

Goats, birds, and emergent diseases: apparent and hidden effects of exotic species in an island environment

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Abstract. Exotic species can have devastating effects on recipient environments and even lead to the outbreak of emergent diseases. We present here several hidden effects that the introduction of goats has had on the Lesser Short-toed Lark, *Calandrella rufescens*, the commonest native bird inhabiting the island of Fuerteventura (Canary Islands). Vegetation structure varied with grazing pressure, and indeed, vegetation was all but eradicated from the locality with greatest goat densities, which was also where the lowest density of Lesser Short-toed Larks was recorded. The impact of habitat impoverishment, however, was partially compensated for by changes in the foraging behavior of birds, which benefited from the abundant food provided to goats on farms. Capture–resighting methods showed that birds visiting farms outnumbered the estimates for birds obtained in the surrounding natural habitat, suggesting that there was recruitment from a much larger area. Stable isotope analyses of feathers indicated that island birds feed largely on the maize supplied at goat farms, showing poorer body condition than birds from populations not associated with farms (peninsular Spain and Morocco). Moreover, larks from Fuerteventura had a very high prevalence of poxvirus lesions compared with other bird populations worldwide and may increase the risk of contracting the disease by feeding on farms, where they aggregate and coexist atypically with domestic birds. The island birds also had lower average productivity, which may be the consequence of the emergent disease and/or the poor nutritional state resulting from feeding on a low-protein diet. Diseased and non-diseased birds from Fuerteventura showed similar body condition and annual survival rates. However, the isotopic traces of $\delta^{13}\text{C}$ indicate that the diet of diseased birds was more uniform than that of non-diseased birds, being based on food from goat farms. Our results show how the combination of species frequently introduced onto islands (goats, poultry, and associated pathogens) can create ecological traps for native species that are not always easy to identify. Moreover, we stress that nutrition and infectious diseases are important determinants of the well-being and dynamics of animal populations, and thus health research must be included in the design of monitoring programs and conservation strategies.

Key words: avian poxvirus; *Calandrella rufescens*; ecological trap; foraging behavior; Fuerteventura, Canary Islands; Lesser Short-toed Larks; nutrition; overgrazing; survival rates.

INTRODUCTION

A wide array of anthropogenic pressures including habitat loss, overexploitation, and the introduction of exotic species has been proposed as some of the principal causes of wildlife extinction (Diamond 1991, BirdLife International 2000). Problems such as habitat loss or overexploitation are in some way correctable, although not always easily (Coblentz 1990). However, exotic organisms, once established, frequently remain as permanent elements in their new ecosystems, constitut-

ing a potential threat to biodiversity (Clavero and García-Berthou 2005, Sax et al. 2007) and an important cause of global change (Dukes and Mooney 1999). In this sense, the introduction of species into areas outside their native geographic ranges can have devastating effects on recipient environments and economies, particularly when they invade islands (Coblentz 1990, Mack et al. 2000). These effects may be direct and operate via predation or competitive exclusion or indirect, for example when introduced species alter habitat composition or introduce new pathogens (Mack et al. 2000). More strikingly, introduced species can interact in multiple ways, making it difficult to distinguish and accurately identify how they are actually

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affecting native species (e.g., Mack et al. 2000, Gurevitch and Padilla 2004, Didham et al. 2007).

Exotic species often change the abiotic characteristics of the recipient ecosystem through their feeding or engineering activities (Mack et al. 2000). Domestic ungulates constitute a particular case of the introduction of nonnative species that have accompanied successive waves of human expansion and colonization (Biber 2002). Although their effects, positive or negative, on plant communities as a result of grazing are still debated (e.g., Tiver and Andrew 1997, Rambo and Faeth 1999, Hayes and Holl 2003), there is a general consensus that the introduction of domestic herbivores onto islands has had a disastrous impact, mainly due to the lack of a history of vertebrate herbivory in the evolutionary background of island plants (Bowen and van Vuren 1997, Donlan et al. 2002, Campbell and Donlan 2005). Goats are among the most destructive ungulates introduced onto islands (Kramer 1971, Coblentz 1978), and their introduction has had a widespread impact due to overgrazing, often leading to ecosystem degradation and biodiversity loss (Coblentz 1978, Campbell and Donlan 2005).

In comparison with habitat loss, infectious diseases have traditionally been considered as a minor problem for conservation. However, diseases can pose serious threats to endangered species, causing extinctions or local population decline (Daszak et al. 2000, Smith et al. 2006). Due to their narrow range distribution and small population size (Pimm et al. 1988), species endemic to islands can be driven to the brink of extinction by introduced parasites and diseases (van Riper et al. 1986, 2002, Milberg and Tyrberg 1993, McCallum and Dobson 1995) that often spread from domestic animals (Milberg and Tyrberg 1993, Wikelski et al. 2004, Gottdenker et al. 2005). Nevertheless, although diseases may represent serious extinction threats to small populations of endangered species, such threats are often identified only once epidemics reach extreme levels and result in severe population decline or local extinctions (McCallum and Dobson 1995). In this sense, emergent diseases, defined as those caused by parasites and pathogens that have (1) recently increased in incidence and occupied new host species or have altered their geographical range, (2) have been newly discovered, or (3) are caused by a newly evolved agent (Lederberg et al. 1992, Daszak et al. 2000, Smith et al. 2006), are but one important result of moving species into new areas. Such diseases are now a subject of intense study given their key role in the dynamics and therefore the persistence of wildlife populations (McCallum and Dobson 1995, Schrag and Wiener 1995, Daszak et al. 2000).

Fuerteventura is one of the seven main islands in the Canary archipelago in the Mediterranean Basin, an important biodiversity hotspot with one of the highest degrees of endemism per unit area in the world (Médail and Quézel 1999, Juan et al. 2000). Introduced goat

herds on the island have dramatically increased in recent years (from 20 000 individuals in 1970 to 118 000 in 2003; Palacios and Tella 2003) and have affected endemic island plant (Rodríguez-Piñero and Rodríguez-Luengo 1993, Gangoso et al. 2006) and bird communities (Osborne 1986, Illera 2001). At present, although there are some wild herds that move freely throughout the island, most goats are semi-stabled for milking and animals wander several kilometers around farms during the day but return to feed on maize and fodder (Gangoso et al. 2006). This high availability of food in these goat farms attracts endemic birds. The most common passerine species inhabiting the surrounding flat steppes is the Lesser Short-toed Lark, *Calandrella rufescens polatzeki* (Illera and Tella 2005), an endemic subspecies to the Canary Islands (Martín and Lorenzo 2001; see Plate 1). Although widespread throughout the island (Illera and Tella 2005), this species congregates in large flocks on farms to feed on the grain provided for goats and poultry. This unusual coexistence with domestic birds (chickens, pigeons, peafowl, ducks, and pet birds) seems to be responsible for the appearance of high numbers of native birds with proliferative signs of poxvirus (Smits et al. 2005) and thus constitutes a potential example of the indirect consequences of species introduction (Fig. 1c).

Avian pox is a mild to severe disease caused by DNA viruses of the family Poxviridae, genus *Avipoxvirus*, which has been reported worldwide in more than 230 avian species belonging to 23 orders (Bolte et al. 1999). Its transmission can occur through accidental introduction into a break in the skin or, more commonly, when vectored by a biting insect. This disease is most commonly characterized by proliferative cutaneous lesions, the most frequently observed form in passerine birds, that harden to thick scabs, although a diphtheritic or wet form with mucosal lesions within the digestive and upper-respiratory tracts also occurs (Gerlach 1999). Although its prevalence in wild populations is usually low (~1%), poxvirus epidemics have been proposed as threats or have even contributed to the extinction of endemic birds in island groups such as Hawaii or Galapagos (van Riper et al. 2002, Wikelski et al. 2004).

The aim of this paper was to analyze the direct and indirect consequences derived from the introduction of an exotic ungulate into an insular ecosystem, using the Lesser Short-toed Lark, a small steppe passerine, as a target species. As the effects of goats on native biota can be extremely complex, we used a multidisciplinary approach by combining results from habitat descriptors, diet (using stable isotope analyses), demography, and the monitoring of the health of individual birds. Specifically, we quantified the effects of goats on vegetation structure and bird abundance and then compared the virus prevalence, dietary composition, body condition, and demographic parameters of island birds with individuals of the same species from peninsular Spain and Morocco (where these larks

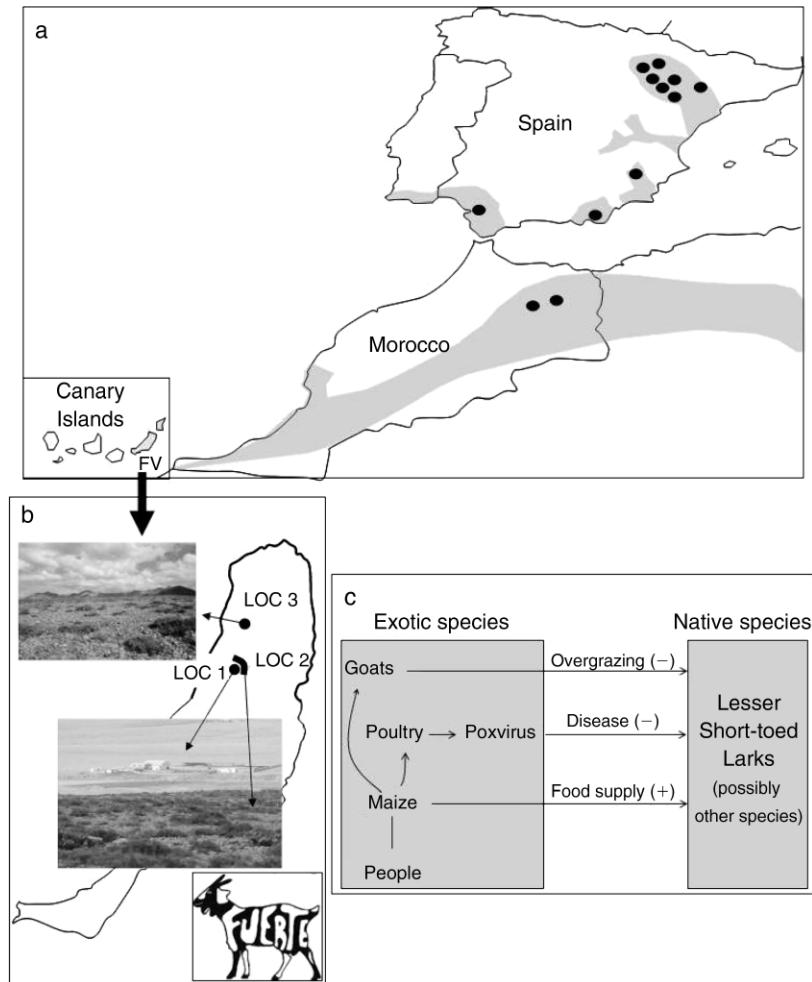


FIG. 1. Study areas (black points) in (a) peninsular Spain and Morocco and (b) Fuerteventura Island (FV). The distribution range of Lesser Short-toed Larks (*Calandrella rufescens*) is shown in light gray. Inset photographs show a general overview of habitats in each island study locality. Note overgrazing around a goat farm in LOC 1 vs. natural habitat in the neighboring LOC 2, which are just separated by a fence. (c) Study model showing the exotic (goats, poultry, poxvirus, and people) and native species (Lesser Short-toed Larks) involved as well as the expected effects of the former species on the latter.

inhabit natural habitats and are not associated with farms). We also made similar comparisons between diseased and non-diseased birds inhabiting Fuerteventura to assess the effects of virus infection at a within-population level.

METHODS

Study areas

Fieldwork was carried out on the island of Fuerteventura, peninsular Spain, and Morocco from 1998 to 2006 (Fig. 1a, b). Fuerteventura is the second largest island of the Canary Archipelago and the closest to the African mainland. Its topography is mostly low (200 m above sea level) and flat, with a maximum elevation of 807 m. Climatic conditions are predominantly arid or semiarid, with the scarce rainfall (150 mm/year) concentrated during autumn/winter months (Illera

2004). Three main flat habitat types can be distinguished in the island, namely sandy steppe, ground-stone steppe, and volcanic lands (Illera and Tella 2005). The vegetation is xerophytic and is dominated by sparse grassland and scrubland (Rodríguez et al. 2000). Study areas in peninsular Spain and Morocco included plains of variable size, topography, and climate, all of which were characterized by xerophytic or halophytic steppe vegetation (for a description see Laiolo and Tella 2005), the typical natural habitat of the Lesser Short-toed Lark (Serrano and Astrain 2005).

Field procedures

Effects of goat grazing on vegetation structure and lark densities.—We evaluated the effects of goat grazing on vegetation structure and bird densities at two complementary spatial scales. First, in the springs of 2002 and 2003 we conducted 72 transects (2 years \times 3 localities \times

12 transects) of 500 m each to compare vegetation structure and bird densities in areas with the same relief, soil, and potential vegetation structure that are subject to different grazing intensities (Fig. 1b). Locality 1 (LOC 1) was a 570-ha area of natural steppe vegetation enclosed by a fence with three goat farms situated inside; here the goats reached the highest densities of the three sites (3.93 animals/ha) and make use of the whole area for grazing. Locality 2 (LOC 2, 350 ha), with the lowest density of goats (0.11 animals/ha), was sited on the periphery of LOC 1 but was separated by the above-mentioned fence, which prevents a free flow of animals between the two localities (see bottom photograph in Fig. 1b). Finally, locality 3 (LOC 3, 625 ha) was 10 km from LOC 1 and held only a few free-ranging herds of goats, with a density of 0.28 animals/ha.

Secondly, during spring 2005 we conducted 151 transects randomly distributed throughout the whole distribution range of the Lesser Short-toed Lark on the island to determine vegetation structure and bird densities at a larger spatial scale. Since bird densities may vary between the three main habitat types, each transect was classified as corresponding to sandy steppe, ground-stone steppe, or volcanic land. Rugged terrain such as mountains and ravines that is not suitable for the species was not sampled (Illera and Tella 2005). Although we were unable to accurately measure goat densities in these 151 areas, goats were widespread across the island at different densities (L. Gangoso, unpublished data), and this large-scale sampling allowed us to confirm that the relationship between the level of vegetation deterioration and bird densities was not just a local phenomenon.

To measure vegetation structure, we established five sampling points at 100-m intervals along each transect. Around each point and within a radius of 25 m, we visually estimated the percentage of herb, shrub, and total vegetation coverage (e.g., Serrano and Astrain 2005) and also measured (to the nearest centimeter) the height of the four plants closest to the central point. To estimate bird densities, the same transects were performed by one person walking at a constant speed. To avoid underestimating bird densities, we did not count during the times when maximum numbers of birds were feeding on the goat farms (i.e., before 10:00; Fig. 2) or during the hottest part of the day (15:00–17:00). Apart from the circumstances described above, previous censuses had shown that the time of the day did not influence our ability to detect Lesser Short-toed Larks in the study area (J. C. Illera and J. L. Tella, unpublished data). All individuals were counted and attributed to one of two belts (nearest belt, <50 m; farthest belt, 50–100 m on each side of the transect line). The inner belt of 50 m was used because it performed better for this species than others (Illera and Tella 2005). Relative densities of birds (D) were estimated as $D = Nk/L$, where N was the total number of birds recorded in both the nearest and the farthest belts, L was the transect length, $k = (1 - ((1$

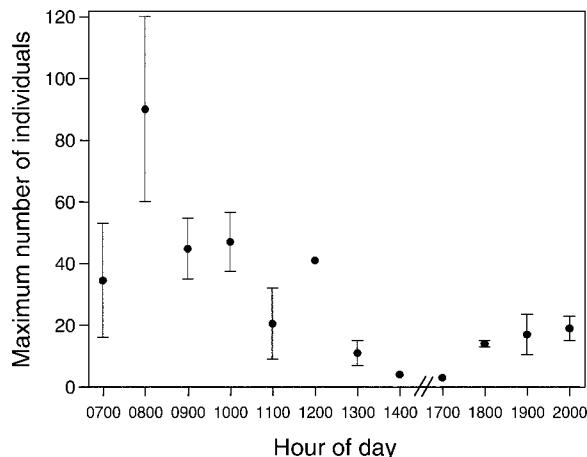


FIG. 2. Changes in the number of Lesser Short-toed Larks (mean \pm SD) feeding on goat farms throughout the daytime. Values were obtained by averaging maximum records of each hour across days.

– N_1/N)/ w , and N_1 was the number of birds within w , the width of the nearest belt (Bibby et al. 1992). Transects were separated by sufficient distance (≥ 500 m) to avoid counting birds more than once.

Use of goat farms by larks.—From 2002 through 2004, we netted and trapped as many birds as possible inside goat farms and marked them with a combination of numbered metal rings (Spanish Ministerio de Medio Ambiente) and colored bands. After marking, we waited two days before beginning observations to avoid any potential effects of trapping disturbance. Larks were observed at goat farms approximately every 15 min during their hours of feeding activity (Fig. 2) with binoculars and telescopes from distances that did not disturb birds. We estimated the number of individuals that daily used the farms as feeding points as $N = M(n + 1)/(m + 1)$, where M is the number of banded birds counted inside goat farms, m is the total number of birds previously banded, and n is the total number of birds counted inside goat farms (including both marked and non-marked individuals). An approximate estimate of the standard error of this value is given by $((M_2(n + 1)(n - 1))/((m + 1)2(m + 2)))$ (Tellería 1986).

Pox virus prevalence, dietary composition, and demographic effects.—We used information from Lesser Short-toed Larks caught on the island (2002–2004) and in different areas of peninsular Spain (1998 and 2002–2006) and Morocco (2005) to compare prevalences of pox infection, body condition, reproductive rates, and dietary composition. Thus, captured birds were aged (juvenile or adult) and the standard biometric measurements such as body mass (± 0.1 g), length of the wing chord and tail (± 1 mm), and tarsus (± 0.1 mm) were taken. The structural measurement that best correlated with body mass was wing chord and so we calculated an index of body condition as the residuals of a multiple regression model of $\log(\text{body mass})$ on $\log(\text{wing length})$

(Laiolo et al. 2004), corrected for birds' age (juvenile or adult) and sex, and the moment of the breeding cycle (reproductive season, including fieldwork done from April to July in peninsular Spain and from April to May in Fuerteventura Island and during the non-breeding season, including fieldwork done from August to December in peninsular Spain and Fuerteventura Island and during February in Morocco). A drop of blood was extracted for molecular sexing (see *Laboratory procedures* below). We also carefully searched the unfeathered parts of their bodies (legs, feet, face at the base of the beak, and eyelids) for avian pox lesions (i.e., proliferative, wart-like projections consisting of epithelial hyperplasia of the epidermis; see Smits et al. [2005] for pictures and a complete description of the lesions). This method gave us a minimum prevalence of pox infection, since birds that were diseased but lacked external lesions were considered to be non-diseased. Sample sizes were large enough to provide reliable estimates of disease prevalence (Jovani and Tella 2006). Finally, we collected one of the outer tail feathers from each adult bird to analyze their dietary composition through stable nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) isotopes. No information on juveniles was used for diet analyses to avoid the confusing effect of possible age differences.

The proportion of juveniles in the different study areas (juveniles caught/total individuals caught) at the end of the breeding season was used as a surrogate for relative population-wide productivity (e.g., Bart et al. 1999). Survival rates of birds from Fuerteventura with and without virus lesions were compared with capture–mark–recapture (CMR) models, in which apparent survival (ϕ) and recapture (p) rates were estimated according to standard procedures (Lebreton et al. 1992). We first tested general assumptions with the program U-CARE (Choquet et al. 2005) and then used the program MARK to implement the CMR models (White and Burnham 1999). Briefly, we built a general fully time-dependent Cormack–Jolly–Seber model with sex and pox infection specific rates of survival and recapture and then fitted constrained versions in order to reduce the number of parameters (see *Results*). Survival and recapture parameters were estimated on a 10-month basis after adjusting time intervals to the time elapsed between sampling occasions. Models within two units of the corrected Akaike Information Criterion (AIC_c) were considered as alternatives. Recapture rates of Lesser Short-toed Larks from peninsular Spain and Morocco were too low to calculate reliable survival rates.

Laboratory procedures

The sex of the sampled individuals was determined from blood cell DNA, using a polymerase chain reaction (PCR) amplification of the CHD genes (see Vögeli et al. [2007] for details of the molecular techniques applied). To prepare samples for the stable isotope analyses, small portions of feathers were first cleaned by ultrasonic shaking for 20 min in 2:1 methanol:chloroform (three

times) and in deionized water. Then, samples were dried in a vacuum at 70°C. Glass vials were used in the cleaning processes. Stable carbon and nitrogen isotope analyses were performed on 0.5–1 mg subsamples by loading tin cups and combusting at 1020°C in a Carlo Erba EA1500 NC elemental analyzer (Carlo Erba, Milan, Italy) on-line with a Finnigan Delta Plus XL mass spectrometer (Finnigan, Bremen, Germany). Stable isotope abundance was expressed in standard notation relative to V-PDB and AIR for C and N, respectively. V-PDB is the Vienna international standard series (supplied by the International Atomic Energy Agency [IAEA]) as opposed to the classical calcite standard from Pee Dee Belemnite (PDB):

$$\delta^{15}\text{N} \text{ or } \delta^{13}\text{C} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$ of the sample and standards, respectively.

All samples were analyzed three times on different days. Usually two standards were measured for every 10 samples. Based on numerous measurements of inorganic and organic international reference standards the analytical precision is about $\pm 0.1\text{‰}$ (1σ). The normalized scale for $\delta^{13}\text{C}$ values of the IAEA standard was used according to Coplen et al. (2006).

Data analyses

We performed generalized linear mixed models (GLMM; McCullagh and Searle 2000) to compare vegetation cover (logit link function and binomial error distribution with denominator for proportion data), vegetation height (identity link function and Gaussian error distribution), and bird density (log link function and Poisson error distribution) between localities (small-scale sampling) and to assess differences in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ composition (identity link function and Gaussian error distribution) between diseased and non-diseased birds on Fuerteventura. When necessary, we included “year” and/or “transect” as random terms to control for the possible effects of spatial and temporal heterogeneity and for the non-independence of data (McCullagh and Searle 2000). Similarly, differences in the proportion of young birds caught at the end of the breeding season (logit link function and binomial error distribution with denominator for proportion data) between peninsular Spain and Fuerteventura were established by GLMM, fitting “year” as a random term to control for interyear variability in breeding performance (Illera and Diaz 2006). Potential differences in the compositions of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in the feathers of birds (identity link function and Gaussian error distribution) between areas (i.e., Fuerteventura Island, peninsular Spain, and Morocco) were evaluated by generalized linear models (GLM; McCullagh and Nelder 1989). Here, we could not include “year” as a random term because one area (i.e., Morocco) was only sampled one year. We also used GLMs to establish the relationships between vegetation structure (herb, scrub, and total coverage and vegetation height) and bird

densities throughout the island (large spatial scale) while controlling for the main habitats used by larks (sandy steppe, ground-stone steppe, and volcanic land; see *Methods*). When necessary, differences between insular sites (LOC 1, 2, and 3 in Fuerteventura Island) and geographical areas (Fuerteventura Island, peninsular Spain, and Morocco) were assessed by multiple comparisons of the least-squares means using the LSMEANS statement. All statistical analyses were performed using the program SAS 8.2 (SAS Institute 2004).

For the diet calculus using stable isotopes, we considered the case of two potential food sources with a distinct isotope ratio (C_3 and C_4 plants), and the calculus of the contribution of C from each food source to the growth of a consumer was based on a two-source mixing model (Delgado and Garcia 2001, McCutchan et al. 2003):

$$\% \text{diet} - A = \left[1 - \left(\frac{\delta^{13}C_A - \delta^{13}C_{\text{cons}} + \Delta\delta^{13}C}{\delta^{13}C_A - \delta^{13}C_B} \right) \right] \times 100$$

where $\delta^{13}C_A$ and $\delta^{13}C_B$ are the isotope ratios of potential food sources, $\delta^{13}C_{\text{cons}}$ is the isotope ratio of the consumer, and $\Delta\delta^{13}C$ is the trophic shift for C (typically assumed to be 0.0‰).

RESULTS

Effects of goat grazing on vegetation structure and lark densities

At a local scale, herb, shrub, and total vegetation coverage, as well as vegetation height, significantly differed between sites ($F_{2,288} = 6.07$, $P = 0.003$; $F_{2,288} = 82.06$, $P < 0.001$; $F_{2,288} = 59.57$, $P < 0.001$; $F_{2,288} = 72.20$, $P < 0.001$, respectively), being greater in areas with lower densities of goats (LOC 2 and LOC 3; Fig. 3) to such an extent that the effects of goat grazing had a significant visual impact (see photographs in Fig. 1b). The relative densities of Lesser Short-toed Larks also differed between sites ($F_{2,68} = 5.52$, $P = 0.006$): the greatest number of birds was found at LOC 3 (5.46 birds/ha) and the lowest near goat farms (LOC 1, 0.58 birds/ha; Fig. 3), with similar figures each year (random term, $P = 0.2987$).

Larger-scale sampling showed that the relationship between bird density and vegetation structure was not local. Indeed, lark densities throughout the island were positively related to herb ($\chi^2 = 39.70$, $P < 0.0001$, $df = 1$), shrub ($\chi^2 = 6.02$, $P = 0.0142$, $df = 1$), and total vegetation coverage ($\chi^2 = 15.41$, $P < 0.0001$, $df = 1$), as well as to vegetation height ($\chi^2 = 8.56$, $P = 0.0034$, $df = 1$), while controlling for the lower lark density in volcanic as opposed to sandy and stony habitats ($P < 0.01$).

Use of goat farms by larks

The capture–resighting method estimated that $\sim 1815 \pm 149$ (mean \pm SE) Lesser Short-toed Larks, all of which were feeding, congregated daily at the three goat

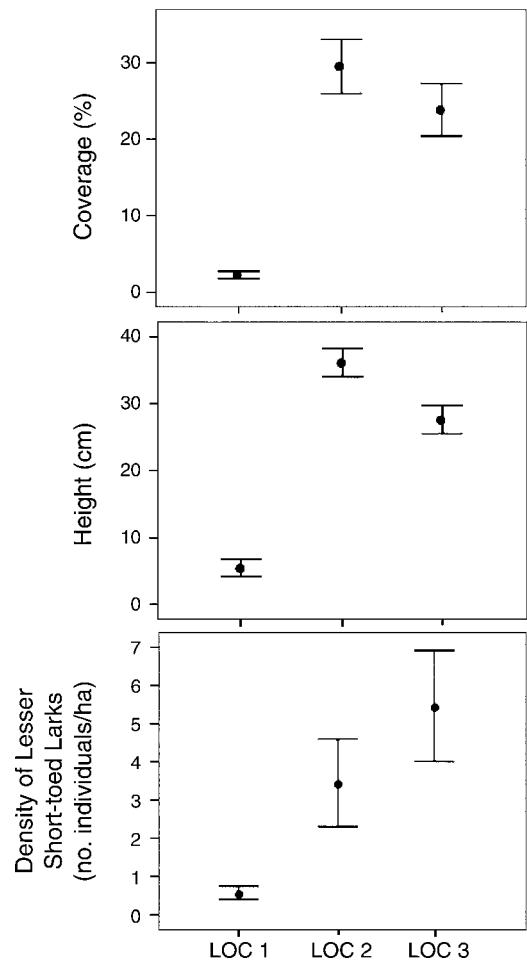


FIG. 3. Vegetation cover and height and density of Lesser Short-toed Larks (mean \pm SD) in localities with different densities of goats (LOC 1, 3.93 animals/ha; LOC 2, 0.11 animals/ha; and LOC 3, 0.28 animals/ha).

farms in LOC 1. This value easily surpasses the quantity of birds expected on the basis of density estimations for LOC 1 (i.e., 0.58 birds/ha \times 570 ha \sim 331 birds). These values were still greater than estimated total population size when the neighboring area (LOC 2) was also included (LOC 1 + LOC 2 \sim 1542 individuals), suggesting that goat farms attract individuals from beyond the limits of LOC 2.

Poxvirus prevalence, dietary changes, and demographic effects

We captured 453 (58 juveniles and 395 adults) Lesser Short-toed Larks on Fuerteventura, 520 in peninsular Spain (228 juveniles and 292 adults), and 46 in Morocco (all adults). While a relatively low proportion of juveniles showed external lesions, adult individuals caught on goat farms on Fuerteventura had a high prevalence of poxvirus, which remained unusually high during the three monitoring years (Fig. 4). Comparison with conspecific birds from peninsular Spain and

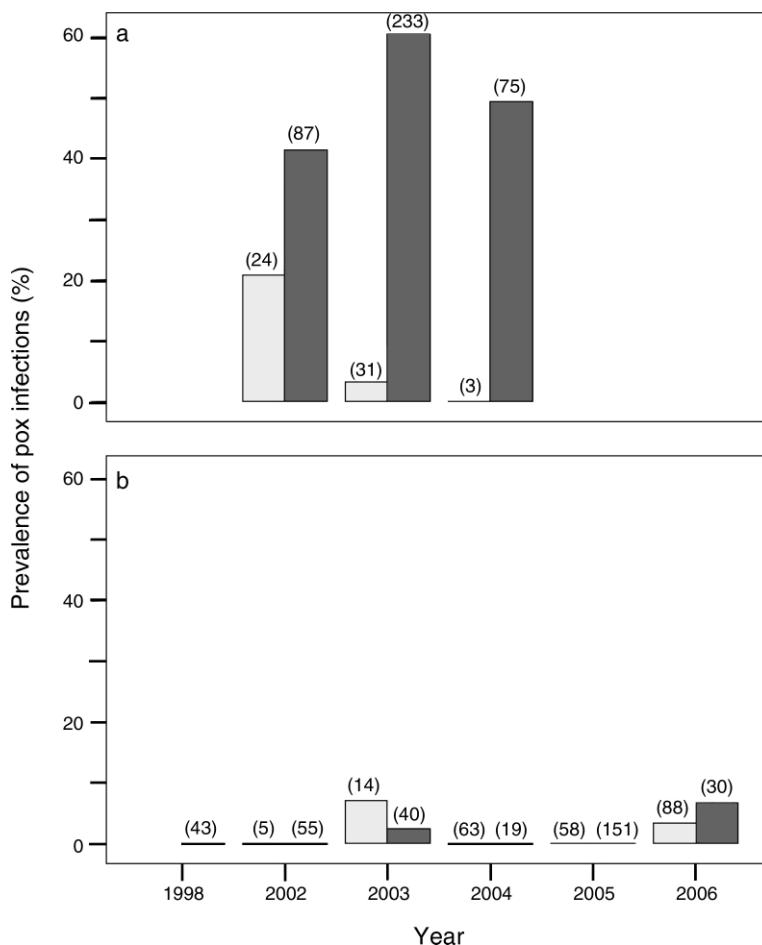


FIG. 4. Prevalence of poxvirus in adult (dark gray bars) and juvenile (light gray bars) Lesser Short-toed Larks from (a) Fuerteventura Island and (b) peninsular Spain and Morocco. Values in parentheses are sample sizes.

Morocco showed that the virus prevalence among Lesser Short-toed Larks on Fuerteventura was extraordinarily high (Fig. 4).

The composition of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ obtained for 219 feathers of adult larks from Fuerteventura ($n = 73$), peninsular Spain ($n = 99$), and North Africa ($n = 46$) showed significant differences in the traces of both isotopes between areas ($\delta^{15}\text{N}$, $\chi^2 = 25.85$, $P < 0.001$, $df = 2$; $\delta^{13}\text{C}$, $\chi^2 = 88.49$, $P < 0.001$, $df = 2$; Fig. 5a). There were differences in $\delta^{15}\text{N}$ values between all three areas ($P < 0.011$), whereas $\delta^{13}\text{C}$ values were only different between Fuerteventura and the other two areas. The $\delta^{13}\text{C}$ values were similar in all samples taken in peninsular Spain and North Africa ($P = 0.47$), since C_3 plants are the main base of the food chain. Interestingly, the isotopic traces quantified in birds from Fuerteventura plot closer to those obtained from the grain collected on goat farms (Fig. 5a), suggesting that their diet is much more dependent on the food provided for goats (mainly maize seeds, a C_4 plant). The photosynthetic cycles of C_3 and C_4 plants are characterized by very different $\delta^{13}\text{C}$ values (approximately -12‰ for C_4

and -27‰ for C_3 ; Cerling 1984, Pate 2001). Maize samples from Fuerteventura goat farms show very narrow $\delta^{13}\text{C}$ values of -12‰ (V-PDB), which are very similar to those reported in the literature for different geographical areas (Keegan and DeNiro 1988, Rossmann et al. 1998, Gonzales-Martin et al. 1999). However, C_3 plants from the Canary Islands show average values of -25‰ (V-PDB) for arid areas (Yanes 2005). The high content of N both in maize and Canarian C_3 plants (Yanes 2005) also explains the high N isotopic values in island as opposed to continental birds, although we expected higher values in continental birds due to their higher consumption of animal proteins (i.e., invertebrates; M. Vögeli, D. Serrano, and J. L. Tella, unpublished data). Moreover, when we compared samples from diseased and non-diseased birds from Fuerteventura, we found a similar composition of $\delta^{15}\text{N}$ in feathers ($+13.06\text{‰} \pm 2.54\text{‰}$ [mean \pm SD], $n = 29$; $+13.02\text{‰} \pm 2.47\text{‰}$, $n = 44$; $F_{1,69} = 0.48$, $P = 0.49$), but a significantly different value of $\delta^{13}\text{C}$ ($F_{1,69} = 4.34$, $P = 0.041$), with less negative values for diseased ($-15.76\text{‰} \pm 2.93\text{‰}$, $n = 29$) than for non-diseased birds (-17.73‰

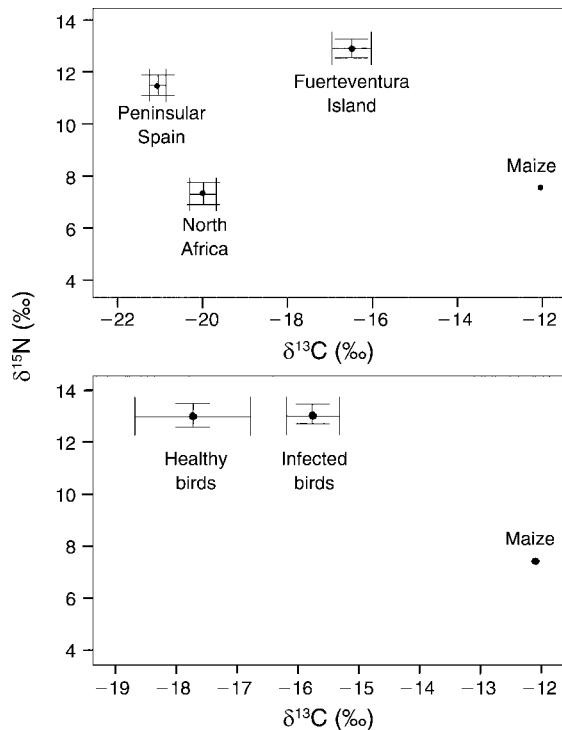


FIG. 5. Isotopic traces (mean \pm SE) in feathers of Lesser Short-toed Larks from (a) peninsular Spain and Morocco vs. Fuerteventura Island and (b) from diseased vs. non-diseased larks in Fuerteventura. International standards for stable isotopes are reported vs. reference standards. For N, we used the isotopic ratio ($^{15}\text{N}/^{14}\text{N}$) of atmospheric air (AIR), while for C we used calcite from Pee Dee Belemnite (PDB; now V-PDB, a Vienna international standard supplied by the International Atomic Energy Agency [IAEA]).

$\pm 5.10\%$, $n = 44$; Fig. 5b). Based on isotopic $\delta^{13}\text{C}$, maize would seem to constitute 70% of the diet of diseased individuals but only 56% of the diet of non-diseased birds. Additionally, the lower variability in $\delta^{13}\text{C}$ (± 2.93) among diseased birds probably indicates a uniform diet as opposed to a polythematic strategy used by non-diseased individuals (± 5.10). This suggests that, although all sampled birds used goat farms for feeding, non-diseased individuals often foraged away from farms, while diseased individuals were more tied to the food supplied by goat farms. Causality cannot be inferred from our data, since diseased birds may feed more frequently in goat farms because of their reduced skills or, alternatively, birds using goat farms more frequently may have a higher probability of acquiring poxvirus. However, our main result, that is, that diseased birds have a more uniform diet (mainly based on maize) than non-diseased birds, remains unchanged.

The body condition index of insular Lesser Short-toed Larks was significantly lower than that of peninsular and African birds ($F_{1,505} = 7.87$, $P = 0.005$; Fig. 6a). However, no differences in body condition associated with virus infection were detected among insular birds ($F_{1,302} = 0.01$, $P = 0.972$).

The best-fitted CMR models indicate that the survival rates of Lesser Short-toed Larks on Fuerteventura were not affected by poxvirus disease, even if this effect is combined with others (ΔQAIC_c range = 4.11–13.40 [ΔQAIC_c , the difference of the corrected quasi-AIC value for avoiding bias in small samples with respect to the best model]) or included by itself ($\Delta\text{QAIC}_c = 20.64$; Table 1). Therefore, disease does not currently appear to be reducing survival rates. If we consider the proportion of juveniles caught to be a surrogate for population-wide annual productivity, then the island population was less productive than populations from peninsular Spain ($F_{1,57} = 16.99$, $P = 0.0001$; year effect, $z = 1.19$, $P = 0.1176$; Fig. 6b).

DISCUSSION

On islands throughout the world waves of extinctions of endemic animals have followed the arrival of humans and their domesticated animals, which have wrought great changes on these peculiar environments (Vitousek 1988, Paulay 1994, Steadman 1995). In particular, the introduction of domestic grazers onto islands has had obvious negative consequences for native fauna due to vegetation degradation and habitat loss (Kramer 1971,

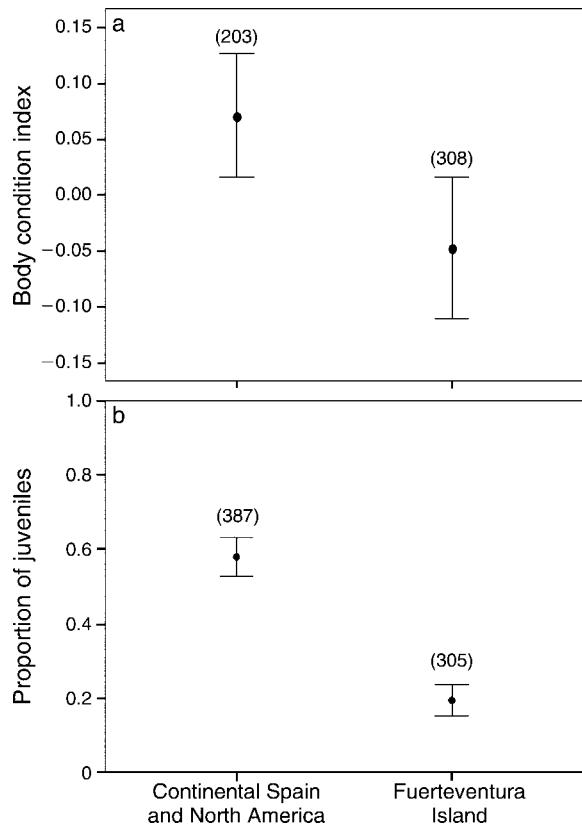


FIG. 6. (a) Body condition index (mean \pm SE) and (b) the proportion of juvenile Lesser Short-toed Larks caught (mean \pm SE) on Fuerteventura Island vs. peninsular Spain and Africa. Values in parentheses are sample sizes.

TABLE 1. Capture–mark–recapture (CMR) models obtained to estimate Lesser Short-toed Lark (*Calandrella rufescens*) survival probabilities in Fuerteventura Island.

Model	QAIC _c	ΔQAIC _c	QAIC _c weights	Model likelihood	No. par	QDev
$\phi_{\text{time}} p$	199.626	0.00	0.86274	1.0000	5	38.724
$\phi_{\text{time} \times \text{virus}} p$	203.737	4.11	0.11041	0.1280	9	34.511
$\phi_{\text{time} \times \text{sex}} p$	206.797	7.17	0.02391	0.0277	9	37.571
$\phi_{\text{time} \times \text{virus} \times \text{sex}} p$	213.026	13.40	0.00106	0.0012	17	26.599
$\phi_{\text{time} \times \text{virus} \times \text{sex}} p_{\text{virus}}$	214.045	14.42	0.00064	0.0007	18	25.414
$\phi_{\text{time} \times \text{virus} \times \text{sex}} p_{\text{sex}}$	214.368	14.74	0.00054	0.0006	18	25.737
$\phi_{\text{time} \times \text{virus} \times \text{sex}} p_{\text{time}}$	214.816	15.19	0.00043	0.0005	20	21.741
$\phi_{\text{time} \times \text{virus} \times \text{sex}} p_{\text{virus} \times \text{sex}}$	217.459	17.83	0.00012	0.0001	20	24.384
ϕp	218.422	18.80	0.00007	0.0001	2	63.648
$\phi_{\text{sex}} p$	219.441	19.82	0.00004	0.0000	3	62.636
$\phi_{\text{virus}} p$	220.267	20.64	0.00003	0.0000	3	63.462
$\phi_{\text{time} \times \text{virus} \times \text{sex}} p_{\text{time} \times \text{virus}}$	223.459	23.83	0.00001	0.0000	24	21.347
$\phi_{\text{time} \times \text{virus} \times \text{sex}} p_{\text{time} \times \text{sex}}$	223.545	23.92	0.00001	0.0000	24	21.433
$\phi_{\text{time} \times \text{virus} \times \text{sex}} p_{\text{time} \times \text{virus} \times \text{sex}}$	236.621	37.00	0.00000	0.0000	32	15.810

Notes: Subscripts relate to effects fitted to survival (ϕ) and recapture probabilities (p), i.e., time, sex (male and female), and virus (diseased and non-diseased). Abbreviations are: QAIC_c, corrected quasi-AIC value for avoiding bias in small samples; ΔQAIC_c, difference of QAIC_c value with respect to the best model; QAIC_c weights, weight of each model with respect to the bulk of models tested; No. par, number of identifiable parameters; QDev, deviance of each model.

Coblentz 1978, Bowen and van Vuren 1997, Donlan et al. 2002). However, subtler indirect effects derived from changes in the behavior of native animals may go unnoticed. Here, we show the manner in which introduced species and their husbandry can create ecological traps for endemic birds by promoting their aggregation and infection with a generalist virus that may impose significant fitness costs.

Lesser Short-toed Larks are specialized steppe passerines that normally distribute at low densities (ranges for Fuerteventura Island, 0–51 individuals/ha; Illera and Tella 2005) across natural, relatively well-conserved steppes (Serrano and Astrain 2005). On Fuerteventura these habitats have been severely transformed by the presence of goats. The negative effects of goat overgrazing on bird densities in Fuerteventura, including those of Lesser Short-toed Larks, were stressed by Osborne (1986). Two decades later, in light of a dramatic increase in goat numbers (Palacios and Tella 2003), we have shown how goats have reduced some natural steppes to stony areas with no or minimal vegetation coverage (Fig. 1b): the relationship between vegetation loss and lark densities is a large-scale phenomenon throughout the island. Nevertheless, birds lose foraging and nesting habitat as a consequence of goat grazing, but gain predictability and probably quantity in their food supply as a result of human husbandry of goats. Goat farms where these ungulates are fed attract birds that mainly eat maize. We might therefore expect that the costs associated with habitat loss would be in some way offset by the benefits of food availability at goat farms. However, when birds visit goat farms they coexist with poultry and other domestic bird species, which are typical reservoirs of many generalist pathogens such as avian poxvirus (Milberg and Tyrberg 1993, Gottdenker et al. 2005; M. Carrete, D. Serrano, M. Vögeli, J. C. Illera, G. López, and J. L. Tella, *personal observations*) and are heavily parasitized by avian fleas that might also

act as vectors (Smits et al. 2005). Conservation concerns related to the introduction of exotic species have traditionally focused on invasive plants and animals, while little attention has been paid to parasites and pathogens as invasive organisms per se (Tella and Carrete 2008) which, as shown here, may have an impact on native biota in combination with the more obvious effects resulting from the introduction of an ungulate.

Recent molecular work on the poxvirus isolated from birds infected in goat farms are inconclusive as to which of the domestic animal species might have transmitted the virus to native birds (Smits et al. 2005, Illera et al. 2008). Nonetheless, current phylogenetic studies indicate that the same poxvirus species may infect many very different avian clades and as such host specificity is much lower than previously thought (Jarmin et al. 2006). Moreover, the high quantity of food available in farms promotes unusually high aggregations of birds that would otherwise feed in much lower densities on the steppe (Serrano and Astrain 2005), thus increasing the horizontal transmission of the disease. Therefore, the naïve immune system of island birds that is unable to fight efficiently against new pathogens (Wikelski et al. 2004, Tella and Carrete 2008), together with an increase in transmission risks due to the larks' behavioral changes, may have promoted an emergent disease. Consequently, a very high proportion of native larks were diseased, with an overall minimum prevalence (adults plus juveniles, 35%) that largely exceeded values found in other populations of this species (1%) and in other continental species (0–1.3%). The proportion of diseased larks was similar or even larger than those recorded from islands (Galapagos, 1–22%; Hawaii, 17–35%) where poxvirus epidemics have been suggested as a threat to several endemic passerines or even in some cases the cause of their extinctions (Tripathy et al. 2000, Vander Werf 2001, van Riper et al. 2002, Wikelski et al. 2004, Kleindorfer and Dudaniec 2006).



PLATE 1. Lesser Short-toed Lark (*Calandrella rufescens*) captured during fieldwork at Fuerteventura Island (Canary Islands). Photo credit: J. L. Tella.

It is worth noting that the picture we reveal here is not a purely local phenomenon. We found an association between vegetation structure and bird densities throughout Fuerteventura and, moreover, non-intensive monitoring has revealed that birds use goat farms throughout Fuerteventura and Lanzarote (Smits et al. 2005; M. Carrete, D. Serrano, M. Vögeli, J. C. Illera, G. López, and J. L. Tella, *unpublished data*), the other island of the Canary archipelago inhabited by Lesser Short-toed Larks (Fig. 1a). Interestingly, other bird species are also attracted to goat farms on both islands, one of which (the Berthelot's Pipit *Anthus berthelotti*) was also heavily infected by poxvirus (prevalence $\sim 30\%$; Smits et al. 2005). Unfortunately, lower sample sizes and the fact that this endemic species is not present on the continent precluded us from conducting a study similar to that performed on larks.

Diseases can drive populations temporarily or permanently to low numbers or densities, predisposing them to extinction as a result of demographic stochasticity or Allee effects. This is particularly true for diseases having reservoirs or affecting populations that are at small pre-epidemic sizes (de Castro and Bolker 2005) or for native island species exposed to new pathogens (Wikelski et al. 2004). However, evidence on the way in which most infections actually affect natural host population dynamics is scarce (de Castro

and Bolker 2005). This is particularly true for avian poxviruses given that, despite being recorded as present in a wide range of bird species worldwide (Bolte et al. 1999), their prevalences are usually extremely low; thus, very little research has been conducted on their effects on host fitness. In wild populations of Serins (*Serinus serinus*), avian pox infections were shown to be very virulent and survival rates of diseased birds were half that of non-diseased ones (Senar and Conroy 2004). Previous studies carried out on the Lesser Short-toed Lark population on Fuerteventura have remarked that poxvirus infection affects the condition-dependent nature of distress calls (Laiolo et al. 2007), which seem to be used by birds as an honest signal of their quality and thus of their ability to escape from predators (Laiolo et al. 2004). Infection has thus the potential to increase lark mortality due to increased predation risks (Laiolo et al. 2007). The scarcity of predators on Fuerteventura compared with continental populations of larks (P. Laiolo, *unpublished data*) might have lessened the potential effect of poxvirus on the predator-mediated survival rates of their avian hosts. We found no evidence for a decline in body condition in diseased Lesser Short-toed Larks that could be associated with the physical deleterious effects of the disease (e.g., losing of feet or changes in the shape of the beak; Smits et al. 2005), probably because the existence of a predictable food

supply, which is provided ad libitum, is compensatory and does not demand particular skills. Hence, similar survival rates between diseased and non-diseased birds may be possible under current conditions of low predation pressure and unusually high food availability. In a potential scenario of sudden inaccessibility to a highly abundant food source, the survival of diseased birds might be threatened, leading to a corresponding reduction in population growth rate. However, and although differences in survival rates on Fuerteventura may be evened out by high food availability, Lesser Short-toed Larks were not able to recover from the disease (only 2% of diseased Lesser Short-toed Larks have healed lesions, $n = 210$; Smits et al. 2005) and thus the species should be considered as very sensitive to the poxvirus (van Riper et al. 2002).

There is growing evidence for the importance of physiological processes regarding the quality as opposed to the quantity of food supplied. Changes in the quality of food intake that do not match animals' requirements may cause nutritional stress that will seriously affect individual development and vital rates (Mayntz and Toft 2001, Nolet et al. 2005). In our case, diseased birds may maintain their body condition and survival rates by using goat farms as feeding sources. Indeed, isotopic traces of $\delta^{13}\text{C}$ in feathers of adult larks showed that all birds sampled on Fuerteventura mostly eat the maize supplied by goat farms (and above all those birds that were diseased). However, these feeding points provide food quantity but not food quality. Maize seeds compared to leguminous plants or food of animal origin are rich in lipids, which can fatten birds, but are a poor source of proteins (ARC 1980, Delgado and Garcia 2001), a basic component for maintaining the immune system (see review in Alonso-Alvarez and Tella 2001), reaching breeding condition and success (e.g., Selman and Houston 1996, Ramsay and Houston 1998), and consequently for dealing with the classical trade-off between self-maintenance and reproduction. This could explain the lower body condition of adults (both diseased and non-diseased birds eat mostly maize) and the significantly lower proportion of young birds on the island, although the possible effects of the disease on mating success (Kleindorfer and Dudaniec 2006) or other aspects such as the loss of genetic diversity or inbreeding depression associated with the "insular syndrome" (Blondel 2000) should not be discarded. Whatever the reason, the effects of the reduction in productivity on the population dynamics of island birds could be doubled as a result of a reduction in growth rate and, therefore, in an erosion of genetic diversity. It is well known that the combined effects of a low growth rate and inbreeding may drive small populations such as those restricted to islands to extinction (Caughley 1994), above all in situations in which inbreeding can erode immuno-competence and entail a greater susceptibility to infectious diseases (Altizer et al. 2003).

Conservation managing and monitoring implications

Although birds have presumably evolved to associate environmental and structural cues with habitat quality (Jaenike and Holt 1991), these cues may become completely decoupled from true habitat quality in landscapes increasingly modified by humans, thereby causing birds to make errors during habitat selection processes. Because these "ecological traps" (sensu Schlaepfer et al. 2002, Kristan 2003) may affect population size or persistence in the long term, our understanding of conservation ecology and population biology will benefit from being able to identify the factors that create these traps and ways to avoid their creation (Kokko and Sutherland 2001). Recently, a few studies have described how introduced species can cause changes in natural environments in such a way that normal behavioral decisions of native species are no longer adaptive (e.g., Tewksbury et al. 2002, Phillips et al. 2003). Here we show the manner in which species commonly introduced into island ecosystems (i.e., goats, poultry, and their associated parasites and pathogens) combined with human husbandry can create ecological traps for native passerines, not only because a new and attractive feeding source (where birds become diseased) has been created, but probably also because the attractiveness of the birds' original habitat has decreased due to overgrazing.

Counts conducted under standardized conditions are regarded as indices of population size that can be used to estimate patterns of relative abundance and species trends over time (Link and Sauer 1998, Sauer et al. 2003). Unfortunately, abundance (i.e., number of individuals) may be a misleading surrogate of habitat quality in source-sink systems if the majority of individuals reside in sink habitats (Pulliam 1988, Pulliam and Danielson 1991). In our example, although census data showed that lark densities were higher in areas with fewer goats, our estimates of birds' daily visits to goat farms suggest that they congregated disproportionately at these points. Moreover, although the great abundance of food available at these sites may help diseased individuals to survive, a diet of low nutritional quality may affect their condition and breeding performance. These indirect effects would remain hidden in the absence of research focused on the nutrition and health status of individuals. Our results add to recent evidence that shows how human-induced habitat and behavioral changes may alter in unexpected ways the incidence and dynamics of wildlife diseases (Gillespie et al. 2005, Blanco et al. 2006) and reveal the need for incorporating health monitoring into population research and conservation programs.

Based on current results, there is enough evidence to warrant the taking of urgent management actions, of which the most obvious are to enclose farms to avoid lark feeding in them and the restoration of native habitat for birds by preventing overgrazing by goats. These actions might have a short-term negative impact on lark

populations because of a reduction of food supplies, at least until natural habitats are restored and the poxvirus epidemic subsides, and so any trade-off in managing actions must be carefully balanced over time. Eliminating introduced goats as in other sites would seem to be an impossible task in Fuerteventura, since goat farming is one of the main economic stays of the island (only surpassed in recent decades by tourism; Palacios and Tella 2003) and is an important part of local culture, to the extent that the symbol of the island is a goat (see it in Fig. 1b). However, strict limits on goat densities should be imposed on farmers to avoid local overgrazing, an action that would also favor a number of other native endemic bird species living in these steppe habitats (Osborne 1986). Actions should be also implemented to avoid disease transmission from domestic to wild birds. Poultry and other domestic avian species are kept in goat farms and houses in poor sanitary conditions (M. Carrete, D. Serrano, M. Vögeli, J. C. Illera, G. López, and J. L. Tella, *personal observations*), a situation that must change if questions about the safety of poultry production and wildlife health are not to arise. In the long term, large-scale survey of individually marked birds might throw some light on the dynamics of poxvirus epidemics, their effects on host fitness, and their contribution to trends in host populations. Moreover, health monitoring should include surveys testing for the potential transmission of other pathogens to larks as well as to other wild bird species also present on the island.

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