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Effect of human activities on bearded vulture behaviour and breeding success in the French Pyrenees

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ABSTRACT

The bearded vulture is a threatened species for which human disturbance has been suggested as an important factor potentially influencing breeding success. Additionally, disturbance remains one of the few factors that is possible to control through directed policy. We evaluated the effect of human activities on the behaviour and breeding success of bearded vultures breeding in the French Pyrenees. Human activities influenced bearded vulture behaviour (primarily through a decrease in nest attendance), but this effect varied in relation to the type of activities and the distance to the nest. Very noisy activities and hunting most frequently provoked nest unattendance even when occurring far (>1.5 km) from the nest. People on foot or cars/planes only affected bearded vulture behaviour if close (<500–700 m) to the nest. We also found a significant relationship between human activities and vulture breeding success: the probability of failure increased with the frequency of human activities. In particular, there was a significant relationship between the probability of failure and the frequency of very noisy activities. We discuss the implications of our results for management schemes and conservation of this species.

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1. Introduction

Conflicts between humans and wildlife may arise because human activities can cause disruption of normal breeding behaviour in wildlife (De la Torre et al., 2000; Verhulst et al., 2001; Quan et al., 2002; Thomas et al., 2003; Rees et al., 2005) and ultimately be a cause of breeding failure (Stevens and Boness, 2003; Ruhlén et al., 2003). Since both human development and human recreational use of nature are likely to increase in the future, the need to understand how wildlife responds to human activities is becoming increasingly important. Science-based management strategies are necessary to minimise the detrimental effects of human activities (Yorio

et al., 2001). Quantitative information about how, when or what type of human activities may be detrimental to wildlife is thus critical to optimise management measures (Carney and Sydeman, 1999).

When evaluating whether human activities are detrimental to wildlife, it is important to evaluate whether they alter behaviour potentially influencing individuals reproductive success (like time spent foraging, or attending the nest) but, more importantly, it is critical to evaluate whether this has an influence in the species' population parameters, such as breeding success. Whereas the former has been assessed for many species (e.g. Lord et al., 1997; Burger, 1998; Gutzwiller et al., 1998; Trimper et al., 1998; Verhulst et al., 2001; Bright

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et al., 2003; Traut and Hostetler, 2003), the latter is more rare (but see, e.g. Fraser et al., 1985; White and Thurow, 1985).

Human activities affect breeding behaviour in many species of raptor (e.g. Trimper et al., 1998; Steidl and Anthony, 2000; Kruger, 2002) and through a reduction in parental care may affect the physiology and condition of the nestlings (Fernández and Azkona, 1993). Thus, spatial and temporal restrictions are commonly prescribed to protect raptors during periods of extreme sensitivity (Richardson and Miller, 1997). Quantitative studies on the behavioural responses to human activities are needed to optimise these management measures (White and Thurow, 1985; Holmes et al., 1993). However, relatively few studies have attempted to quantify this factor, particularly in Europe, and most of the statements about the influence of humans on raptor breeding are based on either qualitative assessments or indirect measures, such as “number of roads” or “distance to villages” (e.g. Donazar et al., 1993, 2002; Ontiveros, 1999; Bakaloudis et al., 2001; Sergio et al., 2003).

The bearded vulture (*Gypaetus barbatus*) is a threatened species in the western Palearctic (Tucker and Heath, 1994; Rocamora et al., 1999). Human disturbance has been described as an important factor influencing breeding success for this species (Layna and Rico, 1991; Donazar et al., 1993; Terrasse, 2001), although no study exists to quantify the effect. In the French Pyrenees, overall productivity for the species is 0.35 fledglings per pair (from 1994 to 2003, Razin unpubl. data), which is relatively low compared to the Alps (0.44 fledglings per pair from 1997 to 2002; Razin et al., 2004) or the Spanish Pyrenees until recently (0.59 fledglings per pair from 1994 to 2000, Heredia, 2000), and there is concern about nest failure rates (Recovery Plan of the bearded vultures in the French Pyrenees). Although no detailed analysis of reasons for failure in this area has yet been carried out, causes of failure potentially include inter- and intraspecific competition, weather, food abundance and disturbance (Razin, 2003). Of those, the latter remains one of the few factors that can be managed through directed policy (in addition to food supply), if proven that it has an effect on breeding success. In the French Pyrenees, weather is particularly cold and humid, and most bearded vulture territories have alpine weather with Atlantic influence (Champeaux and Tamburini, 1995). Additionally, appropriate (sheltered) cliffs for nesting are less numerous than in other areas of its breeding range, whereas human pressure (i.e. human activities and development) is strong. Under these circumstances, if human activities reduce nest attendance, they may potentially influence bearded vulture breeding success.

We thus aimed to assess the effect of human activities on bearded vultures breeding in the French Pyrenees. We first evaluate whether potentially disturbing activities had any effect on bearded vulture behaviour during reproduction (primarily a decrease in nest, clutch or brood attendance). We also evaluated whether this effect varied in relation to the type of activities and the distance to the nest. Second, we tested whether there was any relationship between the frequency of human activities recorded in a nest area and breeding success. Finally, we discuss the implications of our results for management schemes and conservation of this species.

2. Methods

2.1. Data collection

Human activities (or their absence) were recorded during the usual monitoring of the bearded vulture population in the French Pyrenees. This involved weekly (on average) visits to each potential nest area (hereafter called “territory”) throughout the season or until failure was proved, each visit lasting on average 4 h. All observations were made at >700 m from the nests, with binoculars and telescopes, and birds were apparently unaware of observers. Observations were random in relation to other parameters (i.e., they were not longer in the event of observing human activities), since their main purpose was to monitor the population. Each breeding season was defined from 1st October to 30th September the following year, which corresponds to nest selection (October) to the end of post-fledging period (September–October). Visits to each territory were distributed throughout the breeding season. Mean (\pm SD) number of visits to each nest area was 11 ± 9 ($n = 129$) during the pre-laying period, 9 ± 5 ($n = 92$) during the incubation period, 16 ± 15 ($n = 67$) during the nestling period and 6 ± 6 ($n = 39$) during the post-fledging period (see below for definition of the breeding periods). We analysed observations recorded during the breeding seasons 1993/1994–2001/2002, for those territories where human activities (or their absence) were consistently noted by observers. In total, we analysed data for 129 breeding attempts from 22 territories (6 ± 3 breeding attempts per territory, range 1–9). Territories are usually occupied by the same birds year after year (unless one of the birds die), so breeding attempts in the same territory in different years are usually related to the same breeding pair. In all monitoring visits, it was recorded whether birds were present in the territory or not. “Absence” was defined as no member of the pair being visible within 2 km of the nest, for the whole duration of the visit.

Potentially disturbing activities were the following: cars (vehicles on roads close to the nests; most observations involved relatively quick passage of cars on roads that were not directly visible from the nest); motorbikes (in many cases outside roads); helicopters; small planes; gliders; paragliders; forestry activities (tree cutting for forestry exploitation); burning (“controlled” fire lit to create open areas for grazing); hunting (mainly hunting of wildboars, stags, roe deer and mouflon, by groups of 10–40 people, approaching by car and/or by foot); mountain climbing; fire (criminal, as opposed to burning); intervention (by ornithologists to monitor bearded vulture reproduction); military activities (manoeuvres and military planes); farming/shepherding; photographers (people approaching nests to take pictures or to film); “walkers” (people by foot, including hikers, fishermen or bird watchers), infrastructure works (road or path construction, hydroelectric work or other infrastructures). We wanted to test whether the relationship between distance to the nest and the effect of activities on vulture behaviour changed among types of activities, because this has direct implications for management. For analyses, activities were grouped in five categories according to the type of disturbance as potentially perceived by bearded vultures, as

follows: “very noisy” activities (helicopters, motorbikes, infrastructure works, military activities, forestry activities), “noisy” activities (cars and small planes), “least noisy” (“walkers”, climbers, photographers, shepherds, ornithologists, gliders, paragliders), “hunting” (which may be noisy, as well as having a visual impact, depending on the size of the hunting group and on whether or not cars and dogs are included, and the number of shooting events) and “fire” (provoked or controlled).

A total of 490 observations of human activities occurring within 2 km of a nest were gathered. Every time one of these activities was observed, the following variables were noted: the date, the linear distance to the nest (not including altitudinal differences), the duration of the activity (in minutes) and the behaviour of the birds, if possible. Each observation was coded as follows: whether the birds were present or not (birds were considered as “absent” following human activities when none of the members of the pair was visible within the territory, either at the nest or not, neither during the activity nor afterwards for at least 2 h until the end of the monitoring period); if they were present, whether birds showed a reaction to the activity or not (we defined a bird showing a reaction if the nest was unattended, i.e., if they stood up from the nest, left the nest or flew around the nest without perching). Sometimes, it was not possible to identify the behaviour of the birds because the nest was not directly visible from where the observer was. We did not use those observations for the analyses of behaviour, but we included them in the analyses of frequency of human activities (see below).

We also calculated for each breeding attempt the following periods: pre-laying (from October to laying, which usually takes place between late December and early March), incubation (from laying until hatching), nestling, and post-fledging (from first flights to September). Hence, we could allocate a breeding period for those activities occurring in territories where breeding had occurred, and we could calculate also the observation effort (number of visits) for each breeding period.

2.2. Statistical analyses

We analysed whether behaviour was affected by disturbing activities with logistic binary regression models, with “probability of absence” and “probability of reaction” as response variables (as binary variables, see Section 2.1), with a Binomial distribution and a logit link function. As explanatory variables, we included breeding period, distance, duration of the activity, and type of activity. Additionally, we included the interactions between type of activity and distance, and type of activity and breeding period, since they have direct implications for management. Observations carried out in the same territory in the same year, or in the same territory across years, are not necessarily independent, given that, for example, there may exist individual differences in reaction probability, or differences related to characteristics of the territory (like topography) that influence reaction. The best way to analyse those type of data is to use mixed models, including “territory” and “territory * year” as random variables. However, such models did not converge with our data set, particularly when including interactions between vari-

ables (such as the interaction between type of activity and distance). Therefore, we used General Linear Models (using the GENMOD procedure in SAS 8.0, SAS, 1988), with a Type 1 analyses, but including “territory”, “year” and “territory * year” as fixed effects in all models, before including any other explanatory variable. The significance of all variables was thus calculated once the within- and among-year effect of “territory” was taken into account. Additionally, and to double-check that results obtained that way were not the result of biased sampling across territories, we performed an F-test based on the mean deviance of effects vs. the mean deviance of the interaction between that effect and territory. Our assumption was that, if that test was significant, the significance of the effect itself was not due only to differences between territories. We do not present the results of the F-tests in the paper, but have only discussed results if they were significant.

Second, we calculated for each breeding attempt within each territory the total number of human activities recorded for each of the breeding periods (as above). Given that there was variation between territories in observation pressure, we related this figure to the total number of visits to the territory in each of the breeding periods. We evaluated whether frequency of human activities varied among territories and breeding seasons with a General Linear Model analyses, using “number of human activities” as response variable, with a Poisson distribution and a log link function, and using the log of “observation pressure” (number of visits) as an offset, and “territory”, “year” and their interaction as explanatory variables. We subsequently evaluated whether the probability of hatching (if laying had occurred), the probability of fledging (if hatching had occurred) or overall breeding success (probability of producing a fledging if laying had occurred) were related to the frequency of human activities in the relevant period. For this, we used General Mixed Model analyses, fitting the response variable to a binomial distribution, and using a logit link function, and including “territory” as a random variable, to control for among territory differences in variables like altitude or individual differences that may also influence breeding success.

3. Results

3.1. Types and seasonal frequency of human activities

Of 3561 monitoring visits to the bearded vulture territories, a total of 490 observations of human activities was gathered. The activities most commonly reported close to the nests were helicopter flights, hunting and walkers (Table 1). Timing of those activities varied. Hunting occurred mainly in the pre-laying period, because the hunting season coincided temporally with that part of the bearded vulture breeding cycle. Controlled burning occurred most frequently during the incubation and nestling period. Other activities were reported at most times of the cycle (Table 1). Overall, human activities were most frequent in the pre-laying and nestling periods, least frequent during the post-fledging period (Table 1). There were strong differences among territories in the frequency of activities, as seen by the large standard deviation values (Table 1).

Table 1 – Frequency of occurrence of the most common human activities (% of monitoring days in which each type of activity was recorded, data presented as mean ± SD for all territories) in relation to the breeding cycle of bearded vulture

| | Total | Prelying | Incubation | Nestling | Postfledging |
|------------------------|---------------|---------------|--------------|---------------|--------------|
| Helicopter | 4.09 ± 4.3 | 2.82 ± 4.2 | 1.10 ± 2.0 | 5.31 ± 12.1 | 1.19 ± 3.0 |
| Walkers | 3.25 ± 6.7 | 1.87 ± 3.4 | 2.43 ± 4.1 | 2.84 ± 6.4 | 0.93 ± 3.3 |
| Hunting | 3.15 ± 4.4 | 5.86 ± 7.8 | 0.65 ± 1.5 | 0.00 ± 0.0 | 0.00 ± 0.0 |
| Cars | 1.72 ± 2.8 | 1.47 ± 3.0 | 0.54 ± 1.4 | 2.22 ± 6.0 | 0.16 ± 0.7 |
| Climbing | 1.27 ± 5.0 | 0.92 ± 3.8 | 0.00 ± 0.0 | 0.00 ± 0.0 | 0.11 ± 0.4 |
| Planes | 1.12 ± 2.8 | 0.05 ± 0.2 | 0.89 ± 2.7 | 3.05 ± 9.0 | 0.00 ± 0.0 |
| Burning | 0.91 ± 1.6 | 0.18 ± 0.7 | 1.66 ± 4.0 | 2.02 ± 8.9 | 0.00 ± 0.0 |
| Infrastructure works | 0.42 ± 1.0 | 0.22 ± 1.0 | 0.08 ± 0.4 | 0.36 ± 1.1 | 0.00 ± 0.0 |
| Forestry activities | 0.30 ± 0.9 | 0.51 ± 2.1 | 0.21 ± 1.0 | 0.06 ± 0.3 | 1.56 ± 6.3 |
| Motorcycles | 0.23 ± 0.5 | 0.35 ± 1.0 | 0.22 ± 0.5 | 0.17 ± 0.4 | 0.00 ± 0.0 |
| Military activities | 0.21 ± 1.0 | 1.03 ± 4.8 | 0.00 ± 0.0 | 0.00 ± 0.0 | 0.00 ± 0.0 |
| Paragliders | 0.14 ± 0.5 | 0.05 ± 0.2 | 0.00 ± 0.0 | 0.23 ± 1.0 | 0.00 ± 0.0 |
| Intervention | 0.12 ± 0.3 | 0.00 ± 0.0 | 0.26 ± 1.2 | 0.07 ± 0.3 | 0.00 ± 0.0 |
| Wildlife photographers | 0.08 ± 0.3 | 0.00 ± 0.0 | 0.00 ± 0.0 | 0.12 ± 0.5 | 0.00 ± 0.0 |
| Shepperding | 0.07 ± 0.3 | 0.00 ± 0.0 | 0.00 ± 0.0 | 0.28 ± 1.0 | 0.00 ± 0.0 |
| Gliders | 0.05 ± 0.2 | 0.03 ± 0.2 | 0.08 ± 0.4 | 0.06 ± 0.3 | 0.00 ± 0.0 |
| Fire | 0.02 ± 0.1 | 0.00 ± 0.0 | 0.00 ± 0.0 | 0.00 ± 0.0 | 0.00 ± 0.0 |
| Total | 17.19 ± 17.25 | 16.06 ± 17.88 | 8.14 ± 10.47 | 17.31 ± 30.23 | 3.95 ± 8.37 |

3.2. Behavioural responses to human activities

Of the 490 observations in which human activities were recorded, whether the birds were also present could be determined in 375. Birds were absent from the territories in 35% of those cases, almost three times higher than when no human activities were recorded (13%, $n = 3186$). Occurrence of human activities thus significantly influenced territory attendance (Table 2). The probability of being absent from the territory also depended on the breeding period (Table 2) as, even when no human activities were reported, birds were more frequently absent in the post-fledging ($30.3\% \pm 26.2\%$ of cases, $n = 218$ observations from 17 territories) or pre-laying periods (20.5 ± 17.1 , $n = 1267$, 23 territories) than either in the incubation ($0\% \pm 0\%$, $n = 738$, 20 territories) or the nestling periods ($9.98\% \pm 7.8$, $n = 963$, 20 territories). There was also a significant interaction between breeding period and disturbance on territory attendance: birds were proportionally more likely to be absent following human activities if those happened in the pre-laying or the post-fledging periods (Table 4).

In those cases when human activities were reported, even when taking into account the effect of breeding period, probability of absence depended also on the type of activity (Table

3). The activity associated with most absences was hunting (Table 4).

When birds were present, the probability of showing a reaction to the activity that involved not attending the nest depended significantly on the breeding period (being also highest in the pre-laying period, Table 4), and the type of activity (being highest for hunting and very noisy activities, Table 4). In addition, probability of reaction depended on the distance to the nest (the closer to the nest, the higher the probability), the duration of the activity (the longer the activity, the higher the probability), and on the interaction between type of activity and distance (Table 3). The latter arose because, whereas very noisy activities or hunting elicited responses even if far away from the nest, least noisy activities or cars/small planes were tolerated unless within 500–700 m from the nest (Fig. 1).

In all analyses, there were significant differences in response among territories and among breeding attempts within territories (as shown by the “territory * year” interaction, Tables 2, 3).

Table 2 – Results from the logistic regressions explaining the probability of absence in relation to the breeding period and the occurrence of human activities within 2 km of the nest

| Variable | Probability of absence | | |
|-------------------|------------------------|----------|--------|
| | Df | χ^2 | P |
| Territory | 25 | 290.88 | 0.0001 |
| Year | 8 | 20.95 | 0.007 |
| Territory * year | 97 | 351.20 | 0.0001 |
| Breeding period | 3 | 221.50 | 0.0001 |
| Human activity | 1 | 106.45 | 0.0001 |
| Period * activity | 3 | 51.35 | 0.0001 |

Table 3 – Results from the logistic regressions explaining the probability of absence if human activities were reported, and the probability of birds reacting if they were present

| Variable | Probability of absence | | | Probability of reaction | | |
|-----------------------------|------------------------|----------|--------|-------------------------|----------|--------|
| | Df | χ^2 | P | Df | χ^2 | P |
| Territory | 20 | 111.87 | 0.0001 | 18 | 33.89 | 0.01 |
| Year | 9 | 22.39 | 0.008 | 9 | 35.82 | 0.0001 |
| Territory * year | 48 | 138.53 | 0.0001 | 21 | 32.53 | 0.05 |
| Distance (km) | 1 | 3.09 | 0.08 | 1 | 21.90 | 0.0001 |
| Breeding period | 3 | 57.01 | 0.0001 | 3 | 42.58 | 0.0001 |
| Type of activity | 4 | 12.82 | 0.01 | 4 | 16.55 | 0.002 |
| Duration | 1 | 0.00 | 0.95 | 1 | 16.47 | 0.0001 |
| Distance * type of activity | 4 | 6.34 | 0.17 | 4 | 9.30 | 0.05 |
| Period * type of activity | 9 | 14.55 | 0.10 | 9 | 10.01 | 0.35 |

Table 4 – Responses of bearded vultures to human activities in relation to breeding period and type of activity: average ± SD proportion of observations where birds were absent or, if present, the proportion that reacted

| | N | % Absent | Np | % React |
|-------------------------|-----|------------------|-----|------------------|
| <i>Breeding period</i> | | | | |
| Prelaying | 194 | 53.1 ± 38.5 (19) | 52 | 52.7 ± 47.5 (15) |
| Incubation/hatching | 64 | 0.75 ± 2.5 (11) | 63 | 22.2 ± 30.6 (11) |
| Nestling | 101 | 10.7 ± 15.9 (14) | 84 | 31.1 ± 35.8 (13) |
| Post-fledging | 16 | 58.3 ± 50.0 (4) | 9 | 33.3 ± 47.1 (2) |
| <i>Type of activity</i> | | | | |
| Very noisy | 111 | 35.7 ± 34.7 (18) | 49 | 42.0 ± 33.6 (15) |
| Noisy | 71 | 39.3 ± 40.9 (10) | 51 | 36.6 ± 29.6 (8) |
| Least noisy | 84 | 26.5 ± 38.3 (15) | 66 | 35.5 ± 42.4 (12) |
| Hunting | 85 | 64.7 ± 27.5 (12) | 24 | 41.7 ± 51.0 (10) |
| Fire | 24 | 9.25 ± 25.2 (7) | 18 | 11.0 ± 6.4 (7) |
| Total | 375 | 34.7 ± 29.5 (22) | 205 | 35.0 ± 30.5 (20) |

Averages calculated as the average for each territory (in brackets, number of territories). N, number of observations; Np, number of observations where birds were present.

3.3. Relationship between frequency of human activities and breeding success

There were strong significant differences between territories and breeding attempts within territories in relation to the frequency of human activities recorded ($\chi^2_{21} = 300.22, P < 0.0001$ for “territory”; $\chi^2_8 = 68.12, P < 0.0001$ for “year” and $\chi^2_{99} = 224.96, P < 0.0001$ for “territory * year”). Six (27%) territories had none or very few reported incidences per breeding season, whereas in four (18%) an activity within 2 km of the nest was reported every three or four visits on average (Fig. 2). There were also large between-year variations among territories, as seen by the large standard deviations (Fig. 2).

The probability of success decreased with the frequency of human activities reported during the breeding season (GLIMMIX, $F_{1,72} = 3.67, P = 0.05$). Territories where no human activities were reported were on average five times more successful than those where human activities were reported in more than 20% of the monitoring visits (Fig. 3). A regression analyses of the average breeding success for each territory in relation to the average frequency of human activities reported showed a negative significant relationship ($F_{1,20} = 6.60,$

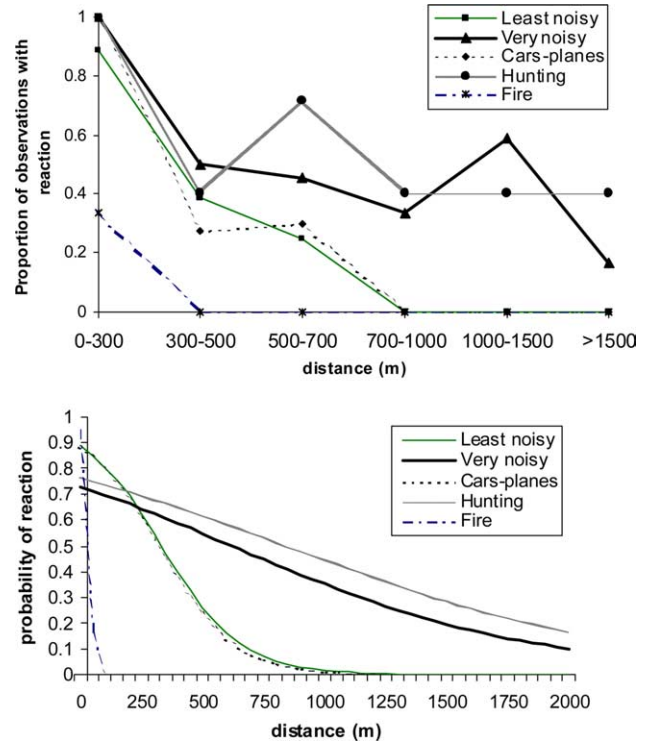


Fig. 1 – Observed (above) and estimated (below) probability of reaction to a human activity in relation to lineal distance between the activity and the nest, and the type of activity.

$P = 0.018, r^2 = 21\%$). In particular, there was a significant relationship between breeding success and the frequency of very noisy activities during the breeding season (GLIMMIX, $F_{1,107} = 4.19, P = 0.04$), but not with the frequency of other activities ($P > 0.10$). Additionally, there was a significant relationship between the proportion of monitoring days with human activities in which the nest was unattended (either because the birds were absent or because they reacted to a human activity) and the probability of nest success (GLIMMIX, $F_{1,76} = 4.07, P = 0.04$). No significant relationship was found between laying date and human activity frequency during the pre-laying period, hatching probability and human activity frequency during the incubation period, or probability of nestling survival and human activity frequency during the nestling period (all $P > 0.10$).

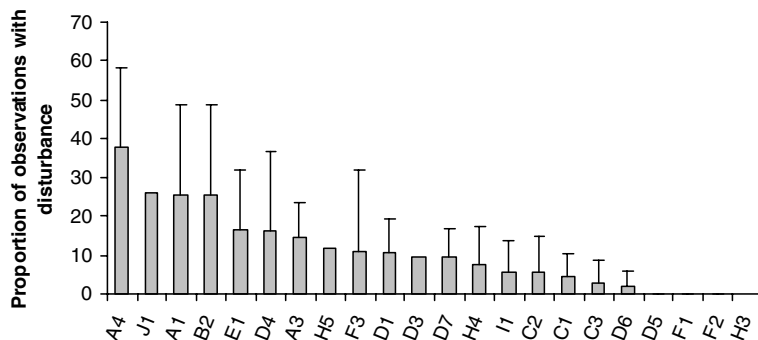


Fig. 2 – Average (±SD) proportion of monitoring visits in which at least one activity was recorded for each study territory.

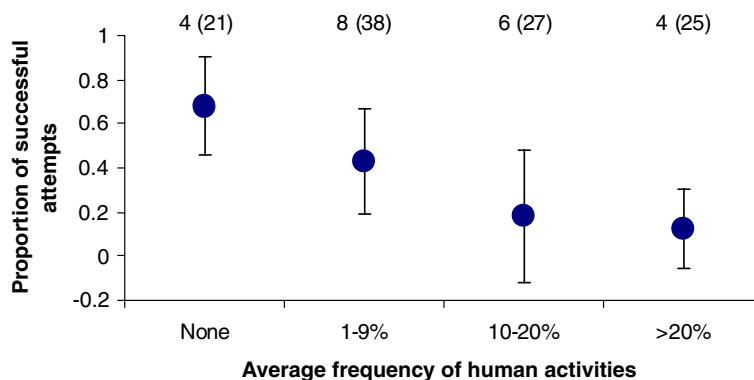


Fig. 3 – Mean (\pm SD) proportion of successful attempts in relation to the average frequency of human activities reported during the breeding season. Data represent the mean of the average success of all breeding attempts for each territory. Sample sizes: number of territories (number of breeding attempts in brackets).

4. Discussion

This study showed that some human activities (particularly when close to the nest) had an influence on bearded vulture behaviour, particularly on the probability of leaving the nest unattended, and that the frequency of human activities in the nest area had an influence on the probability of nest failure. It also showed that the distance at which human activities affected bearded vulture behaviour depended on the type of activity, and that there were significant differences between territories in relation to behavioural reactions.

4.1. Human activities and breeding success

As predicted, the frequency of human activities (particularly those activities that were related to a higher frequency of nest unattendance) had a significant probability of affecting nest success. In raptor species with a breeding cycle longer than six months, laying usually occurs at the beginning of winter, so the nestling period (the time with highest energetic needs) coincides with spring (when food abundance is usually at its highest) (Newton, 1979). This means that incubation/hatching usually takes place in the middle of winter; in those conditions, if disturbance causes the departure of the incubating/brooding bird from the nest area, this may engender thermoregulatory problems for the embryo or young nestling, which may ultimately result in embryo or nestling death (Mearns and Newton, 1988; Bradley et al., 1997). In the Pyrenees, the bearded vultures start laying during late December–early March, period during which temperatures frequently fall below 0 °C (Margalida and García, 2002). Additionally, appropriate (sheltered) cliffs for nesting are less numerous than in other areas of its breeding range, which may explain why disturbance affected success.

The latter result does not take into account individual differences in behaviour, which are important in this and other species (Didier et al., 2002; Van Oers et al., 2004), so human activities do not necessarily have a disturbing effect on all birds. In this study, the effect of human activities on bearded vulture behaviour varied among territories: this may be related to differences in topography between territories, but also on individual differences between the birds. There is

high site fidelity among years in this species, except when one of the birds dies. Therefore, “territory” is probably also a synonym of “breeding pair” and thus of individual differences in behaviour. Nevertheless, and despite these individual differences, results in this study show that human activities occurring around the nest sites of bearded vultures in the French Pyrenees had a high probability of affecting their behaviour and, ultimately, their breeding success. Our analyses did not take into account factors such as lay date, breeding density or age of the parents, which are known to influence breeding in this species (Heredia and Margalida, 2001; Margalida et al., 2003). It could also be that disturbance may be a correlate of other variables (e.g., if more frequently disturbed territories are also worse quality territories or occupied by lower quality parents). However, mixed models allow to analyse hierarchical designs (Littell et al., 1996), so our results show that increased disturbance was associated to increased failure probabilities not only across, but within territories and, ultimately, that human activities and disturbance are an important factor on its own. Breeding attempts within territories that were exposed to higher frequency of human activities, and in particular higher frequency of noisy activities within 2 km, had higher probabilities of failure.

It would be important to evaluate how this reduced productivity affects population dynamics. As specified in Section 1, average productivity in the French Pyrenees is lower than in some other areas, and could thus improve if the frequency of human activities was limited around the nest areas. In fact, results show that a reduction of human activities in the appropriate areas could potentially improve bearded vulture productivity up to 50% in those areas: as seen from data in Fig. 3, on average 8 fledglings are produced each year from the 22 study territories. If human activities occurred less frequently than 10% in all territories, and productivity in the (currently) disturbed territories increased to the level of those territories suffering less than 10% disturbance, the total productivity could increase to 10 young per year. This calculation is possibly an overestimate, since other factors (such as weather and individual quality) also influence breeding success, but it shows that potentially a relatively simple management measure could impact on the population of this threatened species.

Finally, it is also possible that areas that are frequently disturbed are more likely to be abandoned in subsequent breeding attempts, and thus that disturbance may also have delayed effects on bearded vulture reproduction. This study did not include such an analysis, but it may be worthwhile exploring this issue in the future. Such delayed responses to human disturbance have been observed in other species, like Ferruginous Hawks *Buteo regalis* (White and Thunrow, 1985). Absence from the nest area during the pre-laying period may lead to pair instability (leading the pair to move to another nest or territory). Movements between territories may also be due to other factors, such as competition with Griffon Vultures *Gyps fulvus* (Razin, 1997; Margalida and Garcia-Ferré, 1999), but disturbance and the absence from the nest area for extended periods of time may exacerbate this problem. Since the availability of high quality cliffs is low in the French Pyrenees (Razin, 2003), birds moving territories are likely to occupy lower quality ones in terms of availability of cavities protected from weather, which may have important consequences for bearded vulture breeding.

4.2. Management implications

As observed in other species (Grubb and King, 1991), the effect of human activities on bearded vulture behaviour depended on the type of activity and the distance to the nest at which these activities occurred. Furthermore, the effect of distance varied in relation to the type of activity. Assessment of those variations gives input on the best management scenarios to minimise the effect of human activities on bearded vultures since management actions tailored to specific disturbance types may be most effective (Grubb and King, 1991).

Very noisy activities (such as infrastructure works, motorbikes, forestry or military activities and helicopters) seemed to be those most strongly affecting bearded vulture behaviour and breeding success. Noise is particularly transmitted in alpine habitats, as relief provokes echoes and increases resonance. These activities thus provoked a reaction in bearded vultures even if far away from the nest (2 km). Breeding success was significantly negatively associated with the frequency of very noisy activities in a territory during a breeding event, as the probability that nests were left unattended was higher in those territories. These activities should, therefore, be largely avoided around the nests in order to maximise bearded vulture productivity.

Hunting also strongly affected bearded vulture behaviour during the pre-laying period, as it was associated with the absence of the pair from the territory in a significantly high proportion of cases. Bearded vultures were more frequently absent from the territories in the post-fledging period, even in the absence of human activities. However, hunting increased significantly the probability of absence, which, as specified above, may potentially lead to pair instability. Even when the birds were present, hunting frequently provoked a reaction. This effect also occurred when hunting activities took place at large distances from the nest, which may be associated with the fact that hunting as exercised in the French Pyrenees (with groups of people) is also potentially noisy as well as having a visual impact.

Bearded vultures were relatively tolerant of cars or planes, and to people on foot, if they were more than 500–700 m from the nest. The fact that no relationship was found between bearded vulture breeding success and the frequency of cars/planes or least-noisy activities (people on foot and gliders) may be related to this distance effect: it is possible that only the frequency of those activities close to the nest (and not their overall frequency) affects bearded vulture breeding. However, it should also be emphasized that topography, visibility and the relative altitudinal distance between the events and the nests are likely to have a strong influence in explaining how bearded vultures react to human activities where visual, not auditory cues are the most important. In particular, most observations of small planes (as specified in the methods) related to planes passing at high altitude (above the relief), so the actual distance was larger than the linear distance of 500–700 m described. Additionally, most observations of cars involved relatively quick passage (rather than parked) on roads that were not directly visible from the nest: bearded vultures choose sites, if possible, that are far away from roads (Donazar et al., 1993). Visibility and position in relation to the nest significantly influenced whether Bald Eagles *Haliaeetus leucocephalus* reacted to human activities (Grubb and King, 1991). Future work with bearded vultures should include the analyses of those variables (topography, visibility and altitudinal distance) in order to adjust the exact distances at which buffer zones should be implemented. In the meantime, it is probably safer to assume that such activities are not detrimental to bearded vultures beyond 500–700 m from the nests, provided they are not within direct sight of the nest.

Even if breeding failure was related to the frequency of human activities, there did not seem to be a particular period where disturbance was most important in terms of leading to failure. In the Spanish Pyrenees breeding success was overall related to the failure during the hatching and incubation periods (Margalida et al., 2003). We could have thus expected that, if breeding success is influenced by disturbance, it would be during the incubation period that it would be mostly manifested. However, our analyses did not identify that disturbance during the incubation period was more important in determining breeding success than disturbance at other times. One of the reasons for that may be that our analyses do not have enough power to detect differences when analysing data per period (given the smaller sample size in that case). On the other hand, in the French Pyrenees, nest failure does not happen more frequently in the incubation/hatching than in the nestling period. Of 64 failures recorded between 1994 and 2002, half of them occurred during the incubation (29.7%) and the hatching (23.4%) periods, whereas a large proportion (46.9%) of nest failures occurred during the nestling period (particularly in the first month after hatching, 35.9% of failures, M. Razin, unpubl. data). Weather in March–April (when hatching has occurred) is more humid and cold in the French than in the Spanish Pyrenees, which may explain the nestling deaths if nestlings are unattended. Disturbance during the pre-laying period (October–December) also seemed to be important, as stated above, to allow bearded vultures to settle in good nest areas, which are limited. A strong effort should probably be directed to avoid disturbance during

incubation and the first part of the nestling period (end of December to end of April), but it probably would be important that a “tranquillity” zone around the nest is kept year-round (avoiding noisy activities up to 2 km, and other activities close – <500–700 m – to the nest), in order to enhance bearded vulture stability and productivity.

Overall, frequency of human activities varied between territories and between years within territories. Weather may possibly explain annual differences in the frequency of disturbance: access to some sites in the French Pyrenees may be precluded by snow. Results also showed that some territories were much more prone than others to suffer disturbance from human activities. The precautionary principle would probably dictate that protective measures should be implemented more intensively in these disturbed areas.

In summary, this study showed that human activities have a direct effect on bearded vulture behaviour, increasing the likelihood that nest areas would be unattended. Although important factors potentially explaining breeding success could not be controlled for, results also point that an increased probability of nest failure occurred in those areas where disturbance was more frequent. The types of activities that appeared to have stronger effects were very noisy activities and hunting. It will be important to evaluate in the future whether there are any delayed effects of disturbance on bearded vulture breeding (particularly, in increasing the probability of territory or nest change in subsequent years), and the importance of topography on explaining bearded vulture's reaction to disturbance. Conservation measures based on these results may minimise detrimental effects of human activities on bearded vultures in the French Pyrenees.

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