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Reduced food availability induces behavioural changes in Griffon Vulture *Gyps fulvus*

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In natural conditions, Griffon Vultures typically show shy behaviour and escape by flying if approached by humans. According to the state-dependent foraging theory, Griffon Vultures should modify their foraging behaviour depending on food availability and predation risk, humans being the main potential predator. We tested the Reaction Time (RT) and Flight Initiation Distance (FID) in five different artificial feeding schemes over three years in which food availability in the field varied significantly. The first scenario was set in a so-called "vulture restaurant", in which government employees feed vultures that may exhibit tame behaviour and stay within a few meters from a feeding person. Scenario 2 involved similar conditions, but here the researchers not employees placed the food in the vulture restaurant. The vultures did not land at the restaurant until one day had passed, and they flew away when people approached them within 250 m. The third scenario was established in a local zoo several months after the closure of the vulture restaurant. Here, employees fed captive vultures that were often accompanied by wild birds that landed to take food. The RT was 14.2 min and the FID was 50 m. The fourth scenario was established during the subsequent breeding season in a mountain where vultures were fed by the authors of the present study. The RT was 2.8 min and the FID was 15.2 m. The fifth scenario was established in another mountain after the breeding season. Now, the RT was 19.2 min and the FID was 52.2 m. These results demonstrate the ability of vultures to evaluate the predation risk depending on food availability and their state of hunger, and their ability to modify their behaviour from "natural" caution ("shyness") towards a more tolerant ("fearless") behaviour.

1. Introduction

Foraging occupies a substantial amount of the daily time budget of every animal species. In such cases, for a foraging animal, the optimal behaviour may vary both with the quality of the foraging patch and with the internal state of an individual (McNamara & Houston 1986). This variation leads to a trade-off between energy gains and predation risk (Olsson *et al.* 2002). Individuals tend to reduce the risk of predation by altering their behaviour (Houston & McNamara 1989). However, food limitations may force animals to evaluate the trade-offs between predation risk and fitness, which may depend on their future expectations (i.e., breeding success and survival; Olsson *et al.* 2002).

Animals may start behaving tamely or show habituation in the absence of predators (Blumstein *et al*. 2004) when, for example, no aggressive inter-specific interactions occur for long periods of time (Coleman *et al*. 2008). On remote islands, wild animal species may not fear humans or terrestrial predators because they have often not experienced negative impacts that would normally lead them to become alert and escape from a threatening situation (Rödl *et al*. 2007). Such behavioural pattern is problematic for native animals that do not recognize threats from introduced predators (Massaro *et al*. 2008), and it also makes it difficult for individuals to adapt their behaviour to new threats (Blumstein *et al*. 2004). In areas with increasing human use, some species have adapted their behaviour to obtain the benefits of living close to humans, their behavioural flexibility having been conditioned by a favourable situation in which humans do not show or show only little antagonistic behaviour. Such adaptations are obvious in urban areas, with pigeon *Columba* species, gull *Larus* species, rats (e.g., *Rattus norvegicus*), sparrow *Passer* species and crow *Corvus* species serving as good examples. Some birds of prey have adapted to living close to humans by using buildings to nest (Cade & Burnham 2003, Ellis *et al*. 2009) and by hunting in gardens, orchards, parks and even streets (Van Nieuwenhuyse *et al*. 2008). Some evasive raptors, such as the Goshawk *Accipiter gentilis*, tolerate human activities in cities (Kenward 2006). New World vulture species Black Vulture *Coragyps atratus* and Turkey Vulture *Cathartes aura* also live in cities, but this is not true for European vultures that have suffered from human persecution for centuries (Donázar 1993). In Spain, for example, Griffon Vultures *Gyps fulvus* were killed as pests until 1966 after which they have been protected by law (Donázar 1993). Nonetheless, farmers, shepherds and hunters continued to poison and directly persecute vultures until recently (Olea *et al*. 1999, Hernández & Margalida 2008, Margalida *et al*. 2008, Hernández & Margalida 2009). This activity has decreased since the banning of poison use in 1984, after which the Spanish population has been recovering and increasing (Parra & Tellería 2004). From the 1980’s to the 1990’s, the Griffon Vulture population and distribution has rapidly increased, largely thanks to feeding them at feeding stations (artificial “vulture restaurants”) and to the active protection of vulture breeding areas (Del Moral & Marti 2001).

Food is a limited resource for birds, affecting survival, breeding and behaviour (Lack 1954, Newton 1998). The behavioural reaction to variation in food supply has been documented for several bird species (Poulin *et al*. 1992, Brown & Sherry 2006, Robb *et al*. 2008) and is related to predation risk (Olsson *et al*. 2002). However, until now few studies have assessed vulture behaviour in relation to food availability. Due to sanitary restrictions, vulture conservation in Europe is presently conditioned by supplementary feeding activities (Donázar *et al*. 2009a, b). Little is known, however, if these activities lead to behavioural changes in vultures, which could in turn be relevant to vulture conservation.

The present study was done in an area where Griffon Vultures do not depend on feeding stations, and where extensively raised livestock provide the biomass required to ensure the survival of the local population. The systematic removal of livestock from the mountains and the closing of vulture feeding stations in neighbouring provinces have caused the local population to decline, with a simultaneous decrease in breeding parameters (Zuberogoitia *et al*. 2009). Moreover, mortality due to starvation has become increasingly common in recently fledged birds of some vulture colonies. Another sign of food shortage is the recent increase in formal complaints about vultures attacking live livestock (Margalida & Campión

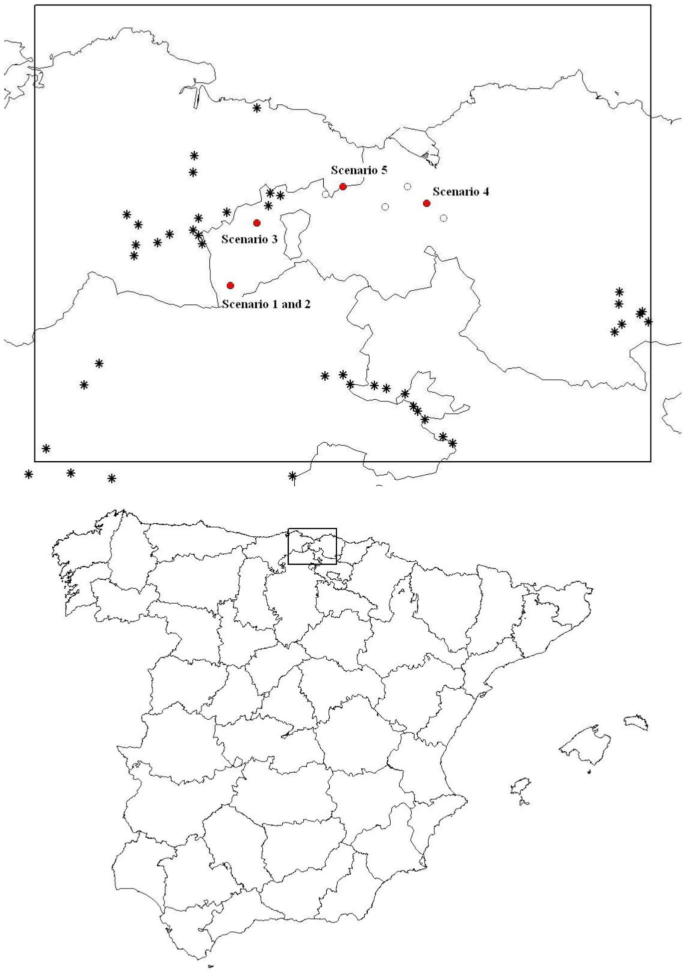

Fig. 1. Study area. Colonies of Griffon Vulture (black asterisks) around sites applied for the five scenarios (full circles; see text), and around sites applied for other scenarios during the breeding season of 2008 (hollow circles).

2009). The only existing feeding station in the study area was closed in 2006. Simultaneously, a policy involving greater control of dead livestock in the field was initiated.

These changes in food availability due to bovine spongiform encephalopathy (Donázar *et al*. 2009a, b, Zuberogoitia *et al*. 2009) enabled us to develop a behavioural experiment, in which the main hypothesis was as follows: according to the state-dependent foraging theory, the Griffon Vulture, a long-lived species that has long survived human persecution, will change its feeding behaviour to maintain high physical fitness according to an artificial feeding programme, i.e., the establishment of feeding stations. Our main goal is to assess the relationship between food availability and foraging behaviour of Griffon Vultures by analyzing (1) the Reaction Time (RT), which is the time lag from the moment food is made available by humans to the moment it is detected by vultures, i.e., until the first vulture lands to feed; and (2) the Flight Initiation Distance (FID), measured as the distance at which feeding vultures allow humans to approach them without escaping by flight. We suggest that vultures would adopt a "tame" or "fearless" behaviour related to the amount of available food.

2. Material and methods

2.1. Study area and design

The study was done west of Biscay, northern Spain, between 43°10' and 43°27'N and 3°27' and 2°31'W (Fig. 1). The study area is hilly and densely populated, with extensive industrial and other urban areas. More than 50% of the area is allocated to forestry at the expense of traditional small-scale farming, and the traditional patchwork of woodland, pasture and small holdings has been greatly reduced.

In 1986 a "vulture restaurant", a vulture feeding station regulated by the local government, was established in the western tip of Biscay, 7.8 km from the nearest vulture colony. This vulture restaurant has been the only regular feeding station in the 7681 km^2 area of the Basque Country (Zuberogoitia *et al*. 2009). Livestock is abundant and spread throughout the mountains, and consequently the number of dead cattle available for scavengers is difficult to estimate, especially in winter months due to the snow cover. The main food source available to scavengers – cattle carcasses – has drastically decreased over recent years due to the rigorous following of laws on the management of livestock carcasses. This was to prevent the spread of certain epidemic livestock diseases, such as bovine spongiform encephalopathy, African swine fever and foot and mouth disease (Del Moral & Marti 2001). Farmers are obliged to notify authorities of every livestock death, and carcasses found by government officials are removed and burned. In the study area, authorities began this activity in 2001, but the vulture restaurant continued to be supplied with meat from butchers twice a week. The vulture restaurant was closed by authorities in August 2006 and reopened in December 2007, after which the quantity and frequency of supplied meat was cut to half the previous level.

We began monitoring the breeding success of Griffon Vultures in 2000, and carried out a study on their feeding behaviour from the summer of 2005 until the autumn of 2008. In these three years, the availability of resources varied depending on government regulations, which were in turn influenced by an increasing number of reports of vultures attacking livestock (Camiña *et al*. 1995, Margalida & Campión 2009). We took the advantage of the fluctuating food availability to develop an experimental assay of vulture feeding behaviour.

We considered five different scenarios that varied in food availability (Fig. 1; for details, see below), for each scenario we measured the Reaction Time (RT), considered as being the time between one vulture flying above a carrion within a 5 km radius and the first vulture landing, and Flight Initiation Distance (FID), measured as the distance at which feeding vultures allowed humans to approach without taking off.

Scenario 1: Predictable food source in a food-rich environment and habituation to humans. We monitored vulture behaviour (eight temporal repeats, i.e., n = 8) in conditions where approximately 300 kg of food was delivered in a lorry driven by a local government employee at 10 AM twice a week, in the vulture restaurant between summer and winter of 2005.

Scenario 2: Predictable food source in a food-rich environment and no habituation to humans. At the same site as Scenario 1, we provided approximately 300 kg of food before sunrise, i.e., several hours before the time in Scenario 1 (n = 6). While the vultures were feeding, we measured the FID when people (mainly hunters and mushroom collectors) visited the area. There was a fence at 250 m, which limited the visibility of vultures and conditioned the FID. Once the vultures were disturbed by at least one person walking beyond the fence, they did not land again as long as someone was walking in the vicinity.

Scenario 3: Predictable food source in a food-poor environment and habituation to humans. After the closure of the vulture restaurant, vultures began to feed at a local zoo located 5.1 km from the nearest colony and 10 km from the restaurant. Managers provided 20 kg of chickens to captive vultures 3–4 times a week, usually at 9 AM. The captive vultures were unable to fly and were in an open enclosure. Wild vultures, Red Kites *Milvus milvus* and Ravens *Corvus corax* landed close to the captive animals to eat their food, an event attracting zoo visitors due to the high concentration of wild birds in close proximity to humans, with more than 300 Ravens and 70 Red Kites and Griffon Vultures simultaneously present. Under this scenario, we monitored vulture behaviour between October 2006 and February 2007 (n = 7). The FID was limited by the fences of the enclosure, but was at least 50 m. The number of people involved in the FID varied considerably depending on the number of visitors but there were always more than five people adjacent to the feeding point.

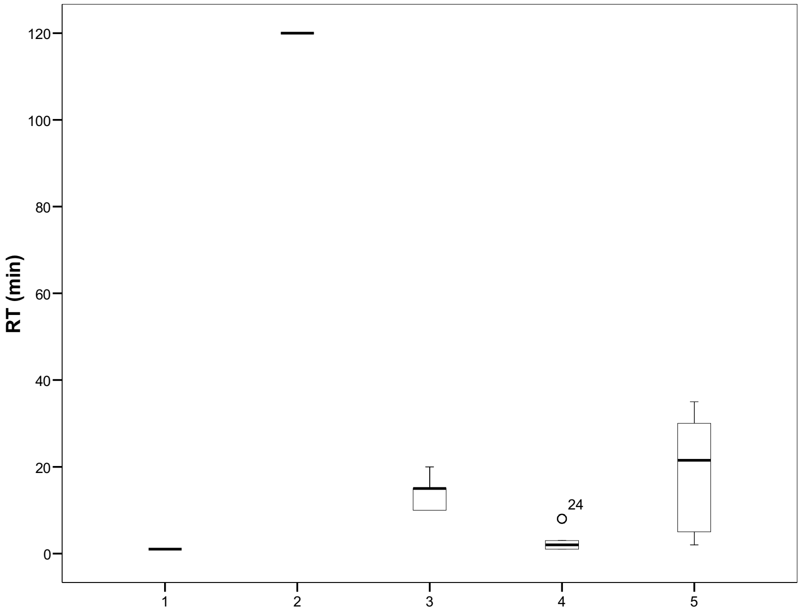

Fig. 2. Box plots (medians, quartiles, minimum and maximum) of the Reaction Time (RT), considered as the time (min) between one vulture flying into the air space above carrion within a 5 km radius and the first vulture landing in the five scenarios (see text).

Scenario 4: Unpredictable food source during the breeding season in a food-poor environment and no habituation to humans. We established an experimental scenario at a mountain top, 15.8 km from the nearest vulture colony, between May and July 2008 (n = 9). Food (64.4 ± 11.3 SD kg of waste meat from butcher shops) was set in a flat plane after sunrise, researchers remaining at varying distances from the plane to observe vulture behaviour. The researchers involved in this experiment were circulated in order to avoid the observer effect, and the experiment was repeated at four other mountain locations 5–10 km from the initial site during the same period (n = 6; Fig. 1).

Scenario 5: Unpredictable food source during the post-breeding season in a food-poor environment and no habituation to humans. We repeated the experiment of Scenario 4 on yet another mountain, 7.5 km from the nearest vulture colony, between August and September 2008 (n = 8), placing the food (49.5 ± 17.7 SD kg of waste meat from butcher shops) in a flat plane nearby a eucalyptus forest *Eucalyptus* species, after sunrise. As in the Scenario 4 experiment, researchers remained at different distances from the food to observe vulture behaviour.

During the autumn and winter of 2005 we trapped 58 adults using cage traps, marked them with alphanumeric colour rings, and intentionally sought for these marked vultures on every occasion concerning feeding vultures in general and during the experiments in particular. Moreover, other ornithologists sent us control data. All data came from an area of r = 15 km within which the five scenarios were established and that supported eight vulture colonies.

We did not attempt to increase the sample size of the experiments (the five Scenarios) in order to avoid the possible effect associated with the learning capacity of vultures. For the same reason we varied the scenarios and people involved in them.

The data were analyzed using non-parametric Kruskal-Wallis and Spearman rank correlation tests, because a priori evaluations of error distributions indicated non-normality and variance heterogeneity (Kolmogorov-Smirnov and Levene tests). The similarity between sampling periods was evaluated using Student's t test. Values presented below are mean ± SD unless stated otherwise, and $P < 0.05$ is considered significant. All tests were computed using SPSS 15.0 software.

3. Results

In Scenario 1, vultures began to land in the restaurant as soon as they saw the lorry approach, even from over 10 km away. When the lorry driver was

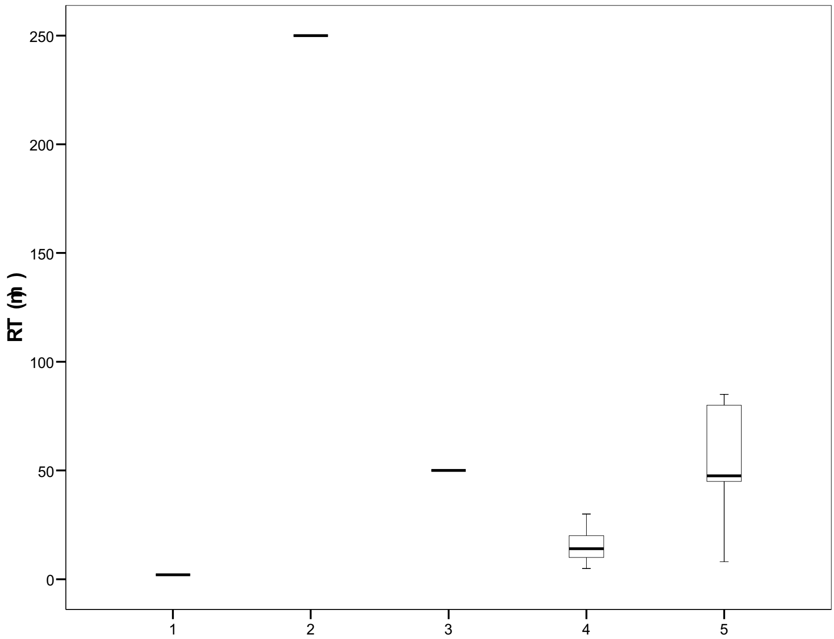

Fig. 3. Box plots (medians, quartiles, minimum and maximum) of Flight Initiation Distance (FID), considered as the distance (m) at which feeding vultures allowed the authors or any other humans to approach, without taking flight during the five scenarios (see text).

carrying out the meat, he often had to use a stick to keep vultures away from himself and was sometimes surrounded by over 400 vultures. However, once the driver had gone, vultures took off when people approached them within 250 m (the distance limited by a fence). In Scenario 2, when we put out the meat, an average of 364.3 ± 103.9 vultures (range 150–450) flew in the vicinity of the restaurant but did not land until one day had passed.

In this case, the FID was the distance between food and the surrounding fence, i.e., 250 m, people often walking close to the fence or even entering the restaurant to watch the vultures feed. In Scenario 3, an average of 60.7 ± 12.4 vultures (range 50–80) landed after 14.2 ± 3.8 min (range 10–20 min) inside the enclosure surrounded by visitors that were kept at a distance of 50 m by the fences. In Scenario 4, during the breeding season, an average of 107.5 ± 29.3 vultures (range 55–150) landed within 2.8 ± 2.7 min (range 1–8 min), even before sunrise. They allowed people to approach within less than 30 m, starting to fly at 15.2 ± 8.8 m (range 5–30 m). In Scenario 5, after the breeding season, an average of 217.2 ± 77.8 vultures (range 161–370) landed within 19.2 ± 13.3 min (range 2–35 min), and the average FID was 52.2 ± 28.0 m (range 8–85 m). Juvenile and 2–5 cy vultures made up less than 5% of individuals in all scenarios.

The feeding behaviour of vultures differed among the five scenarios in terms of RT (Levene's statistic = 11.2, $P < 0.0001$; Kruskal-Wallis H = 26.4, $P < 0.0001$; $n = 30$) and of FID (Levene's statistic = 7.7, $P < 0.0001$; Kruskal-Wallis $H = 27.4$, $P < 0.0001$; $n = 30$). The analysis revealed three groups for both RT and FID: (1) Scenarios 1 and 4, (2) Scenarios 3 and 5, and (3) Scenario 2 (Figs. 2–3).

Group size significantly and positively correlated with food availability ($r = 0.788$, $P < 0.0001$; $n = 44$). The group size during the 2008 breeding season was on average 111.7 ± 78.1 individuals (n = 15, considering Scenario 4 and the other four sites where we repeated that experiment; Fig. 1). During the 2008 post-breeding season, however, it was 206.0 ± 36.9 ($n = 8$). The difference between these periods was significant (Student's $t = -3.928$, $P = 0.001$).

One out of the 58 Griffon Vultures marked in Scenarios 1 and 2 was observed in Scenario 3, another four were observed in Scenario 4, and six were observed in Scenario 5. Eleven marked vultures were observed elsewhere in surrounding areas, and four more were found dead. Hence, some vultures were observed in more than one Scenario.

4. Discussion

The present results demonstrate a "costly" anti-predator response among foraging Griffon Vultures related to food availability. In natural conditions Griffon Vultures are wary and, in order to ensure the absence of threats, it may take more than a day for them to land near a carcass (Donázar 1993). Gavashelishvili and McGrady (2006) showed in the Caucasus that it takes on average 31 daylight hours between carcass appearance and feeding by Griffon Vultures. However, in the present study the RT and the FID in Scenario 1 suggest tame or habituation behaviour once the vultures consider the feeder to be non-threatening, whereas they are more wary if they see other people try to feed or approach them. However, according to the state-dependent foraging theory, "tame" behaviour could also be conditioned by food shortage and hunger level. Food shortage during the 2008 breeding season killed 41.5% of chicks (n = 101 monitored nests; Zuberogoitia *et al*. 2009). Vultures invest remarkable effort in their offspring (Donázar 1993, Margalida & Bertran 2000, Xirouchakis & Mylonas 2007). Hence breeding individuals may have to make a concerted effort to obtain food in order to prevent the fledglings from starving to death. In such a scenario, vultures could switch from shy to "tame" behaviour, or increase the tolerance of risk, even in the proximity of unknown individuals or possible predators.

Our results suggest that the reaction time from the moment that vultures detect food, land and begin to feed when subject to breeding-season food shortage is similar to that observed in the vulture restaurant where habituation behaviour was established after many years (Scenarios 4 and 1, respectively; Fig. 2). Moreover, in such conditions, vultures could tolerate people approaching up to a few metres before flight initiation (Fig. 3). In fact, vultures occasionally allowed researchers to approach within 8–25 m (authors' pers. obs.).

Once the breeding season had passed and vultures were not conditioned by offspring death risk (Scenario 5), the fearless behaviour changed toward increasing RT and FID. According to Bosé & Sarrazin (2007), the group size of foragers correlates with food availability. However, the observed post-breeding group size was almost double that in the breeding season; both adults could then seek food, as there was no need for tending nestlings. Nevertheless, the level of tolerance remained high due to the continuing low food availability, as the tame behaviour of vultures continued. In fact, the time lapsed between setting out the food and the moment that the vultures landed often varied by several hours, delays being usually associated with poor weather. The vultures always landed on the same day, contrary to Gavashelishvili and McGrady (2006) who showed that Griffon Vultures landing on the first day following carcass appearance was rare. Moreover, in their study vultures avoided landing at carcasses in areas with a limited view and a dense adjacent road network, and landing was also delayed at sites near human activities.

We demonstrated how the normally shy behaviour of vultures was conditioned by food availability and hunger level to become tame behaviour within three years. This time lag was confirmed by sightings of individually-ringed vultures. Thus, the distance at which Griffon Vultures take off is not related to individual personality. In fact, predation risk could also be reflected in the synchronization of foraging behaviour (Rands *et al*. 2004). While individuals may vary predictably along a "shy-bold continuum" (Wilson *et al*. 1994), variation in reproductive parameters may influence defensive behaviour and risks that individuals are willing to take (Koops & Abrahams 1998, Blumstein 2006). Parents that invest relatively more in few offspring might be less risk tolerant than those that invest little in many offspring, because their direct fitness is associated with offspring survival. In addition, longevity may be associated with risk-taking and thus overall wariness. Long-lived species are more cautious in risky situations not only because they have acquired more experience but also because they attempt to ensure that they realize their future reproductive potential (Blumstein 2006). However, vultures, like corvids (Nicolakais *et al*. 2003), have relatively large brain and the cost of lost foraging opportunities brought about by wariness might be counterbalanced by rapid habituation to non-threatening situations. Literature on state-dependent foraging (e.g., Clark 1994) provides ample evidence that species often take greater risks under worsening conditions. Individuals with a low expected fitness should be willing to take higher risks and work harder to gain energy, whereas individuals with high expected fitness should be more self-protective (Olsson *et al.* 2002). Taking greater risks in the vicinity of potential predators – in this case humans – might ultimately lead to greater mortality.

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Ravintotilanteen heikentyminen muuttaa hanhikorppikotkien käyttäytymistä

Hanhikorppikotkat (*Gyps fulvus*) ovat luonnonolosuhteissa arkoja ja pakenevat lentäen ihmisen lähestyessä. Olosuhderiippuvaisen ravinnonhankintateorian mukaan hanhikorppikotkien voi odottaa muuttavan käyttäytymistään sen mukaan, mikä kulloinkin on ravinnon saatavuus ja saalistetuksi joutumisen riski; ihminen on lajin tärkein luontainen saalistaja.

Tutkimme reaktioaikaa ja lentoonlähtöetäisyyttä viidessä erilaisessa, kokeellisessa ruokintatilanteessa kolmen vuoden aikana. Jaksolla luontainen ravintotilanne vaihteli huomattavasti. Ensimmäisessä tilanteessa valtion työntekijät ruokkivat korppikotkia, jotka tottuivat ihmisiin päästäen vain muutamien metrien päähän. Toisessa tilanteessa olosuhteet olivat samat, mutta tällä kertaa tutkijat toivat ruuan ruokintapaikalle; korppikotkat eivät laskeutuneet paikalle vuorokauteen, ja pakenivat ihmisen lähestyessä alle 250 m päähän. Kolmas tilanne toteutettiin paikallisessa eläintarhassa, kun ruokintapaikan sulkemisesta oli kulunut useita kuukausia. Nyt eläintarhan työntekijät ruokkivat tarhalintuja, joiden seuraan lyöttäytyi villejä yksilöitä laskeutuen ruokailemaan. Reaktioaika oli 14,2 minuuttia ja pakoetäisyys 50 m. Neljännessä tilanteessa kirjoittajat ruokkivat korppikotkia vuoristoalueella seuraavana pesimäkautena. Tällöin reaktioaika oli 2,8 minuuttia ja pakoetäisyys 15,2 m. Viidennessä tilanteessa korppikotkia ruokittiin toisella vuoristoalueella pesimäkauden jälkeen; nyt reaktioaika oli 19,2 minuuttia ja pakoetäisyys 52,2 m.

Tulokset viittaavat siihen, että korppikotkat kykenevät suhteuttamaan kulloisenkin saalistusriskin ravinnon saatavuuteen ja näläntunteeseen. Tämä ilmenee “luontaisen” varovaisuuden muuttumisena pelottomammaksi käytökseksi.

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