

Regional variation in seasonality affects migratory behaviour and life-history traits of two Mediterranean passerines

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Abstract

Migratory birds may improve fecundity by moving to seasonal breeding areas, but may also suffer higher mortality rates as a cost of movement. However, the covariation among seasonality, migratoriness and life histories should change between species if their ecological features affect site-tenacity, survival or fecundity. In frugivorous birds, for instance, wandering in search of fruits may trigger broader migrations than territorial defence, and also may improve nonbreeding survival by preventing food shortages that eventually happen in discrete territories. We studied the variation in spatio-temporal distribution, life expectancy and fecundity in robins (*Erithacus rubecula*) and blackcaps (*Sylvia atricapilla*) distributed in three Iberian regions with a low, mid or high degree of environmental seasonality. In the Iberian Peninsula, robins and blackcaps are the two most intensive frugivores in winter; however, robins are territorial while blackcaps track fruit abundance among habitat patches. In the most seasonal area, robins and blackcaps decreased abundance in winter and showed a lower breeding-site tenacity, a shorter life expectancy and a larger clutch size. However, blackcaps tended to be more migratory than robins in all regions. Despite their stronger migratory behaviour, blackcaps showed a longer life expectancy and a smaller clutch size than robins in all regions. In robins, winter territoriality could decrease nonbreeding survival but also improve fecundity, because survivors are dominant and hence more efficient breeders. In blackcaps, however, the use of the most profitable habitat patches could improve nonbreeding survival, thereby allowing a similar recruitment than in robins with a lower reproductive investment. These results support that regional-scale changes in seasonality may affect migratory behaviour and hence the tradeoff between reproduction and survival in birds, doing so differently depending on the idiosyncrasy of each species. © 2002 Éditions scientifiques et médicales Elsevier SAS. All rights reserved.

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1. Introduction

Migration is a strategy of seasonal exploitation of habitats through which migratory birds benefit from abundant but transitory resources by increasing offspring production (Bernis, 1966; Greenberg, 1980; Alerstam and Högstedt, 1982). However, migration also involves important costs related to energy consumption, exposure to predators or unpredictable food shortages, which cause a lower nonbreeding survival of migratory birds compared to residents (Alerstam, 1991; Berthold, 1993). It has long been thought that migration is only possible when the benefits of being migratory may balance its costs (Greenberg, 1980; Gauthreaux, 1982; Cox, 1985; Alerstam and Hedenström,

1998), and that migratory behaviour has likely played an important role in the evolution of different avian life histories by adjusting the tradeoff between fecundity and survival (Greenberg, 1980; O'Connor, 1990; Bell, 1996; Young, 1996). However, because of the great difficulty to study survival and fecundity in populations differing in migratory behaviour, these predicted effects of migration on avian life histories have received little empirical support (Alerstam and Hedenström, 1998). To our knowledge, there are no studies that have illustrated the covariation among seasonality, migratoriness, survival and fecundity within species.

The extent to which a species responds to variations in seasonality of its habitats by changing migratoriness should depend on particular features of its biology. For instance, different aspects of the nonbreeding ecology of each species may determine how intense migratory behaviour will be

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(Rappole, 1995). One such aspect may be site tenacity during the nonbreeding season, which has been particularly studied in relation to food-tracking in frugivorous species because of the low predictability of fruits compared to other food resources (Levey and Stiles, 1992; Chesser and Levey, 1998). While leaf production is essential for a plant to obtain energy, the production of fruits is not essential for self-maintenance and hence depends on energy surpluses that vary from patch to patch, season to season and year to year. This means that frugivorous birds may improve nonbreeding survival by tracking fruit availability across wide areas (Herrera, 1985; Levey and Stiles, 1992; Rey, 1995). Given that vagrant birds are also prone to colonise new breeding areas (Rappole, 1995), it has been postulated that the degree to which different frugivorous species track food resources may have affected the extent of their movements to the point of having triggered, in species that originally wandered more intensely, the evolution of migratory behaviour between different regions (Levey and Stiles, 1992; Chesser and Levey, 1998). However, in spite of the survival benefits accrued to vagrant frugivorous birds by tracking the most rewarding habitats for feeding, some frugivores are territorial in winter. Site constancy in winter territories is likely to expose birds to eventual food shortages, and involves the competitive exclusion of subordinates to poorer habitats, causing a stronger population limitation than by the experienced resource-trackers, which better follow an ideal free distribution (Fretwell and Lucas, 1970; Pulliam and Danielson, 1991). The relevant question at this point is whether the dichotomy between vagrancy and territoriality in frugivorous species not only involves a different extent of migratory movements, but also differences in nonbreeding mortality and hence in reproductive investment of birds that follow each strategy (Roff, 1992; Stearns, 1992).

In this paper, we have studied the covariation among seasonality, migratoriness, survival and fecundity in three Iberian populations of robins (*Erithacus rubecula*) and blackcaps (*Sylvia atricapilla*). It is known that these species are sedentary in southern Iberia (Pérez-Tris et al., 1999, 2000a, 2000b; Tellería et al., 2001), but at present the migratory behaviour of most Iberian populations of robins and blackcaps is far from well established (Tellería et al., 1999). However, the winter ecology of both species in the Mediterranean zone has been widely documented. Although in the breeding season they feed on invertebrates (Cramp, 1988, 1992), they shift to a nearly strictly frugivorous diet outside the breeding season, to the point that these two species have been considered to be the most intensive frugivores in the Iberian winter bird communities (Herrera, 1984, 1998). However, robins are territorial in wintering grounds (Cuadrado, 1995), a behaviour that is more related to anti-predatory defence than to the control of food resources (Cuadrado, 1997). Indeed, fleshy fruits may become scarce in robin territories, forcing them to rely on other resources—like ants and oak acorns—which are com-

paratively more predictable (Cramp, 1988; Jordano, 1989). In addition, the likely increase in mortality related to food shortages may be emphasised because robins are distributed according to an ideal despotic distribution in wintering grounds, through which the most dominant individuals monopolise the best habitats and displace subordinates to poorer sites (Tellería et al., 2001). By contrast, wintering blackcaps closely track fruit availability across habitat patches without defending territories (Jordano and Herrera, 1981; Debussche and Issenmann, 1984; Herrera, 1985, 1998; Rey 1995), and in so doing they adjust an ideal free distribution (J.L. Tellería and J. Pérez-Tris, in prep.). We have studied whether the variations in seasonality among Iberian regions may affect the migratory behaviour and hence the life history of robins and blackcaps. Complementarily, given that these two species are similar in most aspects of their breeding and wintering biology (body size, mating system, migratory pattern, year-round habitat preferences, diet and so on [Cramp, 1988, 1992]) but differ in the way they exploit winter resources, we predicted different population dynamics for each one in relation to vagrancy or territoriality, which led to the following hypotheses:

Variation in the seasonal occupation of habitats

Increasing seasonality implies an uneven temporal distribution of food resources, which affects the length of the period birds will spend outside their breeding areas. This period will be as short as environmental conditions may allow, since the early occupation of breeding sites improves reproductive success (von Haartman, 1968; Smith and Nilsson, 1987). Therefore, we expect that birds show a higher breeding-site tenacity in the less seasonal regions, but leave their breeding areas for a longer time with increasing seasonality. However, if wandering in search for fruits is related to a lower site tenacity in Blackcaps (Herrera, 1985; Levey and Stiles, 1992), then we expect that they perform broader migrations than robins.

Covariation between migration, life expectancy and fecundity

The tradeoff between current and future reproduction causes clutch size to be inversely related to life expectancy (Roff, 1992; Stearns, 1992). Migration could affect this tradeoff because migratory populations are likely to achieve a greater fecundity in the most seasonal breeding areas but also are likely to experience a lower survival due to the costs of migration (Greenberg, 1980). Therefore, increasing seasonality of Iberian habitats should be coupled with a shorter life expectancy and an enhanced fecundity of robins and blackcaps. However, this tradeoff could also be modulated by species-specific features. Particularly, if robins suffer a higher mortality in winter than blackcaps because of their winter territoriality, this effect should be counterbalanced through interspecific fecundity adjustments in the opposite direction (Roff, 1992; Stearns, 1992).

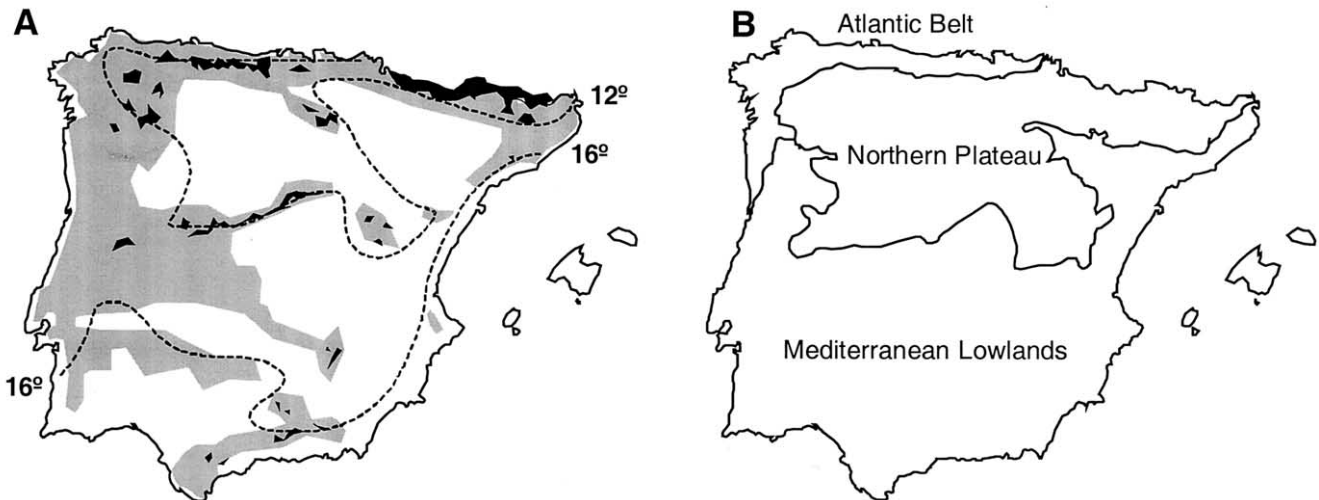


Fig. 1. **A.** Environmental variation in the Iberian Peninsula. Dashed lines represent the mean annual temperature isotherms for 12 °C and 16 °C, and shaded areas correspond to those with mean annual precipitation over 600 mm. Mountain systems above 1500 m (in black) are also shown. **B.** Regional division of the Iberian Peninsula used in this study. Seasonality in Iberia primarily depends on altitude and continentality (Lautensach, 1964), so that it is lowest in the Mediterranean Lowlands and highest in the Northern Plateau, and reaches an intermediate level in the Atlantic Belt.

2. Methods

2.1. Study area

The Iberian Peninsula is located at the southern edge of the Western Palearctic, between 36° N and 43° N. The gradually decreasing oceanic influence towards its south-eastern half, together with elevation in its northern plateau, makes it possible to differentiate three contrasting regions (Fig. 1, see also Lautensach, 1964; Font, 1983). The Atlantic Belt has fresh summers and mild winters, as well as abundant rainfall all around the year. The Northern Plateau (mean elevation around 800 m) shows a marked contrast between temperate summers and harsh winters. The Mediterranean Lowlands have hot summers but temperate and rainy winters (Fig. 1). Therefore, these Iberian regions define a nonlinear gradient of seasonality, in which primary production—and hence food availability—follow a complementary spatio-temporal distribution (Lautensach, 1964; Herrera, 1985). The two northernmost regions, especially the Northern Plateau, are summer habitats for migratory birds, while the Mediterranean Lowlands become the most suitable wintering areas for many Palearctic passerines (Tellería, 1988). During winter, the harsh Northern Plateau contrasts with the Mediterranean Lowlands, which have a peak of primary production and maintain many insects and large stocks of fleshy fruits available for wintering birds (Lautensach, 1964; Herrera, 1985; Tellería, 1988; Fuentes, 1992). The Atlantic Belt shows an intermediate level of primary production during winter that allows invertebrate activity and a moderate fruit production, which sustain small populations of wintering passerines (Lautensach, 1964; Guitián, 1985; Herrera, 1985; Tellería, 1988; Fuentes, 1992).

2.2. Seasonal occupation of habitats

We used two complementary approaches to evaluate the intensity of migratory behaviour of robins and blackcaps in the Iberian Peninsula. The first one, at the population level, consisted of an analysis of seasonal changes in abundance of each species in each Iberian region. The second one, at the individual level, studied the variation in breeding-site tenacity between species and regions.

We studied the spatio-temporal variation in abundance of Iberian robins and blackcaps by using 66 published bird censuses, scattered across the Iberian Peninsula (reviewed by Tellería et al., 1999). We only considered censuses performed in forested habitats (forests, scrublands, olive growths, etc.), where both species may occur along the year (Cramp, 1988, 1992; Tellería et al., 1999). All these data were obtained by means of line-transect counts, and all of them were repeated in spring and winter by the same authors to describe the structure of particular Iberian bird communities. This allowed us to test for seasonal changes in abundance among regions controlling for site-specific habitat characteristics.

We used ringing recoveries (available from the Spanish Ringing Scheme) to study the regional variation in breeding-site tenacity of robins and blackcaps. We explored these data to find native individuals, which were those labelled as local, nesting or nestling (see ringing codes in EURING 1979). We also considered birds ringed or recaptured between April and August (both included), when no migration of these species takes place across the Iberian Peninsula (Cantos, 1995; Bueno, 1998). Following these criteria, we considered 126 robins (recaptured between 1962 and 1996) and 287 blackcaps (1967–1996). A strong breeding-site fidelity was the rule among these birds since

Table 1

Regional variation in breeding phenology of robins and blackcaps. It is shown the mean breeding times (referred to as \bar{B} in the text), with standard errors in days and sample sizes in brackets.

	Robins	Blackcaps
Atlantic Belt	17 May \pm 2 (107)	25 May \pm 3 (46)
Northern Plateau	1 June \pm 3 (51)	31 May \pm 2 (62)
Mediterranean	6 May \pm 3 (6)	8 June \pm 6 (15)
Lowlands		

every one, but a single robin that was excluded, were always recaptured at the same breeding site.

We considered breeding-site tenacity as the time birds remain in the breeding site outside the nesting period. Because the timing of breeding may change among regions or between species, we controlled breeding phenology when estimating breeding-site tenacity. Data on breeding times were obtained from 164 nest-record cards of robins (spread between 1969–1996) and 123 of blackcaps (between 1970–1992) available from the Spanish Ornithological Society. Because of irregularities in the frequency of visits to the nests, in many cases we could not determine the laying date accurately. However, given the broad scale of our comparison, to know the exact laying dates is not necessary to describe breeding phenology in this study. Therefore, we used the average between the dates of the first and last visit to each nest as measures of breeding time. We found that breeding phenology is similar among regions in blackcaps, but robins breed earlier in southern Iberia than in the other regions (Table 1), which could be a means to avoid extending the breeding season into the summer drought period. Indeed, it has been shown that the summer drought negatively affects the reproductive output of south Iberian robins (Pérez-Tris et al., 2000b).

We estimated site tenacity (T) of each local bird i as $T_i = |\bar{B} - D_i|$, where \bar{B} is the mean breeding time value for the species and the region to which the bird i belongs (given in Table 1), and D_i is the farthest calendar date from \bar{B} in which the individual was recorded at the breeding site, regardless if this date corresponds to the ringing or to one of the bird's recaptures. To avoid using birds captured during the nesting period in the analysis of site tenacity, we did not consider time lags shorter than 60 days, which is a safe interval according to the duration of the breeding period—from arrival in spring to departure in autumn—in these species (Cramp, 1988, 1992). This measure of site tenacity assumes that the probability of recapture in the breeding area does not change among regions or species. Because of the importance of the Iberian Peninsula as a migration and wintering area for robins and blackcaps, trapping effort remains high even during autumn and winter in all regions (Santos et al., 1988), so the predicted lower rate of autumn-winter recoveries in the most seasonal region should not be attributed to lower recapture effort. Both species show similar habitat preferences during the breeding season: they go around within similarly sized territories moving into low

and dense vegetation, which makes them easily capturable in mist nets (the main trapping method used by ringers). In addition, their migratory populations stay in breeding territories until departing once the post-nuptial moult is completed, which takes place at a similar time in both species (Cramp, 1988, 1992). Therefore, it is very unlikely that the probability of recapture of robins or blackcaps shows different seasonal changes among regions, unless their populations actually differ in breeding-site tenacity.

2.3. Regional and interspecific variation in life expectancy and fecundity

We estimated life expectancy of each bird as the calendar years it survived, at least, until its last recapture in the breeding area. Although we considered the age at ringing of individuals (whether they were first-year birds or older), we nonetheless underestimated life expectancy. However, this happened in both species and in all regions, so it could not have affected regional nor interspecific variation in life expectancy. Nevertheless, in order to avoid further bias of life-expectancy estimates we did not consider individuals ringed after 1992, a safe boundary according to the variation in life expectancies observed in these species (Cramp, 1988, 1992; Cuadrado, 1994). We could not carry out more refined analyses of survival because the number of birds ringed in each region throughout the study period was not available. Nevertheless, life expectancy in calendar years may be a suitable measure of survival in studies of passerines. Calendar years properly reflect the number of breeding opportunities in these species provided that their mortality rates usually peak in autumn migration and then decline (Greenberg, 1980; Pienkowski and Evans, 1985).

We studied the regional and interspecific variation in clutch size as a surrogate of fecundity (Stearns, 1992). We recorded clutch size from nest record cards considering only accurately complete clutches, which we recognised by their constancy over several days along the incubation period. Regional and interspecific variation in clutch size could be affected by changes among regions or species in nesting success; for instance, egg hatchability rates or fledging rates are known to influence clutch size (Lundberg, 1985; Martin, 1995). To examine the possibility that the patterns of clutch-size variation were confounded by nesting success, we conducted two-way ANCOVAs on the number of hatched eggs and fledged young, controlling for the covariates clutch size or brood size, respectively. Because of irregularities in the frequency of visits, the number of hatched eggs and fledged young were rarely reported in the Mediterranean Lowlands (two nests for each species), so we restricted these comparisons to the two northernmost regions.

A low fecundity due to small clutch size could be counterbalanced by increasing the number of clutches. In our study of clutch size, we assumed that the number of clutches per year was constant across Iberian regions.

Blackcaps rarely lay more than one clutch across their geographic range except in the Cape Verde Islands, where they lay two clutches at two different seasons in the year, showing a genetically-based double reproductive cycle within each year (Shirihai et al., 2001). Robins usually lay two clutches across Europe, and there is no evidence that they lay more in the south of Iberia compared to other Iberian regions (Cramp, 1988). In addition, we have been capturing fledglings of these two species in different localities of these regions (Tellería and Carbonell, 1999; Pérez-Tris et al., 2000b), and we have not detected more than one pulse of production of juveniles in any of the localities (pers. obs.).

We transformed variables to meet the statistical assumptions of parametric statistics. Square-root transformation was applied to clutch sizes, brood sizes and fledgling number, and log-transformation to the remaining variables. All tests were two-tailed, and a posteriori differences among groups were assessed by means of Tukey's tests.

3. Results

3.1. Seasonal occupation of habitats

Both robins and blackcaps showed different seasonal patterns of distribution among regions in the Iberian Peninsula (Table 2). Thus, the abundance of both species decreased in the Northern Plateau (the most seasonal region) and increased in the Mediterranean Lowlands (the less seasonal region) outside the breeding period (Fig. 2). Obviously, the sharp increase in abundance in the Mediterranean Lowlands is mainly due to the arrival of individuals from central and northern Europe (Cantos, 1995; Bueno, 1998), but our results suggest that the arrival of migrants from the most seasonal areas in the Iberian Peninsula could also contribute to this increase. According to our predictions, blackcaps displayed a more seasonal pattern of distribution than robins. Blackcaps disappeared from the Northern Plateau completely and sharply decreased in abundance in the Atlantic Belt, concentrating themselves in the Mediterranean Lowlands during winter (Fig. 2). In robins, however, the populations that remained during winter in both northernmost regions were larger, as only the Northern Plateau showed a significant decrease in abundance (Fig. 2).

Both species showed less breeding-site tenacity in the Northern Plateau than in the other two regions, and robins spent more time in their breeding areas than blackcaps (Fig. 3). Interspecific differences were more intense in the Atlantic Belt, although not significantly so, perhaps because blackcaps behave as partial migrants while robins are more sedentary in this region (two-way ANOVA: among regions $F_{2,305} = 7.03$, $P < 0.001$; between species $F_{1,305} = 14.99$, $P < 0.0001$; region \times species $F_{2,305} = 2.77$, $P = 0.064$).

Table 2

Results of two-way repeated measures ANOVAs on spatio-temporal differences in abundance of Iberian robins and blackcaps. Since each forest was sampled both during the spring and the winter, 'season' has been considered as a repeated measures factor.

Robins:	F	d.f.	P
Region	3.22	2,63	0.047
Season	0.03	1,63	0.863
Region \times season	22.82	2,63	< 0.0001
Blackcaps:	F	d.f.	P
Region	2.17	2,63	0.123
Season	3.94	1,63	0.051
Region \times season	6.37	2,63	0.003

3.2. Patterns of life expectancy and fecundity

Both species had a significantly shorter life expectancy in the most seasonal region, where birds were found to be more migratory. Nevertheless, according to the predicted benefits of wandering compared to territory defence in winter, blackcaps survived more years than robins in all regions (two-way ANOVA: among regions $F_{2,337} = 5.47$, $P < 0.01$; between species $F_{1,337} = 21.22$, $P < 0.0001$; region \times species $F_{2,337} = 3.04$, $P = 0.050$; Fig. 4). Consistent with these results, both species had a greater clutch size in the most seasonal region, but robins laid larger clutches than

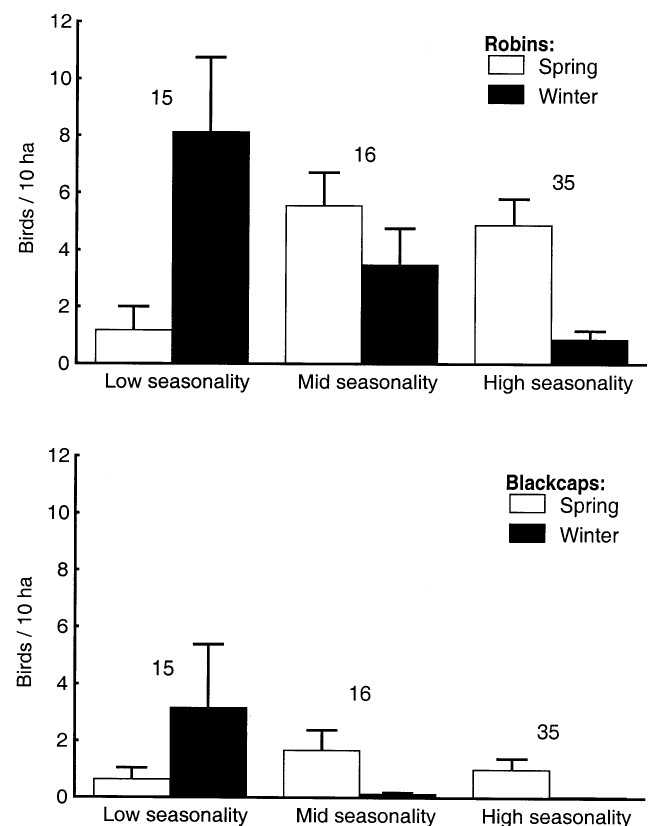


Fig. 2. Spatio-temporal patterns of variation in abundance of robins and blackcaps according to the changing degree of seasonality in the Iberian Peninsula. The levels of seasonality correspond to the regions shown in Fig. 1. Means, standard errors and sample sizes are shown.

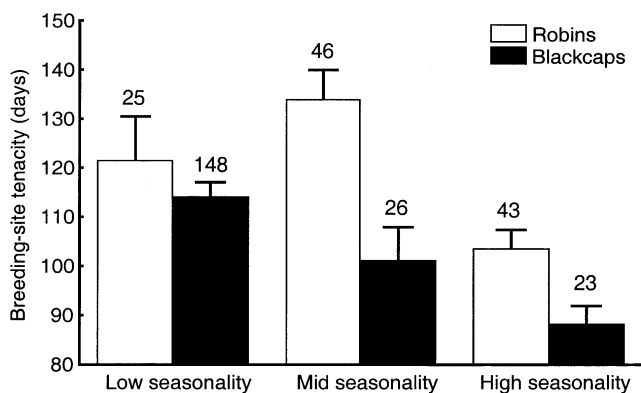


Fig. 3. Regional and interspecific variation in the breeding-site tenacity of robins and blackcaps (means, standard errors and sample sizes), in relation to the changing degree of seasonality in the Iberian Peninsula. The levels of seasonality correspond to the regions shown in Fig. 1. In both species, site tenacity was smaller in the region with the highest seasonality than in the other two regions (Tukey's test, $P < 0.005$).

blackcaps in all regions (two-way ANOVA: among regions $F_{2,257} = 21.27$, $P < 0.0001$; between species $F_{1,257} = 54.07$, $P < 0.0001$; region \times species $F_{1,257} = 0.25$, $P = 0.78$; Fig. 4). It is unlikely that the small sample size in the area with lowest seasonality affected the reliability of these results, as regional and interspecific effects were both large (an average difference of one egg) and highly significant. At a given clutch size, neither regional nor interspecific variation in number of hatched eggs was significant (two-way ANCOVA: between northernmost regions $F_{1,190} = 0.0001$, $P = 0.99$; between species $F_{1,190} = 1.08$, $P = 0.30$, region \times species $F_{1,190} = 0.09$, $P = 0.77$; covariate clutch size: $F_{1,190} = 4.89$, $P < 0.05$). The number of fledged young at a given brood size did not vary either between regions or between species (two-way ANCOVA: between northernmost regions $F_{1,81} = 0.0005$, $P = 0.98$, between species $F_{1,81} = 0.45$, $P = 0.50$, region \times species $F_{1,81} = 0.24$, $P = 0.62$; covariate brood size: $F_{1,81} = 86.40$, $P < 0.001$). No test of parallelism was significant in these ANCOVAs (all $P > 0.77$ and $P > 0.41$, respectively). According to these results, we can consider that regional and interspecific variations in clutch size were not affected by nesting success.

4. Discussion

4.1. Seasonality, migratory behaviour, and life-history traits of robins and blackcaps

So far, the migratory behaviour of Iberian robins and blackcaps had been considered to be nearly homogeneous. Thus, sedentariness would be the most widespread strategy among Iberian populations, which would only shift to partial migration in mountainous areas (e.g., Cramp, 1988, 1992). This view, principally based on the predictions of large-scale latitudinal gradients of migratoriness in the

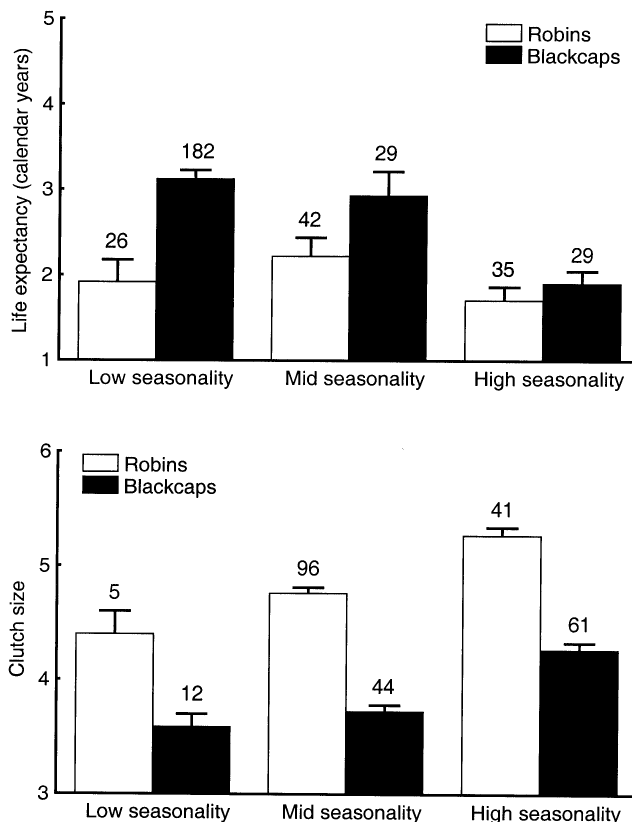


Fig. 4. Regional and interspecific variation in life expectancy and clutch size of robins and blackcaps (means, standard errors and sample sizes), in relation to the changing degree of seasonality the Iberian Peninsula. The levels of seasonality correspond to the regions shown in Fig. 1. In both species, means were smaller in the region with the highest seasonality than in the other two regions (Tukey's test: life expectancy $P < 0.05$; clutch size $P < 0.005$).

Palaearctic, ignores the strong variation in environmental conditions related to elevation in low-latitude areas. In the Mediterranean zone, altitude resembles the effect of latitude, causing sharp variations in seasonality at a much smaller geographic scale (Lautensach, 1964; Font, 1983). Consequently, in the Iberian Peninsula robins and blackcaps tend to be sedentary in the less seasonal areas but migratory in the most seasonal regions, reproducing in a small area their variations in migratoriness with increasing seasonality at the Palaearctic scale (Cramp, 1988, 1992). Along with these intraspecific patterns, we found slight differences between blackcaps and robins in their response to seasonality. In the Mediterranean Lowlands (the least seasonal area of all), blackcaps show a slightly smaller breeding-site tenacity than robins, which could be the outcome of spatio-temporal variations in fruit availability which robins do not track (Herrera, 1985; Rey, 1995). Blackcaps show more seasonal patterns of occurrence in the Atlantic Belt (an area of mid-seasonality), where fleshy fruits shift from abundant in late summer to scarce during winter. Meanwhile, robins—which are less dependent of fruit seasonality—could be as sedentary there as in the Mediterranean Lowlands, or engage in regional-scale movements (Gutián,

1985). Finally, blackcaps completely abandon the most seasonal Iberian area (the Northern Plateau) during winter, when fleshy fruits are absent there, while robins likely behave as partial migrants in that region. In summary, our results not only reveal the predicted increase in migratoriness of Iberian birds with increasing seasonality, but also support that this association may be modulated by other factors, which in turn will determine the extent to which each species responds to environmental instability by leaving their breeding areas. In our study, interspecific differences in the response to seasonality are consistent with the predicted higher site-constancy in the winter territorial robins compared to the vagrant blackcaps (Herrera, 1985; Levey, 1988; Levey and Stiles, 1992).

Our results support the predicted effect of migration on the reproductive tradeoffs of Iberian robins and blackcaps. Some studies had found a correlation between migratoriness and clutch size (Bell, 1996), or between migratoriness and life expectancy (Cuadrado, 1994), but no one had ever illustrated the covariation among migratory behaviour, fecundity and survival in a gradient of increasing seasonality. In Iberian robins and blackcaps, life expectancy decreases and clutch size increases with increasing migratoriness in the Northern Plateau, the most seasonal environment. In this area, primary production concentrates in a shorter breeding season and reproductive restrictions related to the summer drought are less pronounced than in Mediterranean Lowlands (Pérez-Tris et al., 2000b). These environmental conditions could allow birds to lay larger clutches (Sæther, 1994), which might counterbalance the mortality associated to the costs of migration by increasing offspring production (Young, 1996; Pérez-Tris et al., 2000b). On the other hand, the reduced residual reproductive value due to lower survival chances would also mitigate the importance of reproductive costs, inducing a higher reproductive investment in migratory populations (Roff, 1992; Stearns, 1992; Pérez-Tris et al., 2000b). Other factors may influence changes in clutch size among regions, which could affect mortality rates by modifying reproductive effort. For instance, the decrease in clutch size with decreasing seasonality could be explained by a parallel increase in nest-predation rates in the less seasonal areas (Slagsvold, 1982; Lundberg, 1985; Martin, 1995). It is difficult to value a posteriori the extent to which predation pressure could influence life-history variation among robins and blackcaps in the Iberian Peninsula. The few studies that have evaluated nest-predation rates in these species suggest that they are homogeneous both between species and among Iberian regions (De la Puente and Yanes, 1995; Yanes and Suárez, 1995), so nest predation is unlikely to have affected the patterns of clutch size variation that we have found.

It has been claimed that two-species comparisons cannot provide reliable conclusions about interspecific patterns (see discussions in Garland and Adolph, 1995; Harvey and Pagel, 1991). However, a multispecies approach is not always feasible given the difficulty to gather information for

several species. In our study, to obtain enough data of seasonal variation in abundance, ringing recoveries and nest records for a number of vagrant and territorial species would be simply unrealisable: this information does not exist. When faced with these limitations, two-species comparisons may give biologically relevant results provided that independent predictions for between-species differences are formulated a priori. In this case, the probability that all differences are in the predicted directions will be given by the combination of probabilities that each individual difference fits such predictions (Garland and Adolph, 1995). In this study, the probability of obtaining the four predicted interspecific patterns (spatio-temporal distribution, site tenacity, life expectancy and clutch size) by chance is $P = 0.5^4 = 0.063$, which is nearly significant. To improve the reliability of our results we have selected the best model species available. They are the most common in the Iberian forest bird communities (Tellería et al., 1999), the most representative among vagrant and territorial frugivores (Herrera, 1998), and the ones for which a larger body of empirical research has been accumulated so far (Cramp, 1988, 1992).

Despite these methodological shortcomings, our results suggest that differences in winter ecology between robins and blackcaps may modulate the effect of migration on the tradeoff between fecundity and survival in these species. This would have caused, while increasing migratoriness involved a higher fecundity and a shorter life expectancy within species, that between species the most migratory one (the blackcap) showed a lower fecundity and a longer life expectancy than the most sedentary one. These contrasting patterns of covariation within and between species are consistent with the costs of territorial behaviour in terms of survival, which would cause a strong non-breeding population limitation (Fretwell and Lucas, 1970; Pulliam and Danielson, 1991). These costs could be counterbalanced, however, through an increased fecundity of survivors. In partially migratory robins, winter territoriality may favour breeding success of dominant, highly qualified individuals (Adriaensen and Dhont, 1990). In the migratory fraction of the population, dominants may improve survival because they occupy the best places in non-breeding grounds (Tellería et al., 2001). The same happens in the resident fraction, in which survivors benefit from an early occupation of the best breeding territories (von Haartman, 1968; Smith and Nilsson, 1987; Adriaensen and Dhont, 1990). This might constitute a feedback mechanism that could enhance population recruitment although average winter survival is low, since the most qualified individuals would make up the breeding population year after year (Rodenhouse and Sherry, 1997). Blackcaps, however, effectively track food resources during winter (Fouarge, 1981; Herrera, 1982, 1985; Rey, 1995), doing so according to an ideal free distribution (J.L. Tellería and J. Pérez-Tris, in prep.). If this improves their survival (Jordano, 1988), winter vagrancy could enable blackcaps to achieve a similar lifetime breed

ing output to robins without the increased effort associated with large clutches. Obviously, robins and blackcaps are two particular cases in a continuous series of winter behaviours, and evolutionary history, physiology and many other factors may have influenced the evolution of their life histories. Although this makes our results hardly generalisable to other species, they support our predictions and provide an empirical background for future studies on the role that winter ecology and behaviour play in shaping the covariation among migration, fecundity and survival of birds.

4.2. The migrations of Iberian robins and blackcaps in the Palearctic context

The increase of seasonality with increasing latitude likely triggered the evolution of migration in most Palearctic birds (Moreau, 1972; Alerstam and Högstedt, 1982). Thus, migration is a common strategy among birds of highest latitudes that progressively declines southward, both within and among species (Moreau, 1972). Resembling this latitudinal trend, increasing seasonality with elevation should have induced the evolution of migration in mountains and highlands at middle and low latitudes. Our results show that regional differences in the extent of environmental seasonality across the temperate zone may be large so as to cause not only migratory movements, but also life-history adjustments. A number of studies have found morphological differences among Iberian populations of robins and blackcaps that are consistent with this variation in migratory behaviour (Tellería and Carbonell, 1999; Pérez-Tris et al., 1999, 2000a, 2000b), suggesting that migration actually constitutes a relevant selective pressure for these populations. Moreover, the morphological variation found between populations in the very same geographical context is much larger in blackcaps than in robins (Pérez-Tris et al., 1999, 2000a), supporting a stronger response of the former to changes in seasonality.

Operating on the regional scale, the blackcaps' tendency to move could have favoured the development of a complex migratory system in the Palearctic, where several migratory directions have evolved, including a pattern of leap-frog migration with sub-Saharan wintering grounds (Shirihai et al., 2001). Indeed, the rapid evolution of new migratory directions in European blackcaps (Berthold et al., 1992) underlines their plasticity to track newly available wintering areas. By contrast, robins are sedentary or partial migrants in many parts of their range, and do not show such contrasting patterns of distribution between breeding and wintering ranges in the Palearctic as blackcaps (Cramp, 1988). According to our results, the higher site constancy of robins compared to blackcaps likely affects the way each species exploit seasonal environments, which could have constrained the evolution of their migratory patterns.

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