Biological Conservation 144 (2011) 1702–1711

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Dampened behavioral and physiological responses mediate birds' association with humans

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ARTICLE INFO

Article history:
Received 10 January 2011
Received in revised form 20 February 2011
Accepted 5 March 2011
Available online 31 March 2011

Keywords:
Behavioral plasticity
Biodiversity
Birds
Cantabrian Mountains
Corticosterone
Habituation
Mountains
Tourism

ABSTRACT

The study of the mechanisms involved in phenotypic adaptations or plasticity to environmental stressors may serve to evaluate contemporary ecological and evolutionary dynamics in threatened or growing wildlife populations. By addressing human disturbance as a main stressor agent, we investigated anti-predator response (flushing distance), social behavior (degree of gregarism), health (fecal pathogens), and endocrine status (fecal corticosterone levels) as potential mechanisms that permit birds to cope with anthropogenic impact in tourist areas. Our study models were species that are neither urbanized nor invasive, and that are typical of the high mountains of the Palearctic: the Alpine and the Red-billed chough (*Pyrrhocorax graculus* and *P. pyrrhocorax*), and the surrounding alpine bird community. Both chough species showed habituation, reduced flushing distances, fewer parasites and lower corticosterone levels in tourist than in non-tourist sites, and a significant variation in gregarious behavior. Behavioral and physiological adjustments permitted these corvids to optimize resource exploitation depending on habitat quality and in conditions of continuous disturbance. Human-induced changes in chough social behavior had no effect on local avian species richness, a surrogate measure for community diversity. Irrespectively of chough aggregations, bird diversity decreased significantly in recreational areas, thus not all community members tolerated human impact as choughs did. Our findings suggest that species that manage to coexist with humans primarily adjust traits that influence ecological interactions (social, foraging or antipredatory responses) and that vary rapidly (learned behaviors and physiological mechanisms that promote homeostasis).

1. Introduction

Humans are potent agents of natural selection, affecting the fitness of organisms and modifying the configuration and functioning of the physical environment (Carrol et al., 2007). As a major driving force of contemporary evolution, we can promote substantial differentiation among populations in relatively short time frames, either through phenotypic plasticity or microevolutionary responses to natural selection (Stockwell et al., 2003; Yeh and Price, 2004). The study of the adjustments to anthropogenically driven changes can be used to obtain information on the mechanisms that ensure species persistence in adverse environmental conditions (Tarlow and Blumstein, 2007). These mechanisms have great relevance, since they can make the difference between persistence and extinction (Myers and Knoll, 2001).

As a matter of fact, some organisms are doing badly in the face of human-induced rapid environmental changes (e.g. threatened or endangered species, species of concern for conservation), whereas others are doing better than ever (e.g. invasive species, urbanized species). Among these two extremes, there is a plethora of species that interacts with humans without thriving or exhibiting strikingly maladaptive responses to contemporary change, and that varies locally in the way they interact with humans, even within the same population (Carrete and Tella, 2010). A key question transcending the pure conservation application is how to explain variation among species, or among significant subset of individuals within species, in their ability to cope with rapid environmental changes. Behavior is typically the first response when organisms are confronted by changes in the external environment, and also, via choice of environment, it is also a way whereby organism can influence the environmental factor that affect the development and expression of other traits (morphology, physiology, etc.), as well as the interactions with other species (Sih et al., 2010; Laiolo et al., 2011).

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doi:10.1016/j.biocon.2011.03.003

In this study, we focused on the mechanisms that allow tolerance to tourist disturbance as a main environmental perturbation. As an anthropogenic stressor, tourism causes short- and long-term behavioral alterations (Stankowich and Blumstein, 2005; Fowler, 1999; Lord et al., 2001; Martínez-Abraín et al., 2010), and generates adverse physiological responses that reduce survival or breeding success (Müllner et al., 2004; Amo et al., 2006; Laiolo, 2010). These processes may determine the abandonment of otherwise suitable habitats, reducing population sizes and eventually contributing to species endangerment (Czech, 2000; Kerbiriou et al., 2009). When considering species that have become the direct focus for ecotourism, however, some respond adaptively to direct human disturbance through habituation (e.g. individuals become familiar with tourist presence and reduce the intensity of their reaction) (Fowler, 1999; Romero and Wikelski, 2002).

Our study models were two corvids typical of Palearctic mountains, the Alpine and the Red-billed chough (*Pyrrhocorax graculus* and *P. pyrrhocorax* L.). Members of the Corvidae family represent good models for studying plastic responses to environmental challenges, because they have a great ability to respond rapidly to novel conditions (Marzluff and Angell, 2005). Moreover, corvids may have strong cascading effects on the surrounding community via competition or predation processes, thus play a key role in ecological dynamics (Clergeau et al., 2006). Both chough species coexist to a certain degree with humans. The Red-billed chough depends on the maintenance of specific human activities (traditional agro-pastoralism) in large portions of its range (Blanco et al., 1997), whereas the Alpine chough has learned to forage on human food scraps in some highly touristic mountains (Rolando et al., 2003; Storch and Leidenberger, 2003). Accordingly, these corvids are not expected to be especially sensitive to tourist disturbance and should rather engage in close interactions with humans, unlike the majority of mountain species (Laiolo, 2004; Arlettaz et al., 2007; Patthey et al., 2008; Thiel et al., 2008, 2010). Notably, the increase of corvids' populations to the detriment of other species is considered as a major problem in central and northern Europe mountainous areas (Storch and Leidenberger, 2003; Watson and Moss, 2004).

We studied six chough populations exposed to variable levels of summer tourism disturbance in the Cantabrian Mountains (Northwestern Spain). As disturbance indicators we considered bird escape response (flight initiation or flushing distance to an approaching human on foot; Tarlow and Blumstein, 2007), flocking behavior, endocrine status (fecal glucocorticoid levels; Busch and Hayward, 2009) and health condition (fecal pathogen infection, Blanco et al., 2006). Since the target indicators involve learned behaviors or physiological parameters readily affected by bird nutritional status or environmental stimuli (Schoech et al., 2007; Lemus et al., 2008), we expect that these may rapidly respond to the relatively novel environmental settings imposed by tourist activities. We initially analyzed the validity of our indicators, testing whether fecal basal glucocorticoids (fGCs) can be considered as a reliable indicator of individual health (pathogen infection) and behavioral response (flushing distance). Then we addressed the mechanisms choughs adopt to dampen human disturbance. We tested for habituation processes, hypothesizing that individuals and flocks should shorten flushing distances as a result of reduced baseline fGC levels in highly touristic areas, since both mechanisms help maintain homeostasis in disturbed environments (Fowler, 1999). Ultimately, we assessed whether human-induced behavioral shifts in these corvids could cascade negatively to the diversity of the surrounding bird community, as predicted in the case of exacerbated competitive interactions for space and resources between corvids and other birds (Storch and Leidenberger, 2003).

2. Methods

2.1. Study area

The study was carried out in the Cantabrian Mountains, the westernmost mountains of Continental Europe. Originally covered by large areas of deciduous forests, these mountains presently constitute a mosaic of forest patches, pastures and heathlands. The highest, 'alpine-like' massifs are located in the eastern fringes and are embedded in the Picos de Europa National Park, the first National Park established in Spain (Table 1). More than one million tourists visit this area per year, ca. 400,000 in August alone (unpublished report, Picos de Europa National Park). The three massifs of the Picos de Europa (Western, Central and Eastern Massifs, 43°07′–43°16′N, 5°01′–4°39′W) make up the tourist sites we chose for this study. Another three massifs occurring within the chough's range in the Cantabrian Mountains were selected as control, non-tourist sites: Peña Ubiña (43°02′N, 5°57′W), Sierra del Aramo (43°13′N, 5°56′W) and Sierra del Sueve (43°24′N, 5°16′W). Non-tourist sites are those in which sporadic trekking activities occur: the number of people we counted along trekking routes was 20.4 ± 7.7 SE × km in the Picos de Europa Massifs and 0.89 ± 0.33 SE × km in the other massifs in June–September 2009 (Kruskall Wallis $\chi^2 = 14.3$, $P < 0.001$; $N = 22$ routes and 215 km walked). Apart from trekking paths, considerable crowds can be observed in picnic areas, cableway areas and mountain refuges in the tourist sites (up to 150 persons at a time in July–August, pers. obs.). Cattle-grazing is widespread across the entire Cantabrian range, and 80% of overall chough observations in non-tourist sites and 66% in tourist sites occurred in pastures grazed by livestock ($\chi^2 = 1.8$, $P = 0.17$, $N = 153$). The Picos de Europa area shows the greatest proportion of inaccessible limestone cliffs and rocky areas of the Cantabrian Mountains (Appendix 1), offering choughs ample safe roosting and nesting sites a part from attracting crowds of tourists (Baglione, 1997). Each massif under study is inhabited by different breeding populations of the Alpine and Red-billed choughs, with the Picos de Europa Massifs supporting the largest and most continuous chough populations in the Cantabrian Mountains (Baglione, 1997; Cuevas and Blanco, 2009).

2.2. Flushing distance and its potential predictors

Observations were performed in 42 transects along different trekking routes in June ($N = 15$), July ($N = 13$), August ($N = 5$) and September 2009 ($N = 9$), between 7:00 a.m. and 8:00 p.m. The study period corresponds to the breeding period (June-early August) and the early stages of fledgling independence (late August–September) (Laiolo and Rolando, 2001).

Transects lasted 2–11 h and were 2–17 km long (altitudinal range: 800–2415 m a.s.l.). To measure flushing distance we followed the procedure outlined by Kerbiriou et al. (2009): we slowly approached an individual or group of foraging birds with a nearly direct trajectory, at the speed of roughly one step per second. When the bird flushed off, we measured the distance-to-bird location by means of a laser telemeter (Nikon 550 AS and Leica Rangemaster 1200). When birds were in flocks we measured the distance from the central individual of the group (focal individual). In general, choughs behave gregariously (Rolando et al., 1997, 2000), but on some rare occasions only a portion of the flock flew away; in these cases we measured the distance to the first birds that flushed off. After birds flushed off, we recorded focal bird position by means of a Garmin GPSMAP 60 CSX and estimated habitat characteristics within a radius of 100 m (hereafter, the observation plot) from the focal birds, measuring the percent shrub and rock cover in pastures. We also recorded the size (number of individuals) and