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Linking ecology, behaviour and conservation: does habitat saturation change the mating system of bearded vultures?

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The social organization of a population is the consequence of the decisions made by individuals to maximize their fitness, so differences in social systems may arise from differences in ecological conditions. Here, we show how a long-lived species that used to breed monogamously, and at low densities, can change its mating system in response to habitat saturation. We found that a significant proportion of unpaired birds become potential breeders by entering high-quality territories, or by forming polyandrous trios as a strategy to increase their individual performance. However, productivity of territories was reduced when those occupied by breeding pairs changed to trios, suggesting that the third individual was costly. The decision of some individuals to enter into breeding trios as subordinates also had clear negative consequences to population demography. This unusual mating behaviour is thus compromising the conservation effort directed to this endangered species; management to encourage floaters to settle in other suitable but unoccupied areas may be beneficial.

Keywords: polyandry; raptors; population dynamics

1. INTRODUCTION

In many bird species, a proportion of mature individuals in the population do not breed even though they are capable of doing so, mainly because all possible territories are occupied (Newton 1992). These so-called floaters remain in the population as a reservoir from which new breeders are recruited and, therefore, are important for its regulation (López-Sepulcre & Kokko 2005; Carrete *et al.* in press). However, not breeding in a given year has a fitness cost, and mature birds may try to enter into the reproductive population by alternative routes: individuals may occupy poor-quality territories (Rodenhouse *et al.* 1997), or enter into an occupied high-quality territory as a helper (Hatchwell & Komdeur 2000).

Cooperative breeding is a breeding system in which more than a pair of individuals show parent-like behaviour towards young of a single nest. In its broadest sense, it includes reproductive systems varying from helping by non-breeding offspring to various forms of polygamy, in which more than one male or female share breeding status (Brown 1987; Cockburn 1998; Hatchwell & Komdeur 2000). Several hypotheses have been proposed to explain the evolution of this reproductive system. According to the ecological constraints hypothesis, cooperative breeding appears when opportunities for independent breeding are limited because of ecological factors, such as low availability of resources or high risk of mortality during dispersal. The life-history hypothesis, however, states that cooperative breeding is a consequence of certain life-history traits of a species, such as low adult mortality, that reduce the opportunities for independent breeding. Beyond their differences, both hypotheses stress that direct fitness benefits of looking for independent breeding opportunities do not outweigh the indirect fitness benefits of helping relatives (Pen & Weissing 2000).

Although the evolution of cooperative breeding has often been attributed to kin selection (Emlen 1991; Emlen *et al.* 1991), there is increasing evidence that helpers can be unrelated to the young they are raising (Cockburn 1998; Heg & van Treuren 1998). This poses a greater evolutionary paradox than the alloparental behaviour shown by kin helpers that gain indirect fitness benefits. Other rewards such as staying in a restricted area to increase their probabilities to acquire a high-quality territory (Heg & van Treuren 1998; Kokko & Sutherland 1998) or, as in polygamous units, to have some chance of breeding (Hartley & Davies 1994) should tempt birds to joint an existing breeding pair rather than search for an unlikely opportunity of independent reproduction in a saturated environment.

The aim of this paper is to analyse the role of habitat saturation in the mating system of a long-lived, cliff-nesting, territorial and usually monogamous raptor, the bearded vulture (*Gypaetus barbatus*). In Spain, the population of this threatened species reached its minimum in the 1970s (less than 40 breeding territories), but increased to more than 90 breeding pairs in 2002. This increment was within a restricted geographical range (the Pyrenees), so crowding mechanisms severely reduced territory suitability and fitness of territorial birds (Carrete *et al.* in press). In addition to the increase in population size, surprisingly, some territories became occupied by polyandrous trios (Heredia & Donázar 1990). Here, we took advantage of a long-term population monitoring programme to test the ecological constraints hypothesis. Unlike most work of this kind that deals only with fitness benefits for subordinates, we also analysed the consequences of this behavioural change for dominant breeders as well as for the whole population. Our findings have direct implications for conservation.

2. MATERIAL AND METHODS

(a) *Study species and population*

The bearded vulture is a large, long-lived osteophagus raptor with delayed maturity (adult plumage at 5–7 years old) that breeds in sparsely distributed territories. The clutch generally consists of two eggs, but only one chick survives as a consequence of sibling aggression. In monogamous pairs, both sexes share parental duties, although males play a more active role in nest building and territorial defence (Margalida & Bertran 2000). In polyandrous trios, however, the second male is subordinate and, even when its contribution to parental care is limited, it tries to copulate with the female (Bertran & Margalida 2002). As birds were not individually marked, kin relationships among trios members are unknown.

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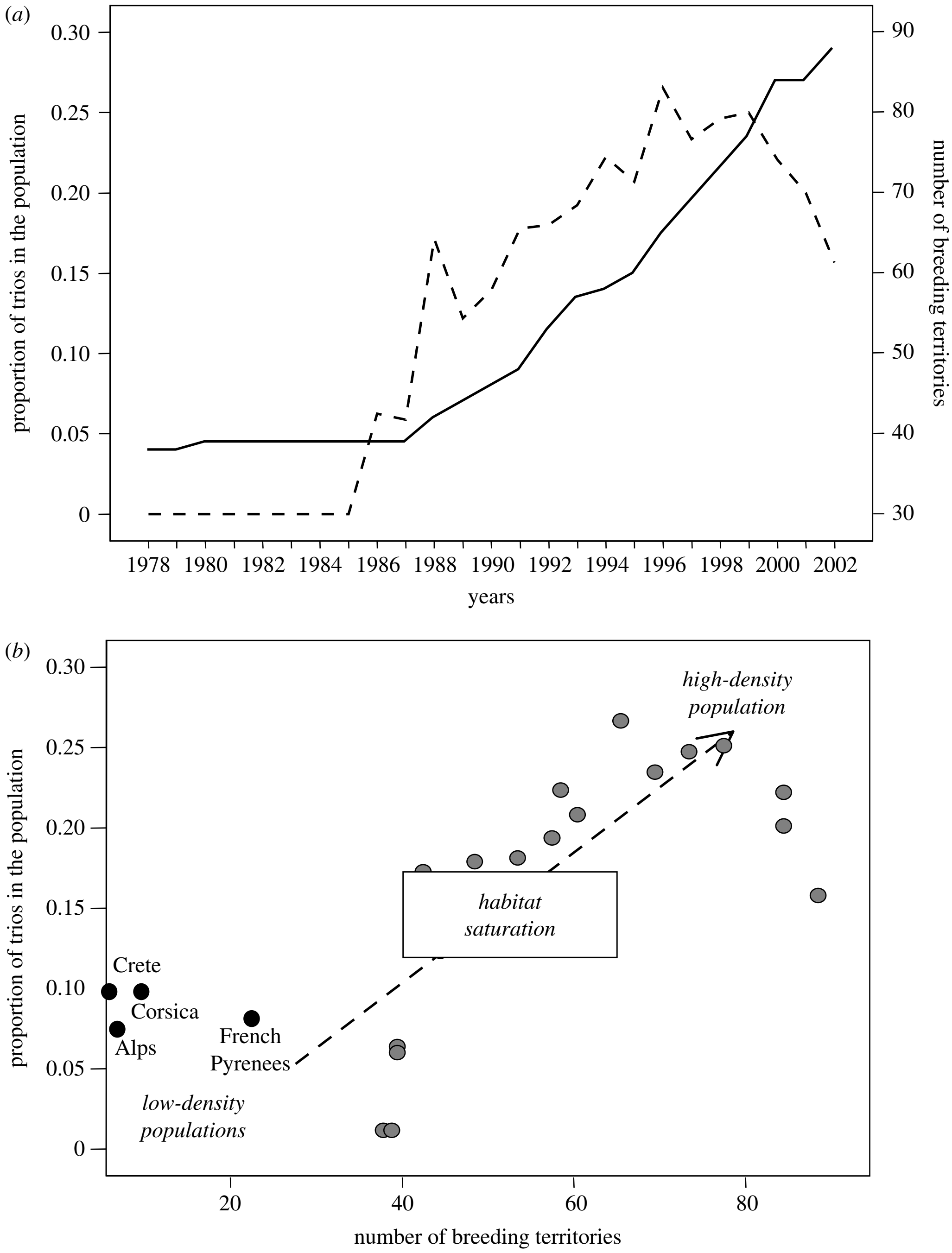

Figure 1. (*a*) Number of breeding territories (solid line) and proportion of trios (dashed line) in the Spanish population of bearded vultures. (*b*) Number of breeding territories and proportion of trios in the Spanish population of bearded vultures (grey dots) compared with other populations (black dots).

The whole Spanish breeding population of bearded vultures, located within an area of 21 000 km^2, was monitored annually from 1978 to 2002. All occupied territories as well as potential breeding areas were searched during the breeding season (November–August). Occupied territories were located through territorial or courtship activity, and repeated visits were conducted to record breeding parameters and identify reproductive units (pairs or trios). Territories occupied since 1978 were categorized as *traditional*, while territories colonized after 1988, when the population increased, were classified as *new*.

We calculated productivity of territories over a sequence of years as the average number of fledglings raised per reproductive unit, including breeding failures. As density-dependent depression in productivity increased with years (Carrete *et al.* in press), we standardized data by subtracting the annual mean and dividing by the variance of the population. This gives the relative reproductive success of a territory as the difference in probability for a nest to be successful relative to the population average. The relationship between the proportion of trios and annual changes in the number of breeding territories (number of breeding territories in year t − number of breeding territories in year $t-1$) was assessed by Spearman's rank correlation. Generalized linear models (GLM) were used to test whether trios formed in high-quality territories, as well as to asses their effects on population productivity (link function: logistic; error distribution: binomial). Territory quality was measured as time since occupation (Sergio & Newton 2003; i.e. traditional versus new territories) and as standardized productivity of the territory when it was occupied by a breeding pair. The reproductive output of trios and breeding pairs in the same territories was compared by Wilcoxon matched-pairs test.

3. RESULTS

The breeding population of bearded vultures as well as the proportion of polyandrous trios increased from 1988 to 2002 (figure 1*a*). Annual changes in the number of breeding territories were positively correlated with the proportion of trios ($r_S = 0.78$, $p < 0.0001$,

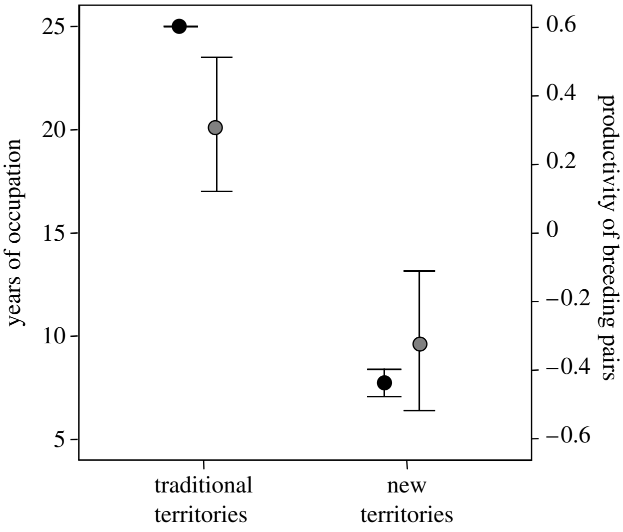

Figure 2. Differences (mean ± s.e.) in time since territory formation (black dots) and mean standardized productivity of territories when occupied by breeding pairs (grey dots) between traditional and new territories.

$n=25$), suggesting that the progressive saturation of the population could be related to their formation. Polyandrous trios tended to appear in traditional territories ($\chi^2_1 = 43.10$, $p<0.0001$), where productivity was higher when occupied by breeding pairs (standardized productivity of traditional and new territories: 0.30 ± 1.13 and -0.32 ± 1.41 fledglings per year, respectively; U-test$=579$, $p=0.031$, $n=81$; figure 2). However, these high-quality territories became less productive when they received a third individual (standardized productivity of breeding pairs and trios within the same territories: 0.63 ± 1.21 and -0.14 ± 1.33 fledglings per year, respectively; Wilcoxon test, $z=-2.10$, $p=0.036$, $n=15$), suggesting that the appearance of another adult could trigger conflicts that affect reproduction among individuals from the same territory. Accordingly, after fitting territory and year into models to control for the density-dependent decay in the productivity of the population during the study period, we found that the formation of trios in some territories caused productivity depression in the whole population (GLM: territory, $\chi^2=328.03$, $p<0.0001$; trio, $\chi^2=14.99$, $p<0.0001$; year, $\chi^2=44.63$, $p=0.0064$).

4. DISCUSSION

Intraspecific variation in mating systems may be determined by ecological features of the environment (Heg & van Treuren 1998) or by conflicts of interest between individuals (Davies & Hartley 1996). This has been supported for small, short-lived birds, usually group-living species, and where coexistence of different types of mate-sharing is common (see examples in Hatchwell & Komdeur 2000). However, there is no solid evidence for long-lived, typically monogamous species that changes in reproductive strategies can take place rapidly (figure 1*a*) compared to their lifespan (in our case 21.4 years for wild birds; Brown 1997). Here, we have shown how a large species that used to breed at low densities can change its mating system when subjected to demographic pressures (figure 1*b*), even when it has negative effects for dominant breeders and the population as a whole.

Management actions for bearded vultures in Spain have fixed dispersers into their natal population (Carrete *et al.* in press), resulting in a large number of surplus birds and habitat saturation. Bearded vultures entered the breeding pool by occupying poor-quality territories (Carrete *et al.* in press) or by queuing in high-quality territories to wait until they are available. Therefore, trio formation may be a strategy for intruders to increase their fitness prospects by mating with a female or by increasing their likelihood of inheriting a high-quality territory when the dominant male dies. Reproductive success of previous owners was compromised when territories changed to trios, suggesting that the third individual was costly. Intruders, however, are not evicted by owners (Bertran & Margalida 2002), perhaps because trios arise from uncommon ecological constraints and thus the energy invested in an unusually developed agonistic behaviour could be higher than the costs of accepting them (Clutton-Brock & Parker 1995; Hamilton & Taborsky 2005).

The decision of some individuals to get into a trio as a subordinate has also clear negative consequences for the whole population. However, since it appears as a consequence of ecological constraints, this behaviour could be reversed through management. The Spanish population of bearded vultures is highly restricted spatially, and both the reproductive and non-reproductive fractions of the population coexist. Although the Recovery Plan of the species claims that management should be directed to promote a geographical expansion of the breeding population to other suitable areas, conservation actions such as the management of supplementary feeding stations are fixing floaters to their natal range. To our knowledge, this would be the second example of unexpected, detrimental effects of food supplementation programmes on the conservation of threatened species (Robertson *et al.* 2006). Reducing food supply or progressively moving feeding stations outside of the Pyrenees may encourage floaters to settle in other areas where they could find breeding opportunities. Even if the management action was different and not directly applicable to our study species, the translocation of floaters of the endangered Seychelles magpie robin *Copsychus sechellarum* from a population-saturated island to an unoccupied one was a successful conservation strategy, since individuals become breeders (Kokko & Sutherland 1998). A similar situation could be expected if ecological and behavioural cues exposed in this paper are linked to direct conservation actions for this endangered vulture.

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