Human–Wildlife Interactions 13(3):459–473, Winter 2019 • digitalcommons.usu.edu/hwi

Similar breeding success of bearded vultures in disturbed and undisturbed areas shows evidence of adaptation capabilities[1]

Vincent Comor, Research and Consulting Agency in Applied Ecology Naturaconsta, 12 rue des bouchers, 67270 Hochfelden, France *v.comor@naturaconsta.com*
Nicolas Poulin, CeStatS, IRMA, UMR 7501, Université de Strasbourg and CNRS, 7 rue René-Descartes 67084 Strasbourg Cedex, France
Mathieu Boos, Research and Consulting Agency in Applied Ecology Naturaconsta, 12 rue des bouchers, 67270 Hochfelden, France

Abstract: Human activities are usually considered as disturbing factors impeding the breeding success of wild animals. Protected areas can then be set up to restrict such activities aiming to improve wildlife's breeding success and conservation. To test for the efficiency of these measures, we compared the breeding success of bearded vultures (*Gypaetus barbatus*) in the western French Pyrenees from autumn 2011 to spring 2017, where eyries are located either within or outside restricted areas, where potentially disturbing activities are restricted (e.g., helicopter flights, forestry works, hunting, paragliding). We monitored reproducing bearded vultures and checked the breeding success at different stages (laying, incubation, hatching, and survival at 2 months) of formed pairs. We then compared the success of each stage between eyries located in restricted and non-restricted areas, including weather data in our model. We found that the breeding success was similar in both types of areas, but that is was negatively impacted by precipitations, which may directly affect the ability of the egg or chick to withstand cold. We also focused on the potential disturbance of hunting parties on the behavior of bearded vultures and found no evidence that hunting was perceived as a threat by bearded vultures; they may in fact benefit from gut piles. Hence, our comparison of the breeding success between eyries located in restricted versus non-restricted areas shows no detrimental impact of human activities and calls for some studies to assess the effectiveness of restrictions in improving the breeding success of bearded vultures, as this species seems to show some degree of tolerance to human activities and may significantly suffer from harsh winter weather in this area.

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Key words: bearded vulture, breeding success, *Gypaetus barbatus*, human disturbance, hunting, Pyrenees, species adaptation, tolerance

Some wild animals require complete solitude (i.e., a place devoid of anthropogenic disturbances) of more remote areas to complete their life cycles. However, even in the more remote areas, some human activities, such as forestry and outdoor recreational activities (Carney and Sydeman 1999, Zuberogoitia et al. 2008), can be highly disruptive for wildlife (Arroyo and Razin 2006). The demand for and development of tourism and leisure activities encourage more people to use natural environments for recreational activities (Gill 2007). Concomitantly, as more remote areas become easily accessible to humans for recreation, these activities create disturbances that animals can or cannot tolerate (Romero and Wikelski 2002, Bathe 2007).

The impact of human disturbances on wildlife has been studied for a long time to determine whether wildlife is actually impacted (Gill et al. 2001*a*) and, if so, the threshold of human disturbance that some species can withstand through tolerance or adaptation (Romero and Wikelski 2002, Gill 2007, Bejder et al. 2009) and resilience (Holling 1973). If they cannot adapt, animals can then suffer from chronic stress (Barber et al. 2010), and some may even abandon suitable habitats where humans are present (Stalmaster and Newman 1978, Burger 1981). Not only do species-specific traits matter in determining the degree of tolerance to and avoidance of a disturbance, but the environment (resource availability, competition, predation) may also influence how an animal will respond

[1]Retraction notice: see page 473.

Figure 1. Bearded vulture (*Gypaetus barbatus*; *photo by J. C. Noreña*).

to a disturbance (Cooke 1980, Smit and Visser 1993). Some species also exhibit a greater degree of tolerance than others (Cooke 1980, Klein et al. 1995).

Birds, such as vultures in the family Accipitridae, which live in very remote areas and nest on cliffs, may be more susceptible to human activities than other bird species. Increased anthropogenic activities in vulture habitats may impact reproduction to such an extent that their breeding success could decrease, even in natural parks (Zuberogoitia et al. 2008). In particular, the bearded vulture (*Gypaetus barbatus*; Figure 1), is assumed to be highly sensitive to human activities in the Pyrenees (Donázar et al. 1993, Arroyo and Razin 2006). This long-lived species feeds on carcasses, mostly from the meat and bone remains of medium-sized ungulates (Margalida and Bertran 1997, 2008).

The bearded vulture is globally classified as a near threatened species (BirdLife International 2017) but as endangered in France (Union internationale pour la conservation de la nature France, Muséum national d'histoire naturelle, Ligue pour la protection des oiseaux 2016). The French Pyrenean population of bearded vultures that breed in the northern part of this mountain range shows some noteworthy differences with other populations concerning its reproduction. The average breeding success on this side of the Pyrenees is relatively low, with 0.35 fledglings per territorial pair per year (Arroyo and Razin 2006), which is lower than the 0.40 fledglings per year for the overall Pyrenean population (Heredia et al. 2013); 0.59 for the Spanish side alone from 1994 to 2000, and also lower than the 0.44 fledglings per year in the Alps (Arroyo and Razin 2006). This low breeding success is characterized by clutch failures, mostly occurring during the hatching period (Margalida et al. 2004), which is considered the most critical stage of breeding success (Margalida et al. 2003*b*).

One hypothesis suggests that the adverse weather conditions occurring in this area at the time of reproduction, characterized by cold and humid weather, may explain the poor breeding success of the French (northern Pyrenean) population (Razin et al. 2008). Indeed, weather conditions have been shown to influence the breeding success of bearded vultures, with snow (Donázar et al. 1993) and rainfall having a markedly negative effect (Donázar et al. 2002), which may be a critical point in the western French Pyrenees, where the climate is characterized by heavy rains and cold spells (Kessler and Chambraud 1990).

The observed low bearded vulture reproduction rate in the Pyrenees could also result from the pressure exerted by some human activities that disturb birds and could lead to multiple breeding failures. The impact of human activities on breeding success has already been shown for several bird species (Madsen 1995, Gutzwiller and Anderson 1999, Verhulst et al. 2001). For example, human activities can affect oystercatcher reproduction, disrupting both the incubation and chick feeding phases (Verhulst et al. 2001). Human presence and/or the noise made by people increase anti-predation vigilance and could, therefore, indirectly reduce breeding success by decreasing foraging time (Quinn et al. 2006). Thus, noisy human activities, though non-lethal and not even aimed at birds, can be perceived as a threat to which birds respond as if they were at risk of predation (Frid and Dill 2002, Beale and Monaghan 2004). Some care should be taken, though, in considering that the avoidance of humans will have a negative impact on bird populations, as animals can avoid human disturbances in time and space to exploit other resources placed in non-disturbed

areas (Gill et al. 2001*b*, Goss-Custard et al. 2019). Concerning the bearded vultures in the Pyrenees, previous studies have concluded that food resources were in sufficient quantity to satisfy their needs (Canut et al. 1987, Margalida and Bertran 1997).

However, in the case of the breeding success of bearded vultures, the most troublesome factor resulting from leaving their nest would not necessarily be the energy spent on fleeing, but the ensuing lack of care of eggs and chicks (Frid and Dill 2002). Left unprotected, an egg or chick would be at the mercy of predators (e.g., corvids; Vulture Conservation Foundation 2016) and exposed to harsh weather conditions (cold, rain, snow, wind). In the case of a prolonged absence of a brooding parent, this can lead to the death of the embryo or chick (Bradley et al. 2012).

Hence, to prevent human disturbances from negatively impacting the breeding success of bearded vultures and based on the observations of Arroyo and Razin (2006), restrictions of human activities have been implemented around certain bearded vulture nests of the French Pyrenees for almost a decade. Within these areas, any supposedly disturbing human activity (mostly noisy and/or aerial ones such as helicopters, forestry, hunting, paragliding) is prohibited from November 1 to August 15 in a perimeter covering a radius of 1,800 m around designated nests deemed at risk (Ministère de l'Écologie 2010). However, evidence that human activities are responsible for the low breeding success of the bearded vultures in the western French Pyrenees remains scant. Therefore, we monitored the reproduction of bearded vultures nesting within and outside restricted areas in order to test the effectiveness of these conservation measures in improving the breeding success of bearded vultures.

In the non-restricted areas, hunting, which represents an important socioeconomic practice (Mateo-Tomás and Olea 2010), may be particularly disturbing for bearded vultures, especially during the prelaying period of territory attendance (Arroyo and Razin 2006). Several studies have determined that, besides the direct mortality hunting induces on quarry species, it can indeed have a disturbing impact on nearby wildlife (Madsen and Fox 1995, Madsen 1998, Laursen et al. 2005). The hunting-related disturbances can be of several types for nontarget bird species. First, birds can see the hunters and their dogs (if present), thereby making a party of hunters more conspicuous than hikers. Then, the noise coming from the talking hunters as well as their barking dogs can also be disturbing. Finally, the noise associated with gunshots may be the most destressing disturbance resulting from a party of hunters, even though shots are not fired during each outing and, if they are fired, they are rather rare.

There are many studies on the indirect impacts of hunting on nontarget waterbirds (Madsen and Fox 1995, Madsen 1998, Laursen et al. 2005, Dooley et al. 2010, Sokos et al. 2013), because the preferred environment of these birds, wetlands, is also favored by hunters due to the great diversity and abundance of game birds in these areas. Regarding raptors, Arroyo and Razin (2006) studied the impact of several human activities on the behavioral responsiveness and nesting of bearded vultures. They assumed that hunting could be responsible for indirectly decreasing the breeding success of bearded vultures because of the disturbance it might create. Significant decreases of the breeding success have also been associated with other noisy activities (i.e., helicopters, motorbikes, military activities, forestry works; Razin and Arroyo 2005). However, the real relative impact of other human activities (including hunting) remains controversial. Compared to areas devoid of human activities, the impact of specific human activities on breeding stages, ranging from the occupation of the breeding area to the fledging of the offspring, remains unclear, especially regarding hunting (White 2005, Dooley et al. 2010, Margalida et al. 2011).

Because an observed behavioral and spontaneous response to a disturbance does not necessarily mean that it has a negative impact on the long-term well-being and conservation of an animal (Beale 2007), we focused on the impact of anthropogenic activities on the breeding success of bearded vultures. We asked whether, once a pair of bearded vultures started nesting, their breeding success in the western French Pyrenees was impeded by the disturbance that human activities may represent, focusing more specifically on hunting. To this end, we monitored 4

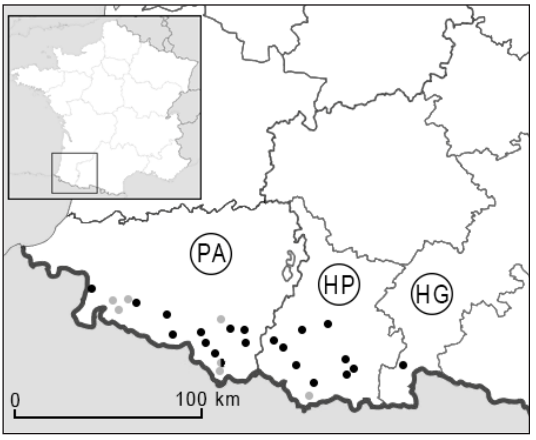

Figure 2. Location of the 27 monitored bearded vulture (*Gypaetus barbatus*) eyries, from autumn 2011 to spring 2017, in the French departments of Pyrénées-Atlantiques (PA), Hautes-Pyrénées (HP), and Haute-Garonne (HG). Gray dots refer to eyries that were in a restricted area from the outset of the study, black dots refer to eyries around which all human activities have remained allowed for the duration of the study, and the half-black half-gray dot represents the eyrie around which human activities were allowed at the beginning of the study and, subsequently, restricted.

Figure 3. The Gavarnie valley, a typical landscape of the French Pyrenees (*photo by Moahim*).

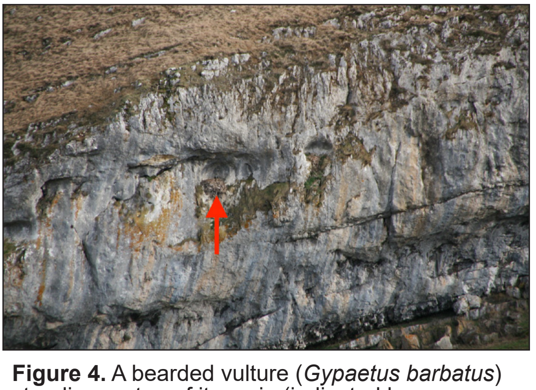

Figure 4. A bearded vulture (*Gypaetus barbatus*) standing on top of its eyrie (indicated by an arrow) in the middle of a cliff (*photo courtesy of D. Acheritogaray*).

stages of bearded vulture reproduction (i.e., egg laying, incubation, hatching, and chick survival up to 2 months). We then compared the success of each stage between nests located in restricted areas and outside of these areas devoid of disturbing human activities. We hypothesized that the breeding success of eyries located within a restricted area would be higher than the one of eyries located where human activities could occur freely, thereby potentially impeding reproduction. The study was conducted over several years (from 2011 to 2017) to take into account the effect of changing weather conditions from year to year, which are suspected to influence bearded vulture breeding success (Arroyo and Razin 2006, Margalida and Bertran 2008).

Study area

Our study was conducted in the western part of the French Pyrenees, in the 3 departments of Pyrénées-Atlantiques, Hautes-Pyrénées and Haute-Garonne, from autumn 2011 to spring 2017 (Figure 2). This area is characterized by mixed forests in the valleys, dominated by oak (*Quercus* sp.) and chestnut trees (*Castanea sativa*) at the lower altitudes, then by beech (*Fagus sylvatica*) and fir (*Abies* sp.) until 1,500 m. Above, mountain pines (*Pinus uncinata*) dominate the subalpine zone, and alpine grasslands can be found above (D. Acheritogaray, personal communication; Figure 3). Many cliffs, which offer more or less suitable habitat for bearded vultures to build their eyries, can be found across the Pyrenees (Figure 4). The forests are exploited for their wood and the grasslands are grazed by sheep. The climate is typical of mountainous areas, but this part of the Pyrenees experiences rather harsh winters, with heavy precipitation coming from the Atlantic Ocean and severe cold spells in winter (Kessler and Chambraud 1990).

We monitored 27 eyries: 6 located within a restricted area, 20 where human activities were permitted throughout our study, and 1 where human activities were allowed for the first year of the study, before being subsequently restricted for the 3 following years. Across all years, 70 different breeding attempts have been followed, 15 within a restricted area and 55 outside. In the non-restricted areas, the minimal distance of a hunting party (hunters

and sometimes dogs [*Canis familiaris*]) to a nest could be as low as 50 m (at the bottom of the cliff, below the nest) and about 150 m from a soaring bearded vulture when shooting game, whereas the minimal distance between an eyrie located in a restricted area and hunters was at least 1,800 m (most of the time several times more; Ministère de l'Écologie 2010).

Methods

We monitored bearded vulture eyries using telescopes. Monitoring was initiated once the pairs had settled, from a safe distance ensuring that they would not be disturbed by the observers (at least 500 m). Although the most critical stage for breeding success is considered to be hatching (Margalida et al. 2003*b*, 2004), success or failure was recorded at different stages of breeding: egg laying, incubation, hatching, and chick survival up to 2 months after hatching, based on Margalida et al. (2003*b*). Egg laying was noted as successful as soon as 1 egg was laid by a pair; it was recorded as failed if no egg was laid. Incubation was considered as failed when parents stopped incubating the eggs before the end of this period (ca. 54 days; Margalida et al. 2003*b*). Hatching was recorded as failed when parents had incubated the eggs up to the end of the usual incubation period, but none of the eggs hatched or none of the chicks survived for >7 days following hatching. If a chick that had survived for the first 7 days of his life was still alive 2 months after hatching, we then recorded this as successful for the survival at 2 months.

Estimation of the noise produced by hunting

The sound tests were performed using a Voltcraft™ SL100 noise recorder with an accuracy of ± 2 dB, in environments similar to the ones where bearded vultures live. The sound intensity of the gunshot from a magnum 12-gauge rifle at 150 m was about 59 dB (wind speed <2 m.s-1) and 47 dB at 1,800 m. This can be compared with the 33 dB of the background noise of a dry temperate forest; the background noise reaches >52 dB in the same environment in rainy conditions (Lengagne and Slater 2002).

We are not aware of any study that investigated the auditory sensitivity of the bearded vulture. However, we found a study carried out on a nocturnal raptor, the Mexican spotted owl (*Strix occidentalis lucida*), showing that this raptor has a 0–7% probability of flushing if the intensity of a noise (here, an operating chain saw) ranges from 50–68 dB, respectively (Pater et al. 2009). Other studies on passerine and shorebirds concluded that sounds whose intensity is <65 dB are not likely to trigger any response from birds nor have any impact on their behavior (Quinn et al. 2006, Wright et al. 2010). Some birds can tolerate anthropogenic noise up to 80 dB (Conomy et al. 1998*a*, *b*). From our measurements, dog barking at 40 m (60 dB) was below that threshold and, at 100 m, ranged from 45–50 dB. As proposed by Arroyo and Razin (2006) to mitigate hunting effects, hunting parties were at least 1,800 m (usually several times more) from the eyries located in the restricted areas; we therefore assumed that hunting parties (gunshots and dogs) could not be perceived as a threat (if even heard) by the bearded vultures as long as they were nesting in a restricted area.

Hunting

Hunting started in September of each year, where it was allowed (outside restricted areas), mostly aimed at medium-sized to big game (ungulates). In October, hunters switched to small game hunting, targeting wood pigeons (*Columba palumbus*), Eurasian woodcocks (*Scolopax rusticola*), and Iberian partridges (*Perdix perdix hispaniensis*). Most of the big game was hunted from November to January, while February was dedicated to reaching the target number of animals that hunters are compelled to cull to fulfil their management hunting plan for ungulates.

In all areas, different weapons were used depending on game; while medium-sized to big game (mostly wild boars [*Sus scrofa*], roe deer [*Capreolus capreolus*], and red deer [*Cervus elaphus*]) were hunted with rifles, small game were hunted with shotguns. Larger game hunting was usually practiced with the help of dogs. During 72 different hunting actions that lasted from 45 minutes to 2 hours, 1 observer (who was not hunting) followed the hunters, scanning the sky for the presence of bearded vultures. The minimal time between 2 hunting actions was 30–60 minutes. This monitoring occurred from early September until late

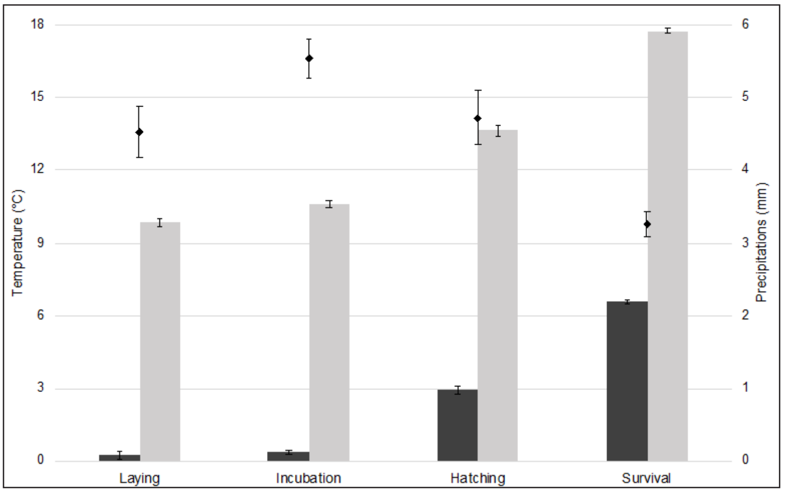

Figure 5. Mean daily minimum (dark gray) and maximum (light gray) temperatures, and mean daily precipitations (diamonds) recorded at all the bearded vulture (*Gypaetus barbatus*) eyries over the whole study period (autumn 2011 to spring 2017) for the 4 breeding stages: laying, incubation, hatching, and survival of the chick at 2 months.

February, from 2013 to 2016. When bearded vultures were spotted, the observer estimated the distance (to the nearest 100 m) between the bird(s) and the closest hunter to the bird (*N* = 34 cases).

Weather

Weather conditions have been suggested to have an impact on the breeding success of bearded vultures (Donázar et al. 1993, 2002); therefore, we also took into account the weather records of the nearest weather stations to each of the 27 eyries. To apply the weather data to our statistical model, we divided the breeding period into 4 periods corresponding to the 4 breeding stages: December 21 to January 20 for egg laying, January 21 to March 20 for incubation, March 21 to April 10 for hatching, and April 11 to June 10 for the survival at 2 months. For each eyrie, year, and breeding period, we calculated the mean minimum daily temperature, the mean maximum daily temperature, and the mean daily precipitations (Figure 5). Precipitations do not provide a distinction between rain and snow. The dataset was provided by Météo France. The maximum distance between an eyrie and the nearest weather station was 30 km.

Statistical analyses

Statistical analyses were performed in R (R Core Team 2018) and SigmaPlot 12.5 (Systat Software). We used the packages lme4 (Bates et al. 2014), car (Fox and Weisberg 2011), and tweedie (Dunn 2017).

The distance between hunters and bearded vultures were analyzed using either a parametric (Student's *t*-test) or a non-parametric test (Mann-Whitney), after checking for normality and equality of variances (using SigmaPlot). Weather data were standardized (mean-centered then divided by the standard deviation).

To compare mean minimum and maximum daily temperatures for each breeding stage between different years, we used linear models with breeding stage, year, and their interaction as fixed effects (in our analyses, year refers to each breeding season, from egg laying to survival at 2 months). To compare mean daily precipitations for each breeding stage across different breeding seasons, we used generalized linear models with a tweedie distribution, which allowed us to account for the semi-continuous, zero-inflated nature of the precipitations data. Breeding stage, year, and their interaction were used as fixed factors in this model. To test for the significance of the interaction terms in both types of models, we used likelihood-ratio tests (LRT), performed by drop1 and Anova (car) functions.

To identify the parameters that influence the survival of the clutch/brood, we fitted generalized logistic mixed models, which allowed us to consider the binary nature of the survival response variable and to control for pseudo-replication, thus taking into account the unbalanced nature of our sample (15 breeding attempts within a restricted area vs. 55 outside). We started with a full model that included 6 variables: year, eyrie status (restricted area or not), breeding stage (egg laying, incubation, hatching, and chick survival up to 2 months after hatching), mean maximal daily temperature,

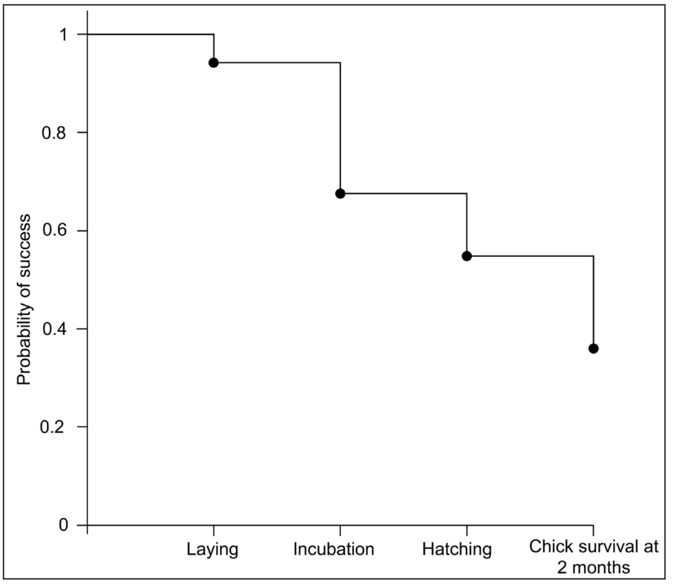

Figure 6. Overall probability of breeding success at each stage of reproduction of bearded vulture (*Gypaetus barbatus*) from both restricted and non-restricted areas in the French Pyrenees, from autumn 2011 to spring 2017. Since the eyrie status did not have any effect on the outcome of the breeding success ($P > 0.81$), the data have been pooled. As precipitation levels did have an effect, we used the mean precipitation level per breeding stage to compute this analysis.

mean minimal daily temperature, and mean daily precipitations of each breeding stage. The first 3 variables were used as fixed variables, the latter 3 as co-variables. Interactions between the fixed variables were also incorporated in the full model. The eyrie site was used as a random variable. Backward selection was performed based on the LRT criteria. For all analyses, significance level was set at 5%. Pairwise comparisons were performed by considering Tukey's *P*-value correction.

Results

Of the 70 breeding attempts of bearded vultures that were monitored (15 from eyries in a restricted area, 55 outside), 25 succeeded: 5 in a restricted area, 20 outside, which represents 33.3% (5/15) and 36.4% (20/55) of breeding success, respectively. When bearded vultures were observed during a hunting action, the distance between the birds and the closest hunter tended to be greater during firing actions (463 ± 60 m, $N = 25$) than during periods without firing (178 ± 55 m, $N = 9$), but the difference was not significant (U = 64, T = 109, $P = 0.06$, Mann-Whitney test). However, the distance between the birds and the hunters was shorter when more shots were fired ($r = -0.52$, $F_{1,20} = 7.39$, $P = 0.013$, $N = 25$, log-transformed data).

The optimal model, chosen by LRT, only included 2 variables: breeding stage ($P = 0.001$) and mean daily precipitations ($P = 0.019$). The mean (± SE) breeding success of the chicks at 2 months was 0.59 ± 0.11 and 0.50 ± 0.06 for restricted and non-restricted areas, respectively. Differences in eyrie status (restricted vs. not restricted), independently of breeding stage, were not significant ($P > 0.81$; Figure 6). Pairwise comparisons between each breeding stage showed that only the survival probability of laying was significantly higher than that of the survival at 2 months ($z = -2.3738$, $P = 0.005$), but that these survival probabilities did not significantly differ from incubation and hatching. Precipitations decreased the survival probability decreased as mean daily precipitations increased ($z = -2.339$, $P = 0.019$).

Discussion

Our study shows no difference in breeding success between bearded vulture eyries located in restricted and non-restricted areas of the western French Pyrenees, at any stage of the breeding cycle (egg laying, incubation, hatching, and chick rearing up to 2 months after hatching). To our knowledge, this is the first time that the effectiveness of the restricted areas implemented in the French Pyrenees has been tested. This contradicts our initial hypothesis and mitigates some results of Arroyo and Razin (2006), who showed that very noisy human activities negatively impacted bearded vulture breeding success, contrary to less noisy activities (and hunting), which were not related to breeding success, although such activities were a focal point considering territory attendance.

The overall breeding success (25 fledglings) of the 70 breeding attempts that we monitored equaled 0.36, which is in agreement with the recorded productivity of 0.35 fledglings per

pair in the French Pyrenees (Arroyo and Razin 2006). However, our analyses did not reveal that any particular breeding stage showed lowered survival probabilities than the other breeding stages.

Precipitations had a negative impact on the breeding success of bearded vultures. This result confirmed previous studies assuming that weather could negatively impact the survival rate of bearded vulture clutch/brood (Donázar et al. 1993, 2002; Arroyo and Razin 2006). Importantly, and independently of the restrictions of human activities, this is the first time the impact of weather conditions on the bearded vulture breeding success has been statistically tested in the French western Pyrenees. This region is particularly subjected to harsh winter weather conditions, characterized by high precipitation levels, due to the proximity of the Atlantic Ocean, which does not affect the rest of the Pyrenean mountain range (Kessler and Chambraud 1990, Arroyo and Razin 2006).

Rain and/or snow may increase egg or chick mortality because of a high sensitivity to cold, lower body mass, and especially as the egg or chick is not yet capable of thermoregulation. Additionally, bad weather may hinder the ability of the brooding parents to rapidly find food, forcing them to spend more time away from their eyrie, leaving the egg or chick unattended and unprotected for a long time, which could then impede its survival (Bradley et al. 2012). The peculiar weather conditions occurring in this part of the Pyrenees may explain the low breeding success from which the bearded vulture population of this area suffers (Arroyo and Razin 2006, Heredia et al. 2013). Therefore, even if the topographic and dietary requirements of the bearded vultures are met in this area, our results support the idea that the harsh weather conditions (especially precipitation) occurring during the breeding period may render this part of the Pyrenees akin to an ecological trap for the bearded vulture.

The distribution of the eyries located in restricted versus non-restricted areas was unbalanced and so were the number of breeding attempts that we observed in restricted non-restricted areas. This imbalance is due to the much lower number of eyries located in restricted areas and to their remoteness, making them hard to access on a very regular basis over a long period of time, which is required to monitor the breeding success of long-lived birds. Moreover, when eyries are located in restricted areas, because potentially disturbing human activities are forbidden, including wildlife photography (Ministère de l'Écologie 2010), it is difficult to monitor birds to negate the potential effect of the presence of an observer. Although this unbalanced dataset could have induced a bias in our results, our statistical analyses took this into account to limit this risk.

In their study on the behavior of bearded vultures in response to human activities, Arroyo and Razin (2006) mainly focused on the behavioral responses and inferred that the observed decreased territory attendance during the pre-laying period was due to hunting, even though there was no clear evidence for a causal relationship in this correlation. Demonstrating causal relationships between human activities and adverse impacts on the life of animals remains difficult (Nisbet 2000), and behavioral responses to human disturbance are deemed as insufficient to draw any conclusion as to the vulnerability to human activities (Gill 2007). For example, in their study on golden plovers (*Pluvialis apricaria*), Finney et al. (2005) stated that, even though these birds showed clear behavioral responses to human disturbance (hikers), their breeding success did not seem to be impacted.

During the hunting actions, bearded vultures cruising close to hunters were common and, when observed, they were usually gliding a few tens or hundreds of meters from hunters (D. Acheritogaray and M. Boos, personal communication). Likewise, during the study, griffon vultures (*Gyps fulvus*) have also been observed gliding close to hunters (D. Acheritogaray and M. Boos, personal communication). These observations are substantiated by our counter-intuitive result showing that bearded vultures were observed soaring closer to hunters when more shots were fired. Therefore, this would suggest that bearded vultures in the western French Pyrenees may have adapted to game hunting activities and tolerate them, since they do not seem to perceive them as a predation risk (Frid and Dill 2002, Bejder et al. 2009). Similarly, waders can learn about predation risk: a western

marsh harrier (*Circus aeruginosus*) approaching a wader colony will force thousands of birds to flush, whereas an osprey (*Pandion haliaetus*) can land in the middle of the same colony without waders showing any sign of wariness (Smit and Visser 1993). Most birds react to shots when they occur at a distance <80 m (Fox and Madsen 1997). Thus, we could assume that hunting on ungulates or forest birds, such as the wood pigeon and Eurasian woodcock, seems to not be perceived as a threat by bearded vultures.

Furthermore, it would appear that bearded vultures may have associated hunting with a feeding opportunity. This hypothesis could be supported by the fact that hunters are allowed to leave the gut piles of game that they field dress; bearded vultures, being bad competitors with other scavengers, could therefore follow hunters as a means of easily finding a food resource (Murn and Anderson 2008, Mateo-Tomás and Olea 2010). Griffon vultures have been shown to adapt their spatio-temporal use of a territory to make it coincide with trophy hunting, to benefit from the carcasses left by hunters (Mateo-Tomás and Olea 2010) and ravens (*Corvus corax*), and they can be attracted by gunshot sounds, expecting to find game gut piles left by hunters (White 2005). If this assumption were to be confirmed, this would then mean that, contrary to popular belief, hunting could benefit endangered vultures in this area.

However, if bearded vultures indeed feed on the gut piles left by hunters who field dress their game, the birds could ingest some lead shards coming from the shattered lead bullets and, eventually, suffer from lead poisoning (Hernández and Margalida 2009, Plaza and Lambertucci 2019). Even though cases of bearded vultures suffering from lead poisoning seem to be rare in our study area, cases have been reported concerning other scavenger species (Razin 2016). Therefore, it would be advisable for hunters to switch to lead-free ammunitions in order to make sure that bearded vultures and any other scavenger species feeding on gut piles are not at risk of lead poisoning. Moreover, even if only a few birds directly die from lead poisoning, low levels of blood lead can be sufficient to weaken a bird, which could then indirectly increase other mortality risks, such as diseases or hitting a power line (Margalida et al. 2008).

Further studies would need to be carried out to determine whether bearded vultures can tolerate the other restricted human activities. Even though we did not specifically study those other activities, our results would suggest that bearded vultures have learned that these activities do not represent a lethal threat, as the breeding success was similar whether these activities occurred or not. Samia et al. (2015) showed that, even though carnivorous birds may not be very tolerant toward human disturbances, large birds and species that produce small clutches are capable of a high degree of tolerance toward human disturbances. This can be explained by the fact that parents that invest a lot per offspring will tolerate more risk to ensure their breeding success and, thereby, to increase their fitness. These parents are, therefore, not likely to easily abandon their nest or territory because of the high fitness cost involved, besides the energetic cost of flight, which is supported by the optimal escape theory (Ydenberg and Dill 1986, Cooper and Blumstein 2015).

Although some human activities influence the breeding success of birds, evidence is poor that the bearded vultures are equally impacted by all of them in the western French Pyrenees to such an extent that it may impede their breeding success. The negative correlation that Donázar et al. (1993) showed between the bearded vulture breeding success and the density of paved roads could be due to the noise and overall activities of humans in such areas, but, most likely, it can be the result of a dearth of food resources in these urbanized areas (which seem to be ecological traps). Other studies have shown that human activities can have no effect or impact on raptors: jet aircrafts on the behavior of ospreys (Trimper et al. 1998) or the vicinity of developed areas on the breeding success of bald eagles (*Haliaeetus leucocephalus*; Fraser et al. 1985). Conversely, breeding failures in bearded vultures have been observed despite the scarcity of human activities (Margalida et al. 2003*a*) and the low, and somewhat random breeding success in the Pyrenees has remained unexplained, probably because weather parameters had not yet been considered to explain breeding failure, at least in the French western Pyrenees.

Our monitoring of the breeding success was only based on settled pairs that had just started

to nest. Hence, we could not assess the potential impact of human activities on pair formation, nor on their settlement during the pre-laying period (October to November). This was due to our limited monitoring capabilities and because previous studies have reported that hatching was the most critical stage for breeding success (Margalida et al. 2003*b*, 2004). It should therefore be mentioned that, as hunting is also practiced during autumn, it might disturb the pair formation and settlement of bearded vultures (Arroyo and Razin 2006). However, the hunting monitoring conducted to study the behavior of bearded vultures subjected to hunting actions took place throughout most of the hunting season, from early September to late February and, as mentioned earlier, hunting does not seem to negatively affect bearded vultures.

A potential cause of breeding failures that has been overlooked is the interspecific competition with other birds, especially ravens and griffon vultures, from which the bearded vultures may suffer, mostly regarding nesting sites (cavities in cliffs). During our monitoring, we repeatedly observed ravens and griffon vultures mobbing bearded vultures, and griffon vultures are well known for usurping bearded vulture eyries (Fernández and Donázar 1991, Margalida et al. 2003*a*, Gil et al. 2014). Although none of the bearded vulture eyries that we monitored was taken over by griffon vultures, the latter have been spotted several times sitting in a bearded vulture eyrie during the settlement period (D. Acheritogaray and M. Boos, personal communication). In their 20-year-old study, Margalida and García (1999) have not been able to observe any direct impact on the breeding success caused by nest usurpation by griffon vultures.

However, the Spanish Pyrenees (oriented southward) offer milder winter climate conditions (higher temperatures and lower precipitation levels) than the northern side, which is subject to high precipitation levels coming from the Atlantic Ocean during winter and spring (Kessler and Chambraud 1990, Arroyo and Razin 2006). Margalida and García (1999) nevertheless stated that some breeding failures had been attributed to negative interactions with griffon vultures and that it ought to eventually happen. Twenty years later, owing to the significant increase of the griffon vulture population, these mobbing and nest usurpations may explain the numerous breeding failures from which the bearded vulture population suffers; the annual population growth rate of griffon vultures reached 14% in the 1990s (Margalida and García 1999). The only information we could find in the literature regarding the evolution of the griffon vulture population in the French Pyrenees mentions that, while the population fluctuated from 580 pairs in 2006 to 525 pairs in 2007 (Razin et al. 2008), it had reached 847 individuals by 2012 (Peyrusqué and Gounot 2017).

Thus, it seems that the griffon vulture population has increased in the last years and this may contribute, at least partially or together with high precipitations during the breeding season, to the lower breeding success of bearded vultures in the Pyrenees (Arroyo and Razin 2006, Heredia et al. 2013). It should also be noted that, when a bearded vulture nest gets usurped by another species, this nest will not be used again by a bearded vulture (Margalida and García 1999). This strong interspecific competition for nesting sites that the bearded vultures lose to the benefit of griffon vultures implies that the former have to renounce to the sheltered cavities (especially protected from storms coming from the west) and resign themselves to poorly located sites, exposed to wind and rain, which may negatively affect breeding success (Donázar et al. 1993, 2002; our study). A similar explanation has been put forward in an attempt to explain the local and past decline of the griffon vulture population (Razin et al. 2008), both this species and the bearded vulture competing for the best nesting sites (at the expense of the bearded vulture, it would appear), as the quality of the eyrie can be an important factor for breeding success in the French Pyrenees (Razin and Arroyo 2005).

Nest characteristics and their surroundings may indeed play a role in the outcome of the reproduction. The surrounding topography, the exposition to wind and rain, and the size and depth of the nest. have indeed been shown to affect the breeding success of some bird species, including vultures (Donázar et al. 1993, Pollo et al. 2003, Margalida and Bertran 2008). These specific characteristics were not included into our analyses and their effect needs to be further investigated.

In some areas of the Pyrenean mountain range, feeding stations have been placed to provide supplementary feeding to necrophagous raptors. However, supplementary feeding does not seem effective at improving the breeding success of bearded vultures (Margalida 2010). During the last 3 years, 6 feeding stations have been put into place in the westernmost part of our study area. These stations are mostly used by griffon vultures, and we have never observed a bearded vulture visiting them. Two nests located very close to some of these feeding stations that had, in the past, been occupied by bearded vultures are now used by griffon vultures (D. Acheritogaray, personal communication).

Therefore, supplementary feeding not only seems ineffective at improving bearded vulture breeding success, but it may rather exacerbate interspecific conflicts with griffon vultures (Bertran and Margalida 2014) and, thus, could be counter-productive. Instead of providing supplementary feeding, Margalida (2010) suggests improving habitat management through the promotion of extensive grazing livestock and hunting, which the author considers as the most efficient and cheapest environmental management solutions to provide natural food resources to scavengers.

The low breeding success of the bearded vulture, with several unexplained failures at different breeding stages, has forced managers to point at anthropogenic disturbances as an etiological culprit. Anthropogenic disturbances are among the few variables that managers can intervene on, hoping to increase breeding success (Nisbet 2000). However, our results show that restricting human activities did not improve the breeding success of settled bearded vultures that seem to have become tolerant to human activities. Moreover, restricting human activities to try to protect 1 species may have counterproductive consequences for nature conservation. For instance, the activity we focused on, hunting, is not only a leisure activity, but is also performed to regulate the oversized populations of wild ungulates, mostly wild boar and deer. Therefore, the restriction on human activities does not appear to be effective at improving the breeding success of bearded vultures, and it also impedes an activity that is acknowledged by the scientific community as necessary to maintain ecosystem functioning (e.g., by preventing saplings from being overgrazed, thereby allowing forest regeneration [Zamora et al. 2001, Kuiters and Slim 2002]), to protect crops from ploughing and grazing (Geisser and Reyer 2004, Schley et al. 2008, Bleier et al. 2012), and also to conserve or restore favorable habitats for some threatened species, such as the capercaillie (Klaus 1984, Pollo et al. 2003).

As the value and demand of wildlife areas increase through their use by the public, they may also suffer from the ensuing disturbing pressure inherent to their being increasingly frequented. To preserve plants, animals, wilderness, and ecosystems functioning in these areas, conservation studies are required to determine the maximum threshold of disturbance that they can withstand without enduring any negative effect (Gill 2007) and provide relevant information for wildlife management and conservation biology in a global backdrop of human–wildlife conflicts (Sutherland 1998).

Management implications

Our results suggest that bearded vultures tolerated potentially disturbing human activities. The vultures we studied do not seem to perceive such activities as threatening or risky, especially as they are a protected species and not targeted by hunters. Our findings also identified the need to better understand in a more comprehensive way how animals actually perceive human activities that we, humans, deem detrimental to them. We need to better understand how human activities impact animal populations in the context of interspecific competition, including the influence of habitat and climate conditions. The results of such studies could then be used as a means of suggesting adaptive management strategies based on the actual impact of human disturbances, and scientific evidence may help in redirecting wildlife conservation funds to tackle the actual limiting factors of vulnerable species.

Acknowledgments

We thank D. Acheritogaray for his technical support in organizing the field work that made this study possible, as well as all the observers

and volunteers for the time they invested in data collection. We also thank Météo France for graciously providing the weather data. Finally, we are grateful to the anonymous reviewers and T. DeVault, HWI associate editor, for their fruitful comments that have contributed to improving this manuscript.

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Associate Editor: Travis DeVault

Vincent Comor is a research associate in the environmental consulting agency Naturaconsta (France). He has worked on tropical, Mediterranean, temperate, and boreal systems and has obtained his Ph.D. degree in community ecology from Wageningen University, the Netherlands. He is now specialized in ecosystem functioning and human–nature conflicts, and he mostly deals with birds and large carnivores.

Nicolas Poulin is a research engineer at the University of Strasbourg, France, in the Department of Mathematics and Computer Science. He is specialized in statistics and has extensive experience in bioinformatics, especially in ethology, behavioral ecology, and bird ecology.

Mathieu Boos is a doctor in ecophysiology and ecology. He specialized in environmental and animal law at the University of Strasbourg, France. He is currently leading the expertise and the research departments of the environmental consulting agency Naturaconsta. Very keen about nature conservancy, he advocates environmental management through the use of adaptive management.

Retraction notice: We have been informed that because of logistical reasons the authors of Comor et al. (2019) were unable able to provide the answers requested by Duriez et al. (2020) regarding the protocols, the quantitative data, or the small and unbalanced sample sizes. At the authors' request, the article by Comor et al. published in *Human–Wildlife Interactions* 13(3) has been retracted.