Animal Behaviour 53: 1305-1311.

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

Bauchinger, U., McWilliams, S.R., Kolb, H., Popenko, V.M., Price, E.R. & Biebach, H. 2011. Flight muscle shape reliably predicts flight muscle mass of migratory songbirds: a new tool for field ornithologists. Journal of Ornithology 152:507–514.

Bell, C.P. 2005. Inter- and intrapopulation migration patterns: ideas, evidence and research priorities. In: Greenberg, R. & Marra, P.P. (eds.) Birds of two worlds. The Ecology and Evolution of Migration. John Hopkins University Press, Baltimore.

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

Bibby, C.J., Burgess, N.D. & Hill, D.A. 1992. Bird Census Techniques. Academic Press, London.

Breitwisch, R. 1989. Mortality patterns, sex ratios and parental investment in monogamous birds. In: Power, D. (ed.) Current Ornithology 6. 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

Campos, A.R., Catry, P., Ramos, J.A. & Robalo, J. 2011. Competition amongst European robins *Erithacus rubecula* in the winter quarters: sex is the best predictor of priority of access to experimental food resources. Ornis Fennica 88: 226-233.

Campos, A.R., Catry, P., Tenreiro, P., Neto, J.M., Pereira, A.C., Brito, R., Cardoso, H., Ramos, J.A., Bearhop, S. & Newton, J. 2011. How do Iberian Robins *Erithacus rubecula* respond to seasonal flooding by conspecific migrants? Bird Study 58: 435–442

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: Ruckstuhl, K.E. & Neuhaus, P. (eds) Sexual Segregation in Vertebrates: Ecology of the two Sexes. Cambridge University Press, Cambridge, pp. 351-378.

Catry, P., Bearhop, S. & Lecoq, N. 2007. Sex differences in settlement behaviour and condition of chiffchaffs *Phylloscopus collybita* at a wintering site in Portugal. Are females doing better? Journal of Ornithology 148: 241-249.

Catry, P., Campos, A.R., Granadeiro, J.P., Neto, J.M., Ramos, J., Newton, J., Bearhop, S. 2016. Provenance does matter: links between winter trophic segregation and the migratory origins of European robins. Oecologia 182: 985-994.

Cramp, S. (Ed.) 1988. The Birds of the Western Palearctic. Vol V. Oxford University Press, Oxford.

Cooper, N. W., Thomas, M. A., & Marra, P. P. (2021). Vertical sexual habitat segregation in a wintering migratory songbird. Ornithology, 138, 1–11.

Cristol, D.A., Baker, M.B. & Carbone, C. 1999. Differential migration revisited. Latitudinal segregation by age and sex class. In: V. Nolan Jr, E.D. Ketterson and C.F. Thompson (eds) Current Ornithology, Vol. 15. 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.

De la Hera, I., Fandos, G., Fernández-López, J., Onrubia, A., PérezRodríguez, A., Pérez-Tris, J., & Tellería, J. L. 2018. Habitat segregation by breeding origin in the declining populations of European robins wintering in southern Iberia. Ibis 160: 355–364.

Debusse, M. & Isenmann, P. 1985. Frugivory of transient and wintering European robins *Erithacus rubecula* in a Mediterranean region and its relationship with ornithochory. Holarctic Ecology 8: 157-163.

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

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

Durell, S.E.A. Le V. dit 2000. Individuals feeding specialisation in shorebirds: population consequences and conservation implications Biological Reviews of the Cambridge Philosophical Society, 75, 503-518.

Ekman, J. 2004. Mass-dependence in the predation risk of unequal competitors; some models. Oikos 105: 109-116.

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

Gauthreaux, S.A. Jr. 1978. The ecological significance of behavioural dominance. Perspectives in Ethology, 3, 17-54.

González, J.M., Basaguren, A. & Pozo, J. 2002. Size-mass relationships of stream invertebrates in a northern Spain stream. Hydrobiologia 489: 131-137.

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.

Gosler, A.G. 1996. Environmental and social determinants of winter fat storage in the great tit *Parus major.* Journal of Animal Ecology 65: 1-17.

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

Gilroy, J.J. & Sutherland, W.J. 2007. Beyond ecological traps: perceptual errors and undervalued resources. Trends in Ecology and Evolution 22: 351-356.

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 B 272: 2319-2323.

Herrera, C. M. 1977. Ecología alimenticia del petirrojo (*Erithacus rubecula*) durante su invernada en encinares del sur de España. Doñana, Acta Vertebrata 4: 35-59.

Herrera, C. M. 1978. Individual dietary differences associated with morphological variation in robins *Erithacus rubecula*. Ibis 120: 542-545.

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

Hobson, K.A., Wassenaar, L.I. 2008. Tracking Animal Migration with Stable Isotopes. Academic Press, London.

Inger, R. & Bearhop, S. 2008. Applications of stable isotope analyses to avian ecology. Ibis 150: 447-461.

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

Krams, I., Cirule, D., Surava, V., Krama, T., Rantala, M.J. & Ramey, G. 2010. Fattening strategies of wintering great tits support the optimal body mass hypothesis under conditions of extremely low ambient temperature. Functional Ecology 24: 172-177.

Latta, S.C. & Faaborg, J. 2002. Demographic and population responses of Cape May warblers wintering in multiple habitats. Ecology 83: 2502-2515.

Latta, S.C. 2003. Effects of scaley-leg mite infestations on body condition and site fidelity of migratory warblers in the Dominican Republic. Auk 120: 730-743.

Leisler, B. & Winkler, H. 1985. Ecomorphology. Current Ornithology 2: 155-186.

Leisler, B. & Winkler, H. 2003. Morphological consequences of migration in passerines. In: Berthold, P., Gwinner, E. & Sonnenschein, E. (eds) Avian Migration. Springer-Verlag, Berlin, pp. 175-186.

López-Sepulcre, A., Kokko, H. & Norris, K. 2010. Evolutionary conservation advice for despotic populations: habitat heterogeneity favours conflict and reduces productivity in Seychelles magpie robins. Proceedings of the Royal Society B 277: 3477-3482.

MacLeod, R., Lind, J., Clark, J. & Cresswell, W. 2007. Mass regulation in response to predation risk can indicate population declines. Ecology Letters 10: 945-955.

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. & Holberton, R.L. 1998. Corticosterone levels as indicators of habitat quality: effects of habitat segregation in a migratory bird during the non-breeding season. Oecologia 116, 284-292.

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.

Morton, E.S. 1990. Habitat segregation by sex in the hooded warbler: experiments on proximate causation and discussion of its evolution. American Naturalist 135: 319-333.

Morton, E.S., van der Voort, M.E., Greenberg, R. 1993. How a warbler chooses its habitat: field support for laboratory experiments. Animal Behaviour 46: 47-53.

Morton. E.S., Lynch, J.F., Young, K. & Mehlhop, P. 1987. Do male hooded warblers exclude females from non-breeding territories in tropical forest? Auk 104: 133-135.

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.

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.

Phillips, R.A, Silk, J.R.D., Phalan, B., Catry, P. & Croxall, J.P. 2004 Seasonal sexual segregation in two *Thalassarche* albatross species: competitive exclusion, reproductive role specialization or foraging niche divergence? Proceedings of the Royal Society of London B 271: 1283-1291.

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:. Nolan, V. Jr., Ketterson, E.D. & Thompson, C.F. (eds) Current Ornithology 14. 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 B 250: 143-150.

Rappole, J.H., Ramos, M.A. & Winker, K. 1989. Wintering wood thrush movements and 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.

Selander, R.K. 1966. Sexual dimorphism and differential niche utilization in birds. Condor 68: 113-151.

Strong, A.M. & Sherry, T.W. 2000. Habitat-specific effects of food abundance on the condition of ovenbirds wintering in Jamaica. Journal of Animal Ecology 69: 883-895.

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.

Van den Hout, P.J., Piersma, T., Dekinga, A., Lubbe, S.K. & Visser, G.H. 2006. Ruddy turnstones Arenaria interpres rapidly build pectoral muscle after raptor scares. Journal of Avian Biology 37: 425-430

Wassenaar, L.I. and Hobson, K.A. 2003. Comparative equilibration and online technique for determination of non-exchangeable hydrogen of keratins for use in animal migration studies. Isotopes in Environmental and Health Studies 39: 211 - 217.

Witter, M.S. & Cuthill, I.C. 1993. The ecological costs of avian fat storage. Philosophical Transactions of the Royal Society of London B 340: 73-92.