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The road to opportunities: landscape change promotes body-size divergence in a highly mobile species

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Abstract

Landscape change provides a suitable framework for investigating population-level responses to novel ecological pressures. However, relatively little attention has been paid to examine the potential influence of landscape change on the geographic scale of population differentiation. Here, we tested for morphological differentiation of red-necked nightjars *Caprimulgus ruficollis* breeding in a managed property and a natural reserve situated less than 10 km apart. At both sites, we also estimated site fidelity over 5 years and quantified the potential foraging opportunities for nightjars. Breeding birds in the managed habitat were significantly larger in size—as indexed by keel length—than those in the natural one. However, there were no significant differences in wing or tail length. Immigration from neighboring areas was almost negligible and, furthermore, no individual (out of 1130 captures overall) exchanged habitats between years, indicating strong site fidelity. Food supply for nightjars was equally abundant in both habitats, but the availability of foraging sites was remarkably higher in the managed property. As a result, nightjars—particularly fledglings—in the latter habitat benefited from increased foraging opportunities in relation to those in the natural site. It seems likely that the fine-scale variation in nightjar morphology reflects a phenotypic response to unequal local conditions, since non-random dispersal or differential mortality had been determined not to be influential. High site fidelity appears to contribute to the maintenance of body-size differences between the two habitats. Results from this nightjar population highlight the potential of human-induced landscape change to promote population-level responses at exceedingly small geographic scales.

Key words: human-induced environmental change, morphology, phenotypic divergence, philopatry, population differentiation.

Human activities may have a severe impact on the direction and strength of selection pressures and, therefore, are an increasingly common influence on the evolutionary trajectories of natural populations (Hendry et al. 2008; Palkovacs et al. 2012). Human-induced landscape change often puts organisms into novel ecological environments that typically induce rapid changes (i.e., at the level of a human life span) in the phenotypic traits of natural populations (Palumbi 2001; Hendry et al. 2008). Although less obvious, human activities may also reduce the spatial scale at which such trait changes occur (see Richardson et al. 2014). Thus, landscape change

can induce spatial isolation through potential barriers to dispersal (Harris and Reed 2002; Bertrand et al. 2013) and/or enhance the diversifying effects of environmental heterogeneity (Franssen et al. 2013). Ensuing fine-scale geographic variation in ecological pressures may then promote population differentiation at exceedingly small geographical scales (Garant et al. 2005; Shine et al. 2012). Human-induced landscape change, therefore, provides a suitable framework for understanding the spatial scale at which microevolutionary processes (e.g., selection, migration, population structure) occur.

Although analyzing population genetic structure in spatially heterogeneous environments is important for evaluating evidence for possible evolutionary changes (Garroway et al. 2013), the study of geographic variation in phenotypic traits is a valuable complementary approach to genetic procedures (Carrol et al. 2007; Lehtonen et al. 2009). Exploring spatial variation in individual morphology still remains essential for understanding local differentiation, as illustrated by the increasingly reported cases of fine-scale population structure (e.g., Shine et al. 2012; Camacho et al. 2013; McDevitt et al. 2013; Arnoux et al. 2014; García-Navas et al. 2014; Langin et al. 2015). Long-term studies involving individually marked, highly mobile animals have demonstrated significant population differentiation resulting from phenotype-dependent (e.g., mass and body size) dispersal over short distances (1–25 km; e.g., Senar et al. 2002, 2006; Garant et al. 2005; Camacho et al. 2013). Nonetheless, spatial proximity does not inevitably result in increased dispersal and mixing of populations. Recent studies have shown that some species are highly reluctant to move over short distances despite high dispersal potential (Lukoschek and Shine 2012; Shine et al. 2012), while many others—typically habitat specialists—may be sensitive to potential dispersal barriers resulting from landscape change (Harris and Reed 2002; Lindsay et al. 2008). Spatial isolation resulting from restricted dispersal over short distances may lead to subdivision of natural populations into separate (nearby) units, and thus promote population differentiation at small spatial scales (Schluter 1998; Shine et al. 2012; Langin et al. 2015).

The red-necked nightjar (*Caprimulgus ruficollis*; henceforth nightjar) is a long-distance migratory bird inhabiting dry warm regions of Northern Africa and Southwestern Europe (Cleere 1999). Nightjars have multiple habitat requirements and, during the breeding season, they typically commute from nesting areas in open shrublands to diurnal roosts in shaded woodlands (Camacho et al. 2014), whereas they use roads for hunting flying insects at night (Jackson 2003). Breeding individuals rely, therefore, on highly heterogeneous landscapes facilitating nightjar access to all these three habitats (Camacho et al. 2014). Due to the general trend toward landscape homogenization, functionally different habitats are usually located some distance apart, and therefore nightjars may find it difficult to commute from diurnal roosts to nocturnal feeding grounds (Camacho et al. 2014). Thus, habitat availability and suitability for nightjars is reduced and they tend to be confined to small, non-continuous habitats in either natural or human-modified areas. As nightjar dispersal over short distances is typically restricted (Camacho 2014), subdivision of nightjar populations into separate units could lead to spatial isolation and thus promote population differentiation at a small spatial scale (e.g., Blondel et al. 1999; Bertrand et al. 2013). Exploring fine-scale variation in nightjar morphology seems, therefore, a promising approach to evaluate evidence for population differentiation and to assess the potential of human-induced landscape change to create microgeographic eco-evolutionary scenarios.

In this study, we estimated site fidelity and explored the patterns of divergence in morphological traits of nightjars over 5 years (>1,100 overall captures) at a managed property and a natural unmanaged reserve situated less than 10 km apart. Specifically, we predict that population clustering and ecologically novel conditions (e.g., shifts in food-related selective pressures) resulting from human-induced landscape change would have the potential to promote local population differentiation in nightjars, particularly because they have specialized habitat requirements and show modest movement propensities (i.e., restricted daily movements and high interannual site fidelity). To evaluate these predictions, we (1) examined divergence in morphological traits (e.g., skeletal body size and wing and tail length) that have been shown to be subject to selection in some avian species (Price and Boag 1987; Siepielski et al. 2009); (2) quantified foraging opportunities, as measured by aerial prey abundance and availability of foraging sites; and (3) assessed adult philopatry, individual exchange, and immigration from neighboring populations. Possible processes underlying morphological differentiation and strong philopatry are discussed.

Materials and Methods

We used data from an intensive study of nightjars inhabiting two close (< 10 km) but contrastingly managed areas in southwestern Spain during 2008–2012 (Camacho 2013). The Doñana Biological Reserve (37°0′N, 6°30′W) is a natural protected area dominated by well-preserved shrubland communities and pine forests. The managed property (37°8′N, 6°34′W) consists of a mosaic landscape of Mediterranean shrublands, cattle-grazed pastures, and plantations of orange and pine trees. In contrast with the natural reserve, where human access and activities are highly restricted, numerous access roads exist in the managed plot and resource exploitation (e.g., agriculture, forest tree crops, cattle raising, and hunting) are common activities. The two sites are separated by a mosaic landscape of intense agricultural and seminatural areas, including heterogeneous vegetation communities and scattered human developments (Figure 1).

Field procedures

From August to October 2008–2010 and from April to October 2011–2012, we conducted weekly transect counts of road-sitting nightjars along two 24-km and 11-km roads crossing the managed and the natural area, respectively. During these transects, we captured individuals using a flashlight and a handheld net (Camacho et al. 2014). To assess the movement patterns of nightjars at a regional scale (i.e., dispersal beyond the study areas), we conducted additional capture sessions of individuals within a 10-km buffer of both study sites, including intervening roads connecting both areas. All individuals were uniquely marked with numbered metal rings, and sexed and aged following criteria described by Forero et al. (1995). Adult individuals were measured for keel length ($\pm$ 0.01 mm), a reliable predictor of avian skeletal size (Senar and Pascual 1997). Tail length and wing chord ($\pm$ 0.1 mm) were measured following Svensson (1992). All measurements were taken by CC, SP, PS and CM after standardization to ensure consistency, and were moderately (wing) to highly (keel) repeatable ($r_{keel} = 0.79$; $r_{tail} = 0.67$, $r_{wing} = 0.42$, P values < 0.001; Lessells and Boag 1987). Only individuals that were not molting wing or tail feathers were used in this study. To reduce the likelihood of inclusion of foreign individuals, we omitted from analyses those nightjars that were only recorded beyond mid August (i.e., potential fall migrants), and only
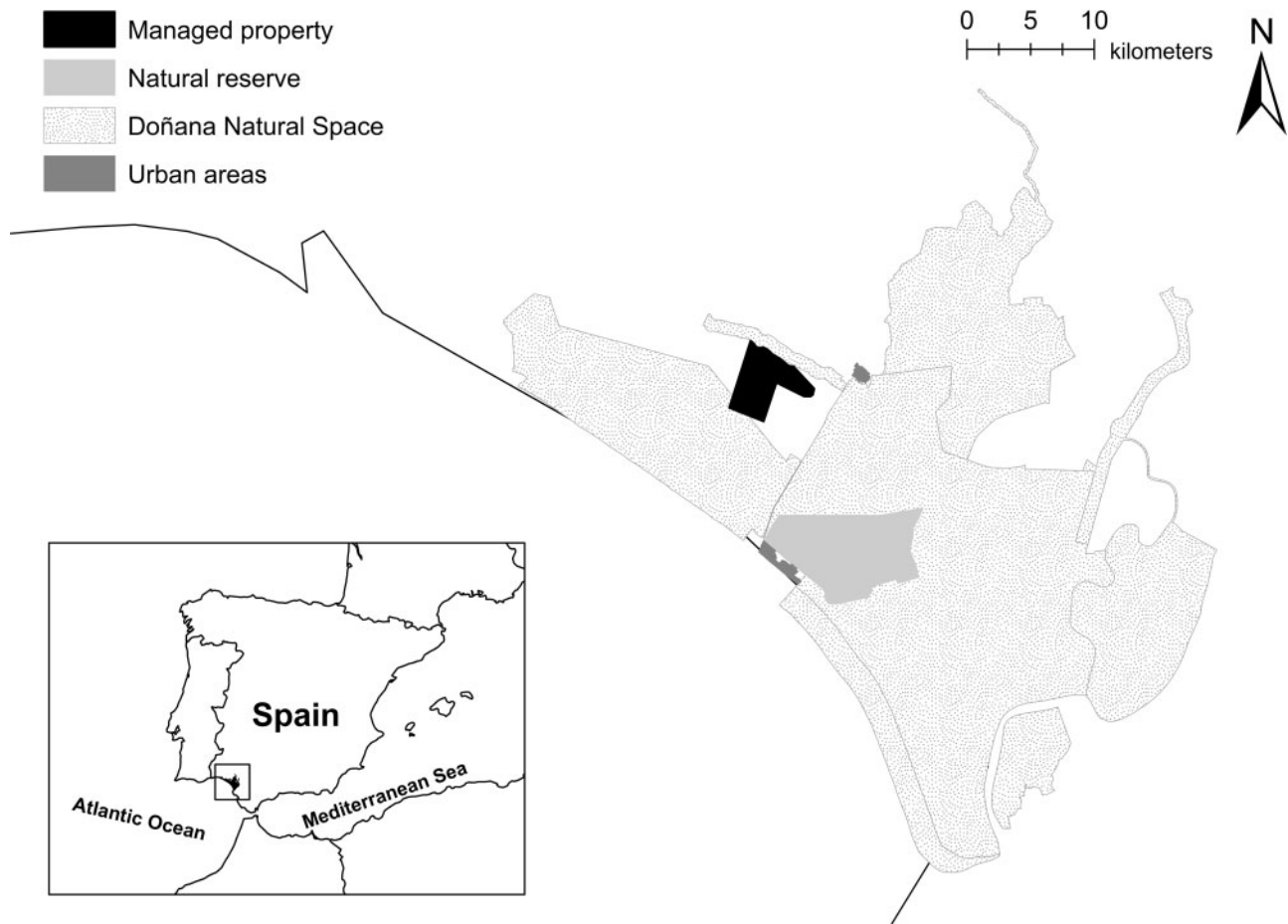
Figure 1. Geographical situation of the study area in southwestern Spain and location of the 2 main study sites (managed property and unmanaged, natural reserve) relative to surrounding and intervening areas.

considered males or females that were captured throughout the breeding season and showed any sign (brood patch) of a recent breeding attempt (i.e., local individuals; Camacho 2013).

Availability of prey and foraging sites

Food availability for nightjars was quantified over a 5-week period beginning in early June 2011. To determine levels of aerial prey biomass, we sampled flying insects at roughly 10-day intervals by driving a vehicle at a constant speed of 40 km/hr along a 4-km road transect with a roof-mounted tow net (50×50-cm entrance, 2-m length, and 0.5-mm mesh size; Jetz et al. 2003). Because seasonal fluctuations in prey availability for nightjars are common (Jetz et al. 2003; Ashdown and McKechnie 2008), paired food samplings at the two study sites were conducted on two consecutive nights, and the sampling order was reversed from night-to-night. All invertebrates were sorted to the level of order, counted, and weighed pooled to the nearest 0.01 mg. Only the orders Lepidoptera, Homoptera, and Neuroptera were considered to be potential prey for nightjars (Jackson 2000a, 2000b; Camacho 2013). Relative food availability was calculated as the prey biomass collected in the tow net during the transect divided by the volume of filtered air. Roads are the main foraging habitat of nightjars in our study area (Camacho et al. 2014) and possibly elsewhere (Jackson 2003), so overall availability of foraging sites was quantified as the surface covered by roads within each study site (Camacho et al. 2014). To measure the width and length of gravel and paved roads crossing each study area, we used the ArcGIS10 software and a high-resolution (0.5 m) orthophotograph.

Statistical analyses

To test for differences in morphology of nightjars between habitats, we used General Linear Mixed Models (GLMMs; normal errors, identity link function), including keel length, tail length, and wing chord as the response variables. Habitat, sex, and their interaction were included as fixed effects in all the three models. Keel length was also included as a covariate in wing and tail length analyses to control for body-size dependent variation in both traits (Green 2001). Individual identity and year (class variables) were always entered in the models as random effects to account for repeated measures of the same individuals and annual heterogeneity in environmental conditions. Visual inspection of a q–q plot and a scatterplot of the residuals plotted against fitted values revealed no obvious deviations from the assumptions of normal distributions and homogeneity of residuals. GLMMs were fitted in R 2.14.0 (http://www.R-project.org) using the function *lmer* in the package 'lme4' (Bates et al. 2011). The significance of the full model was established using a likelihood ratio test (R function *anova* with argument test set to 'Chisq') comparing it to the null model (excluding interactions). To obtain *P*-values, we fitted the models using maximum likelihood (Bolker et al. 2009). *P*-values for the individual

effects were based on Markov Chain Monte Carlo (MCMC) sampling (10,000 iterations) and derived using the function *pvals.fnc* in the package 'languageR' (Baayen 2011). Besides the GLMM, we used a recently developed approach to estimate the 'exchangeability' of individuals among populations by means of classification analyses (Hendry et al. 2013). Briefly, this method uses the full distribution of a particular trait or group of traits to estimate the probability of classification of individuals into each sampled population as a measure of similarity between populations (Hendry et al. 2013). To evaluate exchangeability for the three measured morphological traits, we used discriminant function analyses (DFAs).

To analyze differences between areas in food availability, we used a Generalized Linear Model (GLM; log link function) with a zero-inflated negative binomial distribution to account for overdispersion caused by excess zeros and potential effects of small sample sizes (Zuur et al. 2009). Relative food availability was used as the response variable, and habitat type, sampling period (scaled variable) and their interaction were included as fixed effects to assess whether between-habitat differences in prey abundance were stable over time and in space. To control for the potential effect of intraspecific competition on food availability, the (log-transformed) abundance of nightjars along roads at the time food sampling was conducted was also included in the model as an offset term. The GLM was fitted using the function *zeroinfl* in the package 'pscl' (Jackman 2007).

Results

Nocturnal surveys between 2008 and 2012 (176 trap nights) resulted in 1,130 captures of nightjars at the two study sites (898 and 232 total captures in the managed and the natural area, respectively) and 55 additional captures in the buffer areas, belonging to 791 different individuals (1–8 captures per individual, with 35% of individuals being captured ≥ 2 times). The interval between successive captures ranged from 0 to 3 years, with 40% of recaptures occurring in the year following that of initial capture.

Fidelity to breeding sites
In the managed area, a total of 577 breeding nightjars were marked and all but 2 of them had been first caught and released there. Foreign individuals were 2 adult females first captured in neighboring areas, 6.6 km NE and 4 km W from the managed site (737 and 54 days earlier, respectively). In the natural area, we marked 159 breeding nightjars and the only foreign recapture was an adult male that had been first released 1,052 days earlier 3.6 km W of the natural site. Although all these foreign birds came from nearby areas, none of their capture sites were located along the route between the 2 study areas. Furthermore, not a single marked bird changed areas between years, indicating that site fidelity was very high in the two populations.

Divergence in morphological traits
Overall, 275 breeding individuals (195 and 80 in the managed and the natural area, respectively) were measured in 359 occasions. Despite the sites' close proximity, nightjar distribution across them was not random with respect to phenotype. Local breeders from the managed habitat were significantly larger than those from the natural site, as indexed by keel length (mean $\pm$ SD = 32.70 $\pm$ 1.03 *vs.* 32.34 $\pm$ 1.19 mm; estimate $\pm$ SE = -0.21 ± 0.16, $P_{MCMC} = 0.02$; Figure 2), whereas body size did not differ significantly between the sexes in either area (-0.03 ± 0.15, $P_{MCMC} = 0.56$). Nightjars

showed strong sexual dimorphism (males > females) in wing (208.5 $\pm$ 3.9 *vs.* 207.4 $\pm$ 3.8; sex: -1.32 ± 0.47, $P_{MCMC} = 0.002$; body size: 0.26 $\pm$ 0.17, $P_{MCMC} = 0.01$) and tail length (159.7 $\pm$ 4.7 *vs.* 156.1 $\pm$ 4.4; sex: -3.43 ± 0.54, $P_{MCMC} = 0.0001$; body size: 0.22 $\pm$ 0.19, $P_{MCMC} = 0.057$) relative to body size, but these traits did not differ significantly between areas (wing: -0.1 ± 0.51, $P_{MCMC} = 0.85$; tail: -0.01 ± 0.6, $P_{MCMC} = 0.85$). Full null model comparisons (Chi sq tests, all $P > 0.7$) revealed that all measured traits varied to a similar degree in both populations; the non-significant interaction between area and sex was, therefore, removed from all the final models. DFAs testing for differences between the two populations in the three above mentioned traits gave similar results (i.e., significant differences in keel length only; data not shown). Exchangeability (misclassification) analyses for keel length showed that 72.6% of individuals were correctly classified into the population they originated from, and that 71.5% were accurately cross-classified between populations, indicating low misclassification. To summarize, breeding nightjars in the managed habitat were significantly larger than those in the natural site and, although they are not sexually dimorphic in skeletal body size, males in both areas have more wedge-shaped wings (i.e., they are larger relative to body size) and longer tails than females.

Availability of prey and foraging sites
Relative food availability for nightjars was not significantly different over time in both study sites (area, $Z = 0.34$, $P = 0.72$; period, $Z = 0.89$, $P = 0.37$; area*period, $Z = 1.50$, $P = 0.13$; $n = 20$ counts). However, as a result of the construction of access roads into the managed area, the availability of preferred foraging sites for nightjars was remarkably higher therein (14.1 ha, 0.7% of the total surface) than in the natural site (8.39 ha, 0.2% of the total surface). Therefore, with an equal food supply, the higher availability of foraging sites in the managed property translates into increased foraging opportunities for nightjars breeding therein in relation to those in the natural reserve.

Discussion

We have shown that the spatial distribution of nightjars across contrasting, nearby ($\sim$ 10 km) habitats is non-random with respect to body size, with both males and females being significantly larger in the managed area than in the natural site. Results derived from the exchangeability analyses is compared favorably with those obtained via conventional approaches. Morphological differentiation at small spatial scales has been extensively documented in sedentary bird species (e.g., Blondel et al. 1999; Senar et al. 2002; Chan and Arcese 2003; Garant et al. 2005; Bertrand et al. 2013; Garroway et al. 2013; Arnoux et al. 2014; García-Navas et al. 2014) and, although less commonly (Walsh et al. 2012; Camacho et al. 2013), also in migrants. However, regardless of migratory status, a difference in size close to that of nightjars (1.1%) has rarely been reported at spatial scales comparable to that of our study system (< 10 km, 0.52–0.86% difference; Senar et al. 2002; Camacho et al. 2013; García-Navas et al. 2014).

Non-migratory caprimulgids show strong breeding-site fidelity (Jackson 1985; Doucette 2010), and our results indicate that both natal (Camacho 2014) and breeding (this study) philopatry in the migratory red-necked nightjar are also extremely high. Although nightjars are capable of flying long distances (e.g., from breeding to wintering quarters), they seldom venture far from their hatching site (Camacho 2014). It is possible that selection against long-distance
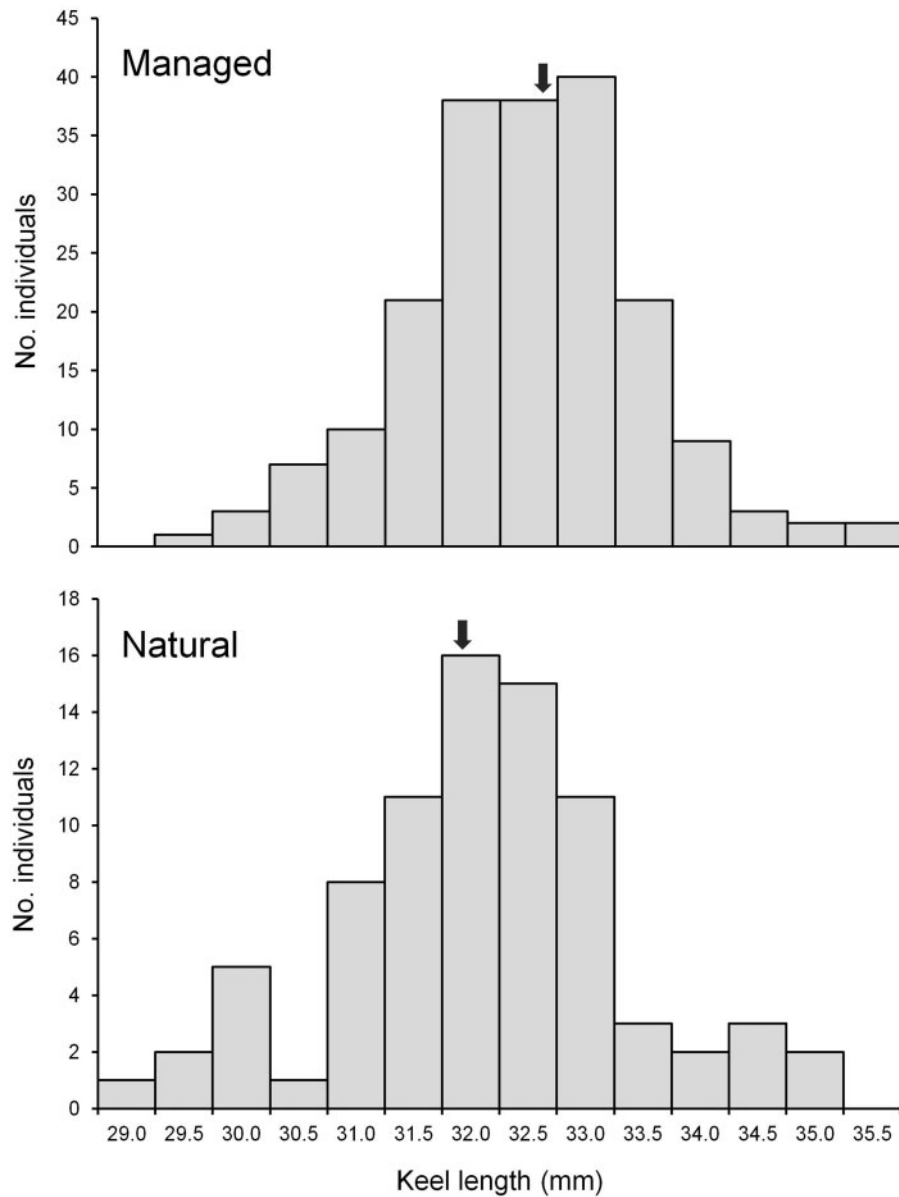
Figure 2. Body size (keel length) distribution of adult red-necked nightjars breeding in 2 close but contrastingly-managed areas. Males and females are pooled together, since no sex differences were observed. Arrows indicate mean values.

dispersers leads to reduced propensity to disperse (Komdeur et al. 2004). However, this seems unlikely since long-distance dispersal in our study population seems an extremely rare event (natal dispersal distances: 0.8–2.2 km; Camacho 2014). Alternatively, strong philopatry might have been driven by conspecific attraction (Stamps 2001), as population density in our study area is moderate to high (0.5–4 birds/10 ha). Another—and mutually non-exclusive—hypothesis is that high site fidelity may have been favored to some extent by the good foraging and nest-site opportunities for nightjars in the study area (Camacho 2013). In addition, landscape structure at the regional scale area might have been influential. Propensity to disperse usually depends on species attributes (e.g., behavior; Bertrand et al. 2013), so that habitat specialists tend to be more sensitive to potential dispersal barriers resulting from landscape change than do habitat generalists (Harris and Reed 2002; Lindsay et al. 2008). In this way, nightjars dispersing away from their natal area may fail to

find breeding sites of suitable quality in the unsuitable human-dominated areas separating the 2 study sites, thereby promoting philopatry.

Several non-mutually exclusive hypotheses can be formulated to explain the body-size divergence of nightjars, namely (1) phenotype-dependent dispersal, (2) microevolution, (3) differential size-dependent mortality (i.e., selection), and (4) phenotypic plasticity in response to resource availability. Below we address each of these possible explanations to the nightjar size differences we found.

Some recent studies have convincingly shown that phenotype-dependent dispersal between nearby (within 1–25 km) populations is as major driver of small-scale differentiation (e.g., Senar et al. 2002; Garant et al. 2005; Shapiro et al. 2006; Bolnick et al. 2009; Camacho et al. 2013), a finding that is in marked contrast to ours. Despite their close proximity, connectivity through dispersal between the managed and the natural area seems to be limited, as

evidenced by the fact that no individual has apparently changed sites during our 5-year study. Misclassification analyses also supported a limited connectivity between these nightjar populations, as low exchangeability levels suggest that gene flow is likely restricted (Hendry et al. 2013). Such a limited connectivity between closely adjacent areas might, however, contribute to maintaining the microgeographic structure of this nightjar population with respect to body size (Nosil 2009; Shine et al. 2012).

Although restricted dispersal and gene flow over short distances does not always lead to population structure (Alcaide et al. 2009), it often leads to spatial isolation (Shine et al. 2012; Bertrand et al. 2013), and hence may drive microevolutionary change through genetic drift or heterogeneous local selection pressures (reviewed in Richardson et al. 2014). Both processes have been repeatedly advanced to explain population divergence at fine spatial scales in a number of bird species (e.g., Blondel et al. 1999, Blondel and Charmentier 2006, García-Navas et al. 2014; Bertrand et al. 2013; Garroway et al. 2013), and could underlie the body-size divergence of nightjars as well. For example, differential mortality of either the smallest individuals in the managed area or the largest ones in the natural reserve could bias the body-size distribution of nightjars and thus influence population structure (Shapiro et al. 2006). We think unlikely that the morphological differentiation is due to selection, as the survival of adults is unaffected by their skeletal size in either habitat (authors' unpublished results from CMR models). Alternatively, increased population density in the managed area may have led to increased intraspecific competition, selecting for a larger size of nightjars in the managed than in the natural area. If this were the case, we could expect displaced, competitively inferior individuals to disperse away of the area. However, as explained above, size-dependent dispersal does not seem to occur in this system.

Landscape changes induced by humans have been shown to drive population structure in several bird species (e.g., Caizergues et al. 2003; Martínez-Cruz et al. 2004; De León et al. 2011), and might also underlie the morphological differentiation in adult nightjars. Food supply is apparently homogeneous across the study area, but the availability of foraging sites (i.e., typically roads; Jackson 2003; Camacho et al. 2014) increased noticeably in the managed area after the construction of the road network. Moreover, roads increased landscape connectivity, leading to better access to foraging areas, particularly for the nearly flightless nestlings (Camacho et al. 2014). Environmental constraints experienced during early development may, therefore, be different for nightjars reared in the managed and the natural area, which would affect nestling growth and ultimately determine adult size (Lindström 1999; Monaghan 2008). Along this line, a cross-fostering study found strong environmental effects on nestling size and condition (Shapiro et al. 2006), suggesting that constraints during early development are reliable correlates of body-size divergence between nearby populations (Aubret and Shine 2007). Recently-hatched nightjars are capable of moving short distances (< 20 m; Aragonés 2003), but dependence on parental food provisioning actually extends well beyond fledging (Camacho 2013). During the night, nestlings in the managed area typically move to roads located in the nest periphery, where they are visited by their parents in close succession (Camacho 2013). However, in nesting areas located far apart (>1 km) from roads, as usually occurs in the natural site, nestlings would presumably be poorly provisioned compared to those in the managed area, where proximity of nests to roads is high (< 300 m; Camacho et al. 2014), young are therefore more commonly found on roads (214 *vs.* 20 fledglings captured in the managed and the natural area, respectively, during the

course of car transect counts in 2008−2012) and adults typically take shorter turns to feed young (CC, SP pers. obs. of radiotagged nightjars). Thus, landscape change would ultimately lead to increased food intake and growth rates of nestlings in the managed area, and there they would attain larger adult sizes therein in relation to those in the natural site (Lindström 1999; Shapiro et al. 2006).

Markedly contrasting foraging opportunities for young nightjars in either study area lend support to the hypothesis that the observed fine-scale variation in body size reflects a phenotypic response to changes in the landscape (Caizergues et al. 2003) rather than contemporary evolution resulting from genetic drift or natural selection (Blondel et al. 1999; García-Navas et al. 2014). Nevertheless, in the absence of genetic data or experimental manipulation of rearing conditions, the latter cannot be ruled out (Ballentine and Greenberg 2010). Caution is also required in extending our results to other disturbed and undisturbed sites, as our sampling is limited to one managed and one natural area.

To summarize, we have shown that the spatial distribution of adult nightjars inhabiting nearby human-managed and natural habitats is non-random with respect to body size despite the small spatial scale (∼10 km), and that nightjars exhibit strong philopatry even in the absence of any obvious barrier to dispersal, which might function to maintain phenotypic variation over time (Shine et al. 2012). Size divergence appears to reflect a phenotypic response to heterogeneous foraging opportunities for nestlings reared in the managed and the natural habitat, resulting from human-induced changes in landscape configuration. Nonetheless, additional alternative processes (e.g., genetic drift or local selection) could also account for the observed body-size variation. Further investigation is therefore needed (e.g., a test for genetic differences) to aid in disentangling the exact process(es) driving the observed pattern. Although fine-scale variation in phenotypic traits may occur in both human-modified and more natural environments, results from this nightjar and many other vertebrate populations (e.g., Hendry et al. 2008; Marnocha et al. 2011; McDevitt et al. 2012; Franssen et al. 2013) suggest that morphological differentiation may be particularly common and/or abrupt in response to anthropogenic disturbance.

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