Articles

The decline of a peripheral population of the European robin *Erithacus rubecula*

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This paper examines the potential effect of some factors involved in the decline of a winter population of the European robin *Erithacus rubecula* in southern Spain. The area receives extra-Iberian immigrants that come into contact with resident conspecifics. Given this interspersed distribution, three hypotheses were tested to explain the decline: a) the depletion of the carrying capacity of the area during winter, b) the decline of the resident population, and c) the reduction of foreign individuals in this wintering area. Winter robin and fruit (a main winter food) abundances were assessed at 43 sites from 1999 to 2014, and the abundance of breeding robins was evaluated from 1998 to 2012. Rainfall and temperatures were recorded throughout this period and changes in forests occupied by breeding robins were assessed in 1999 and 2013. Results showed a decline in winter temperatures and an increase in fruit availability. Given that food increases could buffer the thermoregulatory costs of colder conditions, the depletion of the carrying capacity of the area was discarded as a main driver of robin decline. Spring counts showed a reduction of 45% in the breeding population that was not explained by changes in forest management. However, a significant increase in summer temperatures could boost the pervasive effect of drought on robins inhabiting this marginal area of the species' range. Foreign immigrants, despite the increase in breeding populations in most of Europe, did not buffer the decline caused by the reduction of residents. In fact, an analysis of ring recoveries reported in this area depicted a sharp decrease in extra-Iberian wintering individuals. These results may be related to the effect of global warming on migratory schedules (the northwards retreat of wintering areas) and on the suitability for robins of local habitats in this peripheral region of the Palaearctic.

The Iberian Peninsula has traditionally been considered a main wintering area of Palaearctic birds (Moreau 1956), but the seasonal occupation of this area by migratory birds may be reduced by the effect of some global changes affecting species range (Parmesan 2006). It has been suggested, for instance, that birds involved in migratory movements are moving their wintering areas towards the north due to global warming (Visser et al. 2009, Lehikoinen and Sparks 2010). This may change the relative importance of regions occupied by migratory birds during the year, with concomitant implications on bird biology and conservation. However, despite the need for sound empirical evidence of these patterns, monitoring programs aimed at detecting these changes in these traditional wintering grounds remain scarce (Sanz 2002, Onrubia and Tellería 2012).

This paper explores the features affecting the decline of a winter population of the European robin *Erithacus rubecula* in Campo de Gibraltar (Cádiz, Andalusia, southern Spain) detected during a long-term study on winter bird biology (Tellería et al. 2001, 2005, 2008, 2013). The area receives central European migratory robins that mix with resident conspecifics (Bueno 1998). These local individuals are constrained to some moist forest areas during the breeding period but spread in autumn to winter in scrublands rich

in fruit (Pérez-Tris et al. 2000, Tellería et al. 2001, Tellería and Pérez-Tris 2004). Given the potential depletion of the carrying capacity of the area and the interspersed distribution of resident and migratory individuals, the decline of this winter population could be explained by three hypotheses to be tested in this study:

a) Changes in the carrying capacity of the area during winter

Small birds are constrained in winter by thermoregulatory requirements, implying the active selection of warm and productive habitats during winter months (Meehan et al. 2004, Carrascal et al. 2012). Wintering passerines in Campo de Gibraltar adjust this pattern to avoid colder sites and actively track fruit abundance (Tellería et al. 2005). In this way, inter-winter reduction of fruit resources (a main food for wintering robins, Herrera 1981) and temperatures could complicate the balance of heat loss through an increase in feeding rates (Kwit et al. 2004, Cresswell et al. 2009, Carrascal et al. 2012). This paper tests whether fruit abundance and temperatures have declined in recent years producing a decrease in the attractiveness of Campo de Gibraltar as a wintering area for robins.

b) Reduction of the resident robin population

Residents make up a significant part of the wintering population of robins in Campo de Gibraltar (Tellería et al. 2001, Tellería and Pérez-Tris 2004) where they benefit from the early occupation of the area (Tellería and Pérez-Tris 2004). If migratory individuals outnumber available winter territories, a decline in resident robins may be buffered by migratory birds arriving from the northernmost areas (see hypothesis c). If not, the decline of residents will affect the entire winter population. According to the Spanish Common Breeding Bird Monitoring Scheme, the Spanish population of the European robin has increased during the period 1998–2012 (Escandell 2013), a trend common to other species with preferences for wooded habitats (Seoane and Carrascal 2008). However, this monitoring program is mainly distributed in central and northern areas of Spain and the peripheral southern populations of forest birds are still poorly covered (Escandell 2013). Iberian robins, like other passerines typical of central European forests, are increasingly scarce in southern dry and hot woodlands of the Mediterranean region where it is increasingly difficult to cope with summer drought (Tellería and Santos 1994, Pérez-Tris et al. 2000). This paper tests whether changes in forest structure or summer drought conditions explain the decline of the robin population inhabiting this area at the border of the species' range where bird populations appear more vulnerable to global warming (Cuervo and Møller 2013).

c) Reduction in foreign individuals

The decline of foreign robins could be related to a decrease in migratory populations arriving to overwinter in this southern area (Visser et al. 2009). However, as is the case in Spain, monitoring programs in other European countries from which robins migrate (Bueno 1998) depict a moderate increase in populations (European Bird Census Council <www.ebcc.info/>). This means that, if migratory schedules have not changed, the contribution of foreign birds to the winter population in Campo de Gibraltar should increase. Alternatively, and despite the numerical increase, a decrease in wintering individuals could be caused by a northward shift of wintering grounds resulting from changes in migratory schedules. This study tests whether, all else being equal (resident population and winter conditions), the decline of wintering robins in Campo de Gibraltar can be explained by a reduction in foreign individuals.

Material and methods

Study area

The study area is located on the northern side of the Strait of Gibraltar (Fig. 1). It is crossed by low-elevation mountains (maximum altitude 786 m a.s.l.) covered by cork oak *Quercus suber* forests, mixed with Algerian oaks *Quercus canariensis*. These forests are located within the Parque Natural de los Alcornocales (Cork-oak Woodlands Natural Park), included in the European Natura 2000 network (European Community 1992), which protects many European forest species at the southern limit of the range (Ojeda et al. 2000, Junta de Andalucía 2004). These forests are devoted to cork production, deer hunting and cow ranching. The surrounding lowlands are covered by scrublands, grasslands and croplands that extend westwards to the Atlantic Ocean and eastwards to the Mediterranean Sea (Fig. 1). Both forests and scrublands have fruit-producing shrubs dominated by mastics *Pistacia lentiscus* and wild olives *Olea europaea sylvestris* on which many birds rely in winter (Tellería et al. 2005). We distributed 43 study sites along an altitudinal gradient ranging from sea level to 265 m a.s.l. (mean $\pm$ SE $= 135 \pm 123$) as sites higher than this level were occupied by cliffs and sharp slopes. Half of the study sites were located in forests (n $=$ 23) and the other half (n $=$ 20) in scrublands.

Winter abundance of robins and fruiting shrubs

Robin abundance was assessed in mid January from 1999 to 2009 (with the exception of 2001; in January 2014, a new count was carried out to check the situation). The counts were made in 43 line transects 500 m long and 50 m wide (25 m at either side of the progression line, for a 2.5 ha census area) located in each study site. Fruit abundance was measured in transects during the same sampling sessions by counting the number of plants holding fleshy fruits in a 10 m wide belt, 5 m to either side of transects. A complementary study was performed to confirm that the number of shrubs holding fruits was strongly correlated to the actual variation of fruit abundance (Tellería et al. 2005). Because the same transects were used to assess fruit crops during the study winters, it was accepted that the sampling reflected inter-winter changes in the availability of the resource.

Contribution of foreign birds to winter population

Winter recoveries of ringed robins provided by the European Union for Bird Ringing (EURING) and by the Spanish Office of Migratory Species (Spanish Ministry of Agriculture, Food and Environment) were reviewed to look for changes in the contribution of foreign individuals to winter population. There was a total of 327 ring recoveries obtained in Cádiz Province, the administrative area around Campo de Gibraltar, during winter (December, January and February). After reviewing the distances covered by these birds to reach this wintering area from breeding grounds or migratory stop overs, recoveries were divided into migratory robins ($>$ 1000 km between ringing and recovering) and locals ($<$ 20 km). Just 3 recoveries of individuals coming from intermediate distances were discarded. Finally, to have a temporal perspective, it was explored whether the contribution of foreign birds changed over three periods: before 1970, from 1970 to 1999 and from 2000 to 2009.

Spring abundance of robins and changes in forest structure

Transects in winter were used to assess robin abundance in the 23 study forests. Counts were made in May of 1999, 2004, 2005, 2006, 2008 and 2009 (in 2012, a new count was carried out to check the situation). Changes in habitat structure were assessed in May 1999 and May 2012
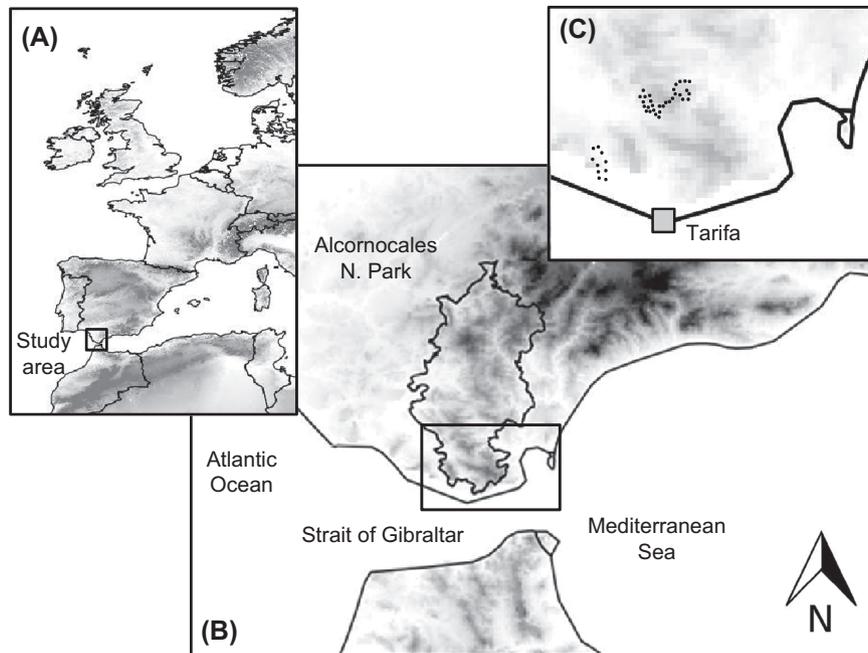
Figure 1. Location of the study area (A) main features (elevation in gray) of (B) and distribution of sampling sites (C) Campo de Gibraltar.

by measuring shrub cover (vegetation below 2 m height), tree cover (vegetation over 2 m height), cork and Algerian oak cover, mastic and wild olive cover and density of trees (number of trunks over 10 cm diameter at breast height). All of these variables were visually assessed in three circular plots of 25 m radius evenly distributed along the 500 m line transects used to count birds and fruit (Tellería et al. 2005).

Climate

Temporal series of rainfall and temperature were recorded from the Tarifa Meteorological Station (36°01′N, 5°36′W, 59 m a.s.l.; available from the Spanish National Meteorological Agency, <www.aemet.es/>). Inter-year changes in temperature were explored by assessing mean and minimum daily temperatures in January and mean and maximum temperatures in August from 1999 to 2012 (data for some years were not available from this meteorological station). These months represent the most extreme winter and summer conditions in the area (Ninyerola et al. 2005). Changes in rainfall were assessed by using annual precipitation and the precipitation accumulated from September to December. The latter describes the rain input after summer drought, which regulates the intensity of the autumnal productive period (vegetation growth, invertebrate activity, etc.) typical of the Mediterranean region (Nahal 1981).

Analyses

Repeated-measures ANOVA were used to look for between-year variation in robin abundance, fruit crop and vegetation traits from 1999 to 2009. In addition, temporal trends in robin abundance, fruit crop and climate variables were studied with TRIM (TRends and Indices for Monitoring data; Pannekoek and Van Strien 2005). This software analyses time-series of counts with missing observations using Poisson regression (log-linear models; McCullagh and Nelder 1989). It suggests a sequential approach to select the best model with and without covariates (e.g. scrubland vs forest in the case of fruit and robin counts). The fit of the models was tested by chi-square tests and likelihood ratios, and the most suitable ones were selected with the Akaike's information criterion (AIC; McCullagh and Nelder 1989). In this way, TRIM assesses temporal trends according to an overall multiplicative slope (OMS = 1, no changes, OMS = 1.05, annual increase of 5%; OMS = 0.95, annual decrease of 5%, etc.) over the study period (Pannekoek and Van Strien 2005).

The effect of variables used to assess changes in forest structure on breeding robins were studied with forward–backward stepwise multiple regressions in the two study springs (1999 and 2012). We introduced a quadratic term of explanatory variables to check for non-linearity in the influence of the forest traits on robin abundance. In this way, we attempted to interpret the potential effect of changes in forest structure on the local population of the species. Additionally, the effect of all of the study variables on robin numbers was studied with a mixed general linear model (distribution: normal; link function: identity) in which the year (1999 and 2012) was included as a random factor. The aim was to test if some habitat changes were sufficient to explain inter-winter trends in robin abundance. All analyses were done with the GLM module in Statistica 7.0 (StatSoft 2004).

Results

Numerical trends of wintering robins

The number of wintering robins declined in Campo de Gibraltar during the study period. The changes occurred
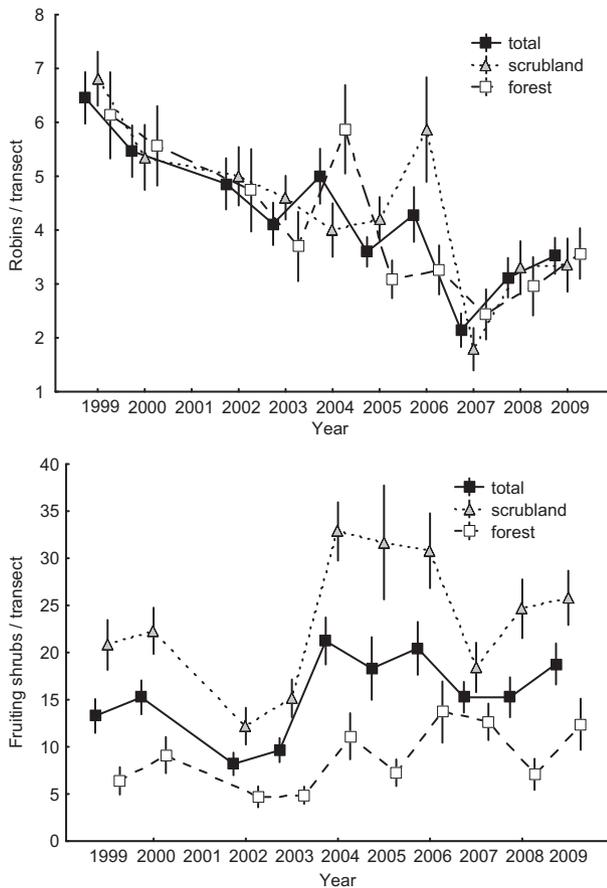
Figure 2. Top panel: mean numerical trends of wintering robins (± SE) in the study area and within the two main habitats occupied by the species. Bottom panel: mean abundance trends of fruit availability (± SE) in the study area and within the two main habitats considered in this study.
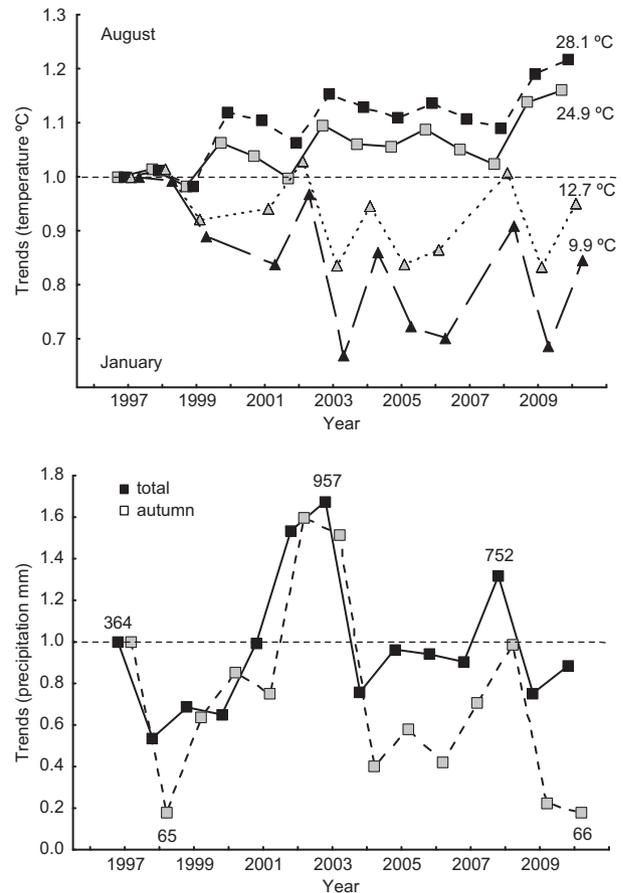

Figure 3. Top panel: trends in August and January mean, minimum and maximum temperatures, with scores at the end of the study period. Bottom panel: trends in total and autumn precipitations (September–December). Mean, maximum and minimum scores are represented.

conjointly in scrublands and forests despite some asynchrony outputs in the trends of the two habitats (Fig. 2; repeated measures ANOVA, year: $F_{9,315} = 10.79$, $p < 0.001$; habitat: $F_{1,35} = 2.08$, $p = 0.158$; year × habitat interaction: $F_{9,315} = 2.44$, $p < 0.011$). The number of robins showed a significant decline ($p < 0.01$), with OMS = 0.9271 (SE = 0.0066) and similar trends in scrublands and forests (Wald chi-square text 0.06, $p = 0.8091$). Thus, the population wintering in 2009 declined by around 45% of the initial population in 1998.

Trends of winter conditions

Fruit crop differed between years, with higher fruit crops in scrublands (Fig. 2; repeated measures ANOVA, year: $F_{9,315} = 7.00$, $p < 0.001$; habitat: $F_{1,35} = 26.66$, $p < 0.001$; year × habitat interaction: $F_{9,315} = 3.43$, $p < 0.001$). The most significant contrasting situations were reported in the winters of 2003–2004 (low resource availability) and 2004–2006 (high availability), which showed significant differences in availability of this resource when compared to the rest of the winters (Tukey HDT test, $p < 0.05$, in all cases). Fruit availability increased moderately ($p < 0.01$) according to TRIM categories, with OMS = 1.0505 (SE = 0.008) and an uneven distribution of fruit abundance

in scrublands and forests (Wald chi-square 34.52, DF = 9, $p = 0.0001$). During this period, a decline ($p < 0.01$) was observed in January temperatures. Average temperatures changed from 13.4°C to 12.7°C ($p < 0.05$; OMS = 0.9908, SE = 0.0042) and minimum temperatures from 11.7°C to 9.9°C (decline, $p < 0.01$; OMS = 0.9774, SE = 0.0081). Annual and autumn rains depicted an uncertain trend and strong temporal changes (Fig. 3).

Contribution of foreign birds to the winter population

Around half of the 324 ringed robins recovered in winter in Cádiz Province arrived from more than 1000 km away (Table 1). However, the relative contribution of these birds changed over time: despite the fact that the number of controlled birds increased from 2000 onwards, the presence of extra-Iberian birds showed a sharp decline.

Trends of environmental conditions for breeding birds

The forests occupied by resident robins changed between 1999 and 2012. In this period, forest management led to a decrease in trunk density and shrub cover species and an

Table 1. Distribution of ring recoveries (n) according to periods and the distance covered by robins between the wintering grounds in Cádiz province (southern Spain) and the ringing localities.

Period	Local robins	Migratory robins	Total	% migrants
1959–1970	4	44	48	91.67
1971–1999	19	62	81	76.54
2000–2009	193	2	195	1.02
Total	216	108	324	50.00

increase in grass cover. Forest management did not affect tree cover or the main fruit-producing shrubs (wild olives and mastics; Table 2). The reaction of robins to the most dramatic changes in vegetation traits differed among years. In 1999, robin abundance increased in areas with 20–50% shrub cover and sharply decreased beyond this limit suggesting the avoidance of close undergrowth (Fig. 4). In 2012, robins occurred in the most tree-covered stands (Fig. 4). Forward-backward stepwise multiple regression analyses were unable to detect any effect of the study variables on robin distribution in 1999. However, in 2012 robins were more abundant in the most tree covered sectors ($\beta = 0.73$, $F_{1,20} = 15.38$, $p < 0.001$) and in the less shrub covered stands ($\beta = -0.40$, $F_{1,20} = 4.65$, $p < 0.043$; model: $R^2 = 0.44$, $F_{2,20} = 7.80$, $p = 0.003$). Combining the two study periods, robin abundance was strongly affected by the effect of year ($F_{1,43} = 34.16$, $p < 0.001$) and tree cover ($\beta = 0.29$, $F_{1,43} = 7.42$, $p = 0.009$; model: $R^2 = 0.51$, $F_{1,43} = 22.61$, $p < 0.001$).

During the study period, August temperatures increased moderately ($p < 0.01$) in the mean (from 21.5°C to 24.9°C; OMS = 1.0085, SE = 0.0024) and maximum temperatures (from 23.1°C to 28.1°C; OMS = 1.0120, SE = 0.0028, Fig. 3).

Numerical trends of breeding robins

The breeding population of robins in Campo de Gibraltar showed sharp inter-annual changes (repeated measures ANOVA, year: $F_{6,132} = 11.21$, $p < 0.001$). During the period 1999–2008 (we used a period similar to that used for winter counts to compare the trends), robin abundance showed a significant decline ($p < 0.01$) with OMS = 0.9263 (SE = 0.0125, Fig. 5). This means that the population breeding in Campo de Gibraltar in 2008 was around 45% of the initial population in 1998.

Table 2. Changes in forest structure and species composition (mean ± SE) between 1999 and 2013. Results of repeated measures ANOVA for the study variables are also reported.

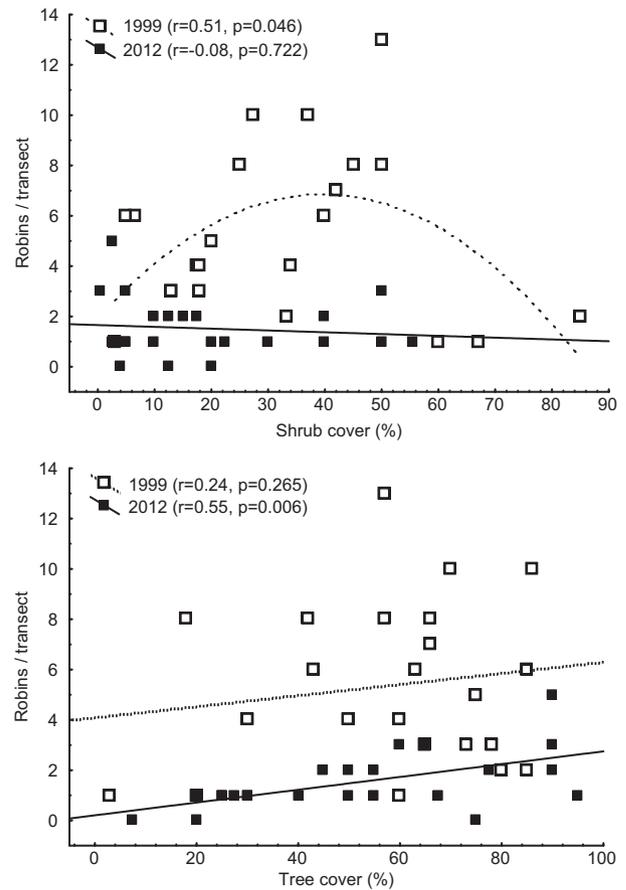|	1999 (n = 23)	2013 (n = 23)	$F_{1,22}$	p
Grass cover (%)	17.23 ± 3.60	41.07 ± 5.06	19.24	< 0.001
Shrub cover (%)	31.95 ± 4.36	18.83 ± 3.58	5.99	0.023
Tree cover (%)	57.91 ± 4.75	51.74 ± 5.46	1.60	0.220
Trunk density (no. per sample)	38.05 ± 5.69	20.54 ± 3.46	7.51	0.012
Quercus canariensis (%)	30.49 ± 6.39	24.83 ± 6.40	0.05	0.824
Quercus suber (%)	27.03 ± 4.28	24.28 ± 4.15	0.55	0.468
Olea europaea (%)	1.83 ± 0.56	2.21 ± 0.82	0.01	0.947
Pistacia lentiscus (%)	0.14 ± 0.11	0.80 ± 0.53	0.93	0.344

Figure 4. Relationship between robin abundance and shrub and tree covers. Dashed and solid lines represent the best regression adjustments (linear or polynomial) for the first (1999) and second (2012) study years.

Discussion

Changes in the carrying capacity of the area during winter

The most significant change in winter conditions in Campo de Gibraltar was related to a moderate decrease in temperature, which could affect the thermoregulatory balance of wintering robins. Winter temperatures are usually below the thermo-neutral zone for small birds (situated between 20–30°C; Calder and King 1974; Fig. 3). This produces behavioral changes in birds because they feed more actively to cope with thermoregulatory requirements (Gosler 2002, Krams et al. 2010). Alternatively, they may avoid colder situations by selecting warmer or sunnier areas at different spatial scales (Root 1988, Cresswell et al. 2009, Carrascal et al. 2012). Thus, if food supply is insufficient to cope with increasing food requirements related to temperature drops, birds could be compelled to leave the area. Results from this study do not suggest any strong interaction between cold weather and food availability able to produce a sharp decline in the suitability of this wintering area. The temperature decline was relatively small and, more importantly, was within the range of mild conditions when compared to northern areas where many robins remain in winter (Cramp 1988). In addition, the potential effect of the temperature drop could
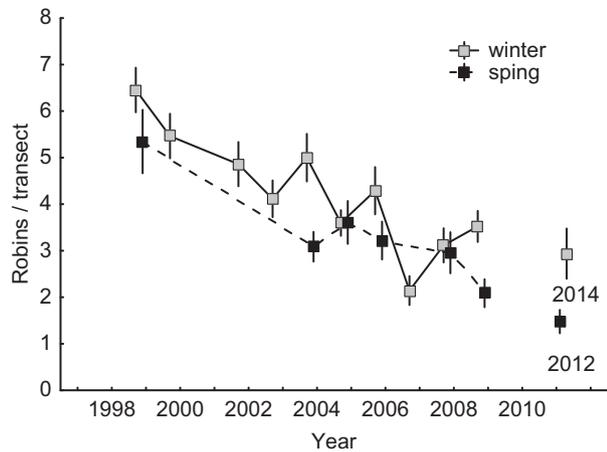
Figure 5. Mean numerical trends of breeding robins (± SE) in the study area in relation to the patterns depicted during the winter. The scores reported in controls during spring and winter (2012 and 2014) are also reported.

be buffered by the moderate increase in fruit availability and the related facilities to meet thermoregulatory requirements (Kwit et al. 2004; Fig. 2). It is important to emphasize that the fruit available for birds in Mediterranean scrublands and woodlands in southern Spain is highly energetic (e.g. wild olives and mastic fruits are among the most energetic fruits, Herrera 1987) and usually exceeds the food requirements of wintering birds (Hampe 2008, Tellería et al. 2013). It can thus be presumed that the drop in temperature is insufficient to explain the steep decline in the winter robin population in Campo de Gibraltar.

Reduction of the resident robin population

The results indicate a sharp reduction in the breeding population of the robin in Campo de Gibraltar. The most noticeable change affected the structure of forests where robins breed. These forests have been managed to reduce undergrowth and to improve grass cover and the growth of cork and Algerian oaks (Table 2). These are targets of the management regulations of Parque Natural de los Alcornocales, which also include the conservation of fruit-producing shrubs in isolated patches within the forest (Junta de Andalucía 2004). As a result, the changes in the forest did not affect tree cover or fruit-producing shrubs (wild olives and mastics). Because, according to our results, tree cover is a main correlate of robin abundance in spring (Fig. 5) and fruit availability is the main correlate of robin abundance in winter (Tellería et al. 2008), changes in forests do not suggest constraints on resident robins over the course of the year. In addition, according to robin preferences in spring 1999, shrub reduction in densely covered areas benefited the species (Fig. 4), a trend also shown in other dense Mediterranean woodlands (De la Montaña et al. 2006). The robin has been reported as a forest generalist (Díaz 2006) able to tolerate intermediate levels of clearing and thinning in Mediterranean forests (Camprodon and Brotons 2006) such that the forest changes reported in this study do not explain the sharp decline in this population (Fig. 4). However, this does not exclude the possibility that undergrowth clearing led to

changes in the microclimate of the otherwise humid, dense oak forests suitable for this hygrophylic species (Camprodon and Brotons 2006).

Our results show a significant increase in summer temperatures in Campo de Gibraltar, a trend related to global warming in the Mediterranean region (Solomon et al. 2007). These changes may induce structural changes in Mediterranean habitats, including the retreat of moist forests (e.g. the study cork oak and Algerian oak woodlands, de Dios et al. 2009), and the regional extinction of related species (Carnicer et al. 2011, Jiguet et al. 2011). In the Iberian Peninsula, forest occupation by robins is mainly related to moist conditions (Tellería and Santos 1994), which suggests that summer environmental moisture could determine a threshold of habitat quality for the species. In fact, the ground runs dry in Mediterranean environments as the summer progresses (Joffre and Rambal 1993) causing a decrease in the primary production of pastures that limits the availability of invertebrates in both soil and grass (Herrera 1981, Mooney 1981). It has been suggested that because robins feed principally upon ground invertebrates (Cramp 1988), the need for a high soil moisture throughout the breeding season could constrain their distribution in a gradient of increasing dryness. In fact, former studies in Campo de Gibraltar have suggested that the harshness of summer conditions, probably due to the effect on food availability, may actually be a major proximate determinant of changes in condition and mortality of juvenile robins (Pérez-Tris et al. 2000). Thus, it may be presumed that global warming, through changes in environmental conditions of the breeding habitat during summer, could be a putative cause of the decline of the robin population in this marginal area of the species' range where the European robin seems to face increasingly unsuitable conditions.

Reduction in the number of foreign individuals

This study suggests that the resident population plays a main role in the decline of wintering robins in Campo de Gibraltar and discards the depletion of the suitability of the area for wintering birds as a credible reason to explain this trend. However, these results also support the hypothesis that foreign immigrants do not play a major role. This assumption is supported by the evident inability of migratory birds to buffer the decline of resident populations in a context of an overall increase of European robin populations (European Bird Census Council <www.ebcc.info/>). It has been suggested that densities in wintering grounds tend to magnify the trends of breeding populations through the effect of recruited juveniles and due to crowding in the most suitable habitats (Terborgh 1980). This occurs in the wintering grounds of the Iberian Peninsula where robins gather in suitable Mediterranean woodlands and scrublands in the warmest areas (Tellería et al. 1999). However, the numerical trend of the wintering population was similar to that observed in the breeding population (Fig. 5) suggesting a lack of buffer effects by foreign individuals. More explicitly, it suggests a constant numerical contribution of foreign birds over the years or, alternatively, a similar reduction of these birds in this wintering area. This last interpretation is supported by ring recovery trends, with a decreasing

number of foreign birds over the last decade despite the increasing numbers of winter records and the increasing ringing activity in recent years in Spain and Europe (European Union of Bird Ringing: <www.euring.org/>). The absolute lack of foreign birds (with just two reports) strongly supports a strong reduction in extra-Iberian birds in this wintering area.

Conclusions

The results reported here provide the first empirical evidence of the numerical weakening of the wintering and breeding populations of a bird species in the Mediterranean region. The changes are consistent with the hypothesis that climate warming is changing the role of the Mediterranean region as a wintering ground for birds and, interestingly, also support current ideas on the vulnerability of some southern bird populations to global warming (Santos and Tellería 1995, Cuervo and Møller 2013). While this process should be tested in other populations, species and areas, these results demonstrate the ability to report significant changes in bird biology and distribution over short time periods in critical areas and should encourage researchers to promote intensive monitoring programs for target populations (Lehikoinen et al. 2014).

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