Food availability affects parental anti-predator behaviour in red kites

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Abstract

Parental investment theory proposes two non-mutually exclusive hypotheses to explain variation in anti-predator behaviour in relation to the age of offspring: the “reproductive value of offspring” hypothesis and the “harm to offspring” hypothesis. The relative importance of the two factors underlying the hypotheses, reproductive value and harm, may change depending on environmental conditions such as food availability. To test the relative importance of the two hypotheses under different food conditions, we conducted a supplementary feeding experiment in red kite (Milvus milvus) breeding pairs and used a live eagle owl (Bubo bubo) as decoy nest predator to trigger anti-predator behaviour. We used time-to-capture in mist nets mounted next to the decoy predator as proxy for mobbing intensity. Under natural food conditions we found a nearly constant mobbing intensity throughout the entire nestling period. However, under food-enhanced conditions mobbing intensity was reduced in parents with young nestlings and increased in parents with old nestlings. These results suggest greater importance of the “reproductive value of offspring” hypothesis in situations of favourable food availability. Moreover, mobbing intensity depended on brood size and weather conditions. The results suggest that parental anti-predator investment increases with the reproductive value of the brood under favourable breeding conditions, but that this pattern is adjusted to the current context, including the vulnerability of the brood and environmental conditions.

Introduction

In many animals, parental care involves not only provisioning food and protection from inclement weather, but also active nest defence against predators (Clutton-Brock 1991). Parents may prevent nest predation through mobbing, i.e. behaviours such as approaching and harassing the predator, or through loud vocalization and physical attacks (Caro 2005). The resulting departure of a predator from the nest area has a direct benefit (Curio 1978) for offspring survival (Ajie et al. 2007; Andersson et al. 1980; Lind and Cresswell 2006; Montgomerie and Weatherhead 1988), but driving off a predator is costly in terms of time and energy for the parents (Dugatkin and Godin 1992), and includes the risk of being injured or killed by the predator (King 1999; Mo 2017; Sordahl 1990). Hence, mobbing represents a form of parental investment, and according to life history theory, the level of this investment should depend on its cost-benefit-ratio for the parents (Clutton-Brock 1991). Thus, it is expected that mobbing behaviour varies in relation to a number of internal and external factors associated with the benefits of parental efforts (Caro 2005; Mahr et al. 2015).

Parental investment theory proposes two non-mutually exclusive hypotheses to explain intraspecific variation in mobbing intensity and risk-taking during reproduction (see Dale et al. 1996; Swaisgood et al. 2003). The reasoning underlying the two hypotheses results in contrasting predictions. According to the “reproductive value of offspring” hypothesis, there should be a positive relationship between anti-predator investment and the value of the brood (i.e., large brood size, old offspring, good body condition) due to the increase in expected benefits associated with brood survival (Greig-Smith 1980; Montgomerie and Weatherhead 1988; Tryjanowski and Golawski 2004). On the other hand, the “harm to offspring” hypothesis (also called
“offspring vulnerability” hypothesis) assumes that parents should increase their anti-predator investment based on the harm the nestlings would suffer from a period of no parental care (i.e., in vulnerable situations where continued care is required). According to this hypothesis, the benefits of the parental investment are generally expected to be highest for broods in poor condition or broods that are unable to manage on their own (i.e., in young offspring; Dale et al. 1996; Listoen 2000). Previous studies investigated these hypotheses by quantifying age-dependent mobbing intensity or risk-taking; however, results are equivocal, providing support for either, or both hypotheses (Crisologo et al. 2017; Fernandez and Llambías 2013; Tryjanowski and Golawski 2004). The reason for this might be that the age-dependent benefits of mobbing behaviour in the two hypotheses may change with breeding conditions, while the age-dependent costs remain similar (for theoretical details, see Dale et al. 1996). While adjustments to mobbing behaviour and risk-taking with different predators or different levels of predation risk were supported in many studies (Carlson et al. 2017; Curio 1983; Dassow et al. 2012; Mahr et al. 2015; e.g. Patterson et al. 1980), only few empirical tests exist examining the effect of breeding conditions on the relative importance of the two hypotheses (but see Hakkarainen and Korpmäki 1994; Listoen 2000).

In many birds, including raptors, high food availability is associated with a high offspring survival rate and reduced harm during periods of parental absence (Fuller 2012; Grüebl et al. 2018; Martin 1987; Nägeli et al. 2022; Perrig et al. 2014; Wellicome et al. 2013). Under such conditions, the importance of the brood’s reproductive value for parental investment decision-making is high, and parents should invest more into protecting old than young broods (Dale et al. 1996). In contrast, under poor food conditions, the deciding factor may shift towards the harm offspring would suffer if they received no care. Thus, under poor food conditions, parents should invest more into young broods than they would under favourable food conditions, and more into young than old broods (Dale et al. 1996; Listoen 2000). Manipulating food availability through supplementary feeding experiments could, therefore, be a suitable approach to test these predictions of food condition-dependent mobbing behaviour in birds.

Techniques to catch adult raptors often take advantage of their anti-predator behaviours. A stuffed or live predator as decoy is presented near the nest to trigger anti-predator reactions and capture the parents (Bloom et al. 1992; Bloom et al. 2007; Zubero-goitia et al. 2008). During capture events, predator placement therefore can also be used for the investigation of mobbing behaviour (Arroyo et al. 2001; Carlson et al. 2017; Sternalski and Bretagnolle 2010; e.g. Tolonen and Korpmäki 1995). Capturing success and time-to-capture should be associated with the intensity of the mobbing behaviour. However, in this context, the time until detection of the decoy predator represents a source of bias in the temporal patterns of the capturing history. This is particularly an issue, because food availability and supplementary feeding affect foraging and movement behaviour (Catry et al. 2013; Grüebl et al. 2018; Pfeiffer and Meyburg 2015; Staggenborg et al. 2017), potentially affecting predator detection.

Here, we aim at testing the food condition-dependent change in the relevance of the “reproductive value of offspring” and the “harm to offspring” hypotheses in a large raptor species, the red kite (Milvus milvus). We quantified the intensity of mobbing behaviour in relation to offspring age for pairs provided with supplementary food and those without, while accounting for confounding factors such as brood size, natural food availability, weather conditions, and site characteristics. We used capture probability and time-to-capture when responding to a living eagle owl as a measure of mobbing intensity. We also considered the time to detection of the predator and analysed the factors affecting detection time. This study therefore contributes to a more holistic understanding of parental investment under different environmental conditions.

Methods

Study area and study species

The study was conducted within the red kite breeding period (March to July), during the years 2016 to 2018 in the cantons of Fribourg and Bern, Switzerland (46°5’N, 7°15’E). The study area has an extent of approximately 17.5 x 22.5 km (c. 394 km²), covers elevations from 530 - 1500 m a.s.l., and is characterized by agriculture (56.25%) and managed forests (26.95%) interspersed with settlements. The agriculture is
dominated by dairy farming and meat production, resulting in large areas dominated by grassland (Nägeli et al. 2022; Scherler et al. 2023b; Welti et al. 2020). The red kite is a facultatively scavenging European raptor species that also profits from anthropogenic feeding (Cereghetti et al. 2019; Orros and Fellowes 2015) and builds nests in forest patches, tree rows or single trees (Aebischer and Scherler 2021). The well-known study population shows a very high density of c. 30 pairs per 100 km² (Aebischer and Scherler 2021; Knaus et al. 2018). Egg laying occurs mostly at the beginning of April and clutch size is 2.57 ± 0.62 eggs (range 1 - 4; Scherler et al. 2023a). Brood survival and survival of nestlings depend on weather conditions and food availability (Nägeli et al. 2022). After hatching, parental attendance at the nest declines continuously throughout the nestling period and Carrion crows (Corvus corone), Northern Goshawk (Accipiter gentilis), and Eagle Owls (Bubo bubo) represent the most common avian nest predators (Scherler et al. 2023a).

**Supplementary feeding experiment**

Supplementary feeding started before or during incubation and ended around fledging at a brood age of c. 52 days. We mounted feeding platforms in the territory of selected red kite breeding pairs in open fields near the nest (distance to the nest: 20 – 200 m), where they were easily accessible to the red kites. Platforms consisted of a 0.6 m x 0.6 m wooden board on a 2 m post. Every second day, we placed five dead individuals of day-old chickens per adult and per nestling on the platforms when nestlings were > 9 days old, and ten chickens per nestling when they were > 9 days old (for details on the supplementary feeding experiment, see Nägeli et al. 2022; Scherler et al. 2023b).

**Natural food availability**

Small rodents are an important food source for red kites, especially during the breeding season (Andereggen 2020; Davis and Davis 1981). To quantify natural food availability, we therefore monitored the rodent activity in a total of 180 monthly transects representing the main agricultural habitat types in the region, evenly distributed across the study area (following Apolloni et al. 2018). We derived a monthly rodent activity index from traces in meadows as a proxy for the red kites’ natural food availability, as meadows represent the main vole-foraging habitat of red kites (for details on the rodent activity index, see Nägeli et al. 2022).

**Predator exposure trials**

Predator exposure trials were carried out from early May to mid-July, during the rearing time of the nestlings. To trigger mobbing reactions in the breeding pairs, a human-habituated eagle owl was used as decoy predator. The eagle owl was set on a perch at forest edges in the vicinity of the focal red kite nests. To capture mobbing red kites, a Dho-gaza net (height: 4 m; length: 6 m; 60 mm mesh) was set up next to the eagle owl, just out of its reach to avoid entanglement (Bloom et al. 2007). The Dho-gaza net was mounted perpendicular to the treeline and to the wind direction in order to guide the course of the swooping. We selected breeding pairs with nestlings older than 6 days to avoid disturbance during the very early nestling period. Exposure trials were carried out between 6 am and 9 pm. The trial generally ended 90 minutes after the placement of the decoy predator. We managed to conduct a maximum of five trials per day at different nests. Other bird species also reacted to the eagle owl and had to be removed from the net. Because this could have negative effects on the mobbing behaviour of red kites, predator exposure trials were categorized into trials disturbed by bycatch and undisturbed trials (resulting in a binary variable denoted as “disturbance”). Moreover, mobbing behaviour might differ with vicinity to the forest edge due to limited manoeuvrability. This was recorded in a binary variable denoted as “proximity to trees” (decoy predator closer than 5 meters to the forest edge).

In a subset of trials, we recorded the number of swoops and calling intensity (binary: few callings = 0; frequent calling = 1). Capture success was highly associated with the number of swoops (Estimate: 0.32; 95 % CI: 0.19 – 0.44), and with calling intensity (Estimate: 1.75; 95 % CI: 1.14 - 2.37). As variation in mobbing intensity is expected to result in different time-to-capture, we recorded the time-to-capture if capture occurred. Therefore, we used capture success as a measure of mobbing intensity. To account for differences between pairs in the time-to-detection of the decoy predator, we split the trials into two periods:
detection time (the time from predator placement until the first reaction of one of the members of the breeding pair) and mobbing time (the time from detection until capture). It was not possible to record data blindly because our study involved focus animals in the field and included capturing of focus individuals. No individual identification of the parents was possible; thus, mobbing behaviour reflects the behaviour of breeding pairs.

Statistical analysis

Data analysis was done in R, version 3.4.0 (R Core Team 2017). To investigate the probability of predator detection and mobbing behaviour in red kites, we used mixed effect cox-proportional hazard models with both a binary success variable and a time-to-event variable as response, and date-ID and nest-ID as random effects (coxme function; R package coxme; Therneau 2018). As detection of the decoy predator and mobbing behaviour represent different processes, we analysed the two processes in separate models using detection success (binary) together with time-to-detection as responses to model detection probability (detection model) and capture success (binary) together with time-to-capture to model mobbing intensity (capture model). This allowed for differentiation between factors affecting detection probability and capture probability.

Brood size and age (of the oldest nestling) on the day of the exposure trial, rodent activity index, and food supplementation were included as focus predictors in both models. Mean daily precipitation (Source: MeteoSchweiz), ambient temperature (measured at the beginning of the exposure trial), wind (binary: low vs. high, recorded at the beginning of the exposure trial), distance between decoy predator and red kite nest, and year (categorical) entered as fixed control variables. In the capture model, we included three more control variables potentially affecting capture probability: proximity to trees, disturbance, and whether repeated trials on the same nest within the same season had been performed (denoted as “repetition”). All numeric explanatory variables were centred and scaled before including them in the analyses. The initial models included all two-way interactions between focus variables. Age of nestlings was added as a quadratic term, whereby orthogonal polynomials were used to avoid collinearity. Interactions and quadratic terms with 95 % CI of effect sizes overlapping zero were excluded by backward elimination, while all main effects remained in the model. Effects with 95 % CI not overlapping zero were considered as important effects.

Results

Within the three breeding seasons, a total of 371 predator exposure trials were carried out at 248 red kite broods, over 105 catching days (Table 1). The minimum age of the brood during predator exposure trials was 6 days and the maximum age 74 days (mean +/- sd = 34.7 +/- 16.5 d, n = 371). The broods contained between 0 and 3 nestlings (mean +/- sd = 1.8 +/- 0.7 nestlings, n = 371) with 1.5 +/- 0.6 nestlings in 2016 (n = 51), 1.9 +/- 0.7 nestlings in 2017 (n = 149), and 1.8 +/- 0.7 nestlings in 2018 (n = 171). Mean ambient temperature during the attempts was 20.6 +/- 4.3 degC (min = 7 degC, max = 32.5 degC, n = 371), and the distance between the eagle owl and red kite nests was 47.3 +/- 29 m (n = 371).

Detection model

Most red kite breeding pairs detected the decoy predator within the first 20 to 40 minutes from the start of the trial (Fig. 1). In 31 trials the predator was not detected at all. The interaction between rodent activity and supplementary feeding affected time-to-detection (Table 2). The feeding treatment reduced time-to-detection during periods of low rodent densities, but increased time-to-detection during periods of high rodent densities (Fig. 1). We also found an interaction between nestling age and number of nestlings. While brood size showed only marginal effects on time-to-detection during large parts of the nestling period, time-to-detection was shorter with increasing number of nestlings towards fledging (Table 2). In addition, wind reduced, and precipitation increased time-to-detection (Table 2).

Capture model

The overall capture probability of birds that detected the decoy predator was 0.21 (SE = 0.022, n = 340 trials). The interaction between supplementary feeding and age of nestlings strongly affected the time-to-capture, our measure of mobbing intensity (Table 2). Food supplemented parents showed considerably
shorter time-to-capture with old than young nestlings. This relationship disappeared in un-supplemented parents which showed constant time-to-capture throughout the nestling period. This resulted in increased time-to-capture in fed parents with young nestlings (Fig. 2a), and reduced time-to-capture in fed parents toward the end of the nestling period (Fig. 2b). Time-to-capture was shorter in parents with large than small broods (Table 2, Fig. 3). Control variables also affected the time-to-capture. Disturbance by bycatch, repeated capturing attempts at the same brood, and a decoy predator positioned close to the forest edge increased the time-to-capture (Table 2). Also, the weather variables wind and high temperatures resulted in increased time-to-capture.

Discussion

This experimental study investigated the effect of food availability on the intensity of the anti-predator behaviour of breeding red kites. Under experimentally enhanced food conditions, the intensity of anti-predator behaviour was higher in red kite parents with old broods than with young broods. This age-dependence disappeared in the un-supplemented control group, where anti-predator behaviour was constant over the entire nestling period. These results support the previous theoretical prediction of Dale et al. (1996) that the “reproductive value of offspring” hypothesis has greater relevance under favourable breeding conditions, while the “harm-to-offspring” hypothesis becomes more relevant under poor breeding conditions. These results suggest that food availability affects parental anti-predator behaviour by changing the nestlings’ body condition which represents a new pathway of how food conditions drive parental investment.

Under a wide range of food conditions, food supplementation to parents might mainly affect parental condition rather than vulnerability of the brood (Boutin 1990; Michel et al. 2022; Ruffino et al. 2014). However, in recent studies we showed that enhanced food conditions due to our experimental food supplementation increased nest and nestling survival, as well as body condition of nestlings compared to control broods (Catitti et al. 2022; Nageli et al. 2022). This confirms that food supplementation reduces the harm that offspring suffer due to a period of parental absence by increasing their baseline body condition – and probably also increases the reproductive value of the brood due to increased post-fledging survival probability of nestlings (Naef-Daenzer and Gruebler 2016).

The greater relevance of the “harm-to-offspring” hypothesis under normal than enhanced food conditions suggests that also large species, such as the red kite, can be affected by predator presence in the nest area. Field observations during predator exposure trials support that, even if mobbing intensity is low, red kite parents invest time in supervising their brood and the predator; time that could otherwise be spent in food provisioning (Ghalambor et al. 2013; Ibanez-Alamo et al. 2015; Martin and Briskie 2009; Mutzel et al. 2013). In this respect, parents of nestlings that are susceptible to predation are faced with a trade-off between time invested in nest guarding and time invested in foraging (e.g. Komdeur 1999; Rothenbach and Kelly 2012). The outcome of this trade-off likely represents the underlying mechanism of adjustments in mobbing intensity. During food shortages, when nestlings have more urgent food requirements and are more susceptible to harm from starvation or developmental stress (see Catitti et al. 2023), chasing away predators should expedite the return to foraging. On the other hand, during favourable food conditions, breeding pairs can spend more time passively guarding the nest and, thus, can save energy and avoid risking themselves during active mobbing behaviour. This might be true for bird species where nest guarding and attendance can be efficient anti-predator strategies (Catry et al. 2006; Dewey and Kennedy 2001; Hu et al. 2017; Rothenbach and Kelly 2012; Samelius and Alisauskas 2001). We suggest that nest guarding and mobbing represent two different nest defence strategies that both reduce nest predation (Cato 2005; Montgomerie and Weatherhead 1988), but their cost-benefit ratio changes with food availability and vulnerability of the brood.

As the two hypotheses show contrasting predictions for the effect of nestling age on mobbing behaviour, we used nestling age to investigate the relevance of the two hypotheses under different food conditions. However, also brood size showed a clear effect on mobbing behaviour. While the “harm-to-offspring” hypothesis does not give a clear prediction regarding brood size, the “reproductive value of offspring” hypothesis does (Montgomerie and Weatherhead 1988) and is supported by increased mobbing intensity in parents with large

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versus small broods. We recently showed that large brood sizes were associated with reduced body mass and increased corticosterone levels in red kite nestlings (Catitti et al. 2022; Nageli et al. 2022), illustrating the general life-history trade-off between offspring number and offspring quality (Stearns 1992). Since it is the body condition of the nestlings that is expected to affect parental mobbing behaviour under the “harm-to-offspring” hypothesis (Dale et al. 1996), these results suggest both, increased harm to offspring, as well as increased reproductive value in large broods. Thus, increased anti-predator investment into large broods suggests that the reproductive value of an additional nestling is larger than the increased costs of reduced body condition arising in a period of absence no parental care. This might be a general pattern as increased parental care investment into large broods, including anti-predator investment, has been shown in many studies (Clutton-Brock 1991; Lazarus and Inglis 1986; Royle et al. 2012).

Quantifying time-to-detection was important in this study because differential detection could bias the investigation of capture probability, which was used as proxy for mobbing intensity. Predator detection time is not only a methodological issue, but is also likely associated with nest predation risk, should low detection probability be due to parental absence from the nest area (Behrens et al. 2019; Duncan Rastogi et al. 2006; Samelius and Alisauskas 2001; Schmidt and Whelan 2005). Under poor natural food conditions, parents detected the decoy predator later than under favourable food conditions probably due to longer foraging trips. Supplementary feeding resulted in earlier detection under poor natural food conditions, but later detection under favourable food conditions. In addition, parents with large broods detected the decoy predator earlier than parents with small broods indicating a higher nest visitation rate. These results are in line with recent studies showing that, in years with low food availability, the home-range size of red kite pairs is considerably larger than in years with high food availability (Pfeiffer and Meyburg 2015), and that prey delivery rate is elevated in large versus small broods (Andereggen 2020), but can be reduced under ad libitum food conditions. Together, these results indicate that time-to-detection depends on factors affecting movement behaviour within home-ranges and corroborates that nest predation risk by avian predators can be increased in pairs with large home-ranges (Lameris et al. 2018), in situations of low food availability (Duncan Rastogi et al. 2006), and in pairs with small brood-sizes (Schmidt 1999), all being consequences of low habitat quality.

Finally, weather conditions during the predator exposure trial affected time-to-detection probability, as well as time-to-capture. This was expected for time-to-detection, because weather conditions are shown to affect ranging behaviour (Baucks 2018) and food delivery rates (Andereggen 2020). However, while we added weather variables mainly to account for potential biases in the analysis of time-to-capture, our study is one of the very few showing that weather conditions affect mobbing intensity (but see Fisher et al. 2004). Mobbing intensity strongly decreased i.e. time-to-capture increased with high ambient temperatures and windy conditions. When ambient temperatures are outside their thermal neutral zone, birds face additional energy costs during activities, which could affect their decisions regarding nest defence (Fisher et al. 2004). Also, windy conditions can affect control of swoops and, thus, increase injury and predation risk of parent birds. This is also supported by the fact that time-to-capture was increased when the predator was placed closer to trees, impeding manoeuvrability. Both underlying mechanisms, energetic trade-offs and increased threat of injury, might be particularly relevant in large bird species exhibiting predominantly soaring flight, such as red kites, where flapping flight is energetically costly, and manoeuvrability limited (Sapir et al. 2010; Shepard et al. 2013; Shepard et al. 2016; Shepard et al. 2019).

In conclusion, we show that nest defence depends not only on predation risk due to predator type and behaviour, but also on environmental conditions. While, in general, parental anti-predator investment seems to be adjusted to the reproductive value of the brood, this investment is modulated by a multitude of factors associated with the brood, the environment, and the approaching predator. In particular, this study provides evidence that food availability affects anti-predator behaviour by altering the body condition of nestlings. The vulnerability of the offspring is therefore important for the choice of the nest defence strategy. It represents a driver of mobbing intensity and is important for the outcome of trade-offs between different forms of parental care. Thus, low food availability might have mobbing-mediated consequences for reproduction and reproductive costs beyond the consequences mediated through changes in foraging
behaviour, even if predation rate remains unchanged. In addition to potential survival costs for the parents, the additional parental effort due to frequent mobbing may even be a reason for brood desertion under poor environmental conditions (see Nageli et al. 2022). Ultimately, large-scale environmental factors affecting investment into nest defence may have significant demographic consequences.

**Tables and table legends**

**Table 1** Number of predator exposure trials (N attempts) and number of captured adult red kites per breeding season in unfed and fed breeding pairs

<table>
<thead>
<tr>
<th>Year</th>
<th>N attempts</th>
<th>N captured red kites</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unfed</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2016</td>
<td>42</td>
<td>16</td>
</tr>
<tr>
<td>2017</td>
<td>101</td>
<td>18</td>
</tr>
<tr>
<td>2018</td>
<td>162</td>
<td>27</td>
</tr>
<tr>
<td>Fed</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2016</td>
<td>9</td>
<td>5</td>
</tr>
<tr>
<td>2017</td>
<td>48</td>
<td>4</td>
</tr>
<tr>
<td>2018</td>
<td>9</td>
<td>1</td>
</tr>
<tr>
<td>Total</td>
<td>371</td>
<td>71</td>
</tr>
</tbody>
</table>

**Table 2** Results of the mixed cox-proportional hazard models investigating factors affecting detection and capture probability (n = 371 trials at 248 nests). Effects with 95% CI not overlapping zero are printed in bold

<table>
<thead>
<tr>
<th>Variable</th>
<th>Detection model</th>
<th>Detection model</th>
<th>Detection model</th>
<th>Detection model</th>
<th>Detection model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Year 2017</td>
<td>Year 2017</td>
<td>-0.01</td>
<td>-0.45</td>
<td>0.44</td>
<td>-0.16</td>
</tr>
<tr>
<td>Year 2018</td>
<td>Year 2018</td>
<td>0.33</td>
<td>-0.15</td>
<td>0.81</td>
<td>-0.26</td>
</tr>
<tr>
<td>Rodent activity</td>
<td>Rodent activity</td>
<td>0.08</td>
<td>-0.09</td>
<td>0.24</td>
<td>0.07</td>
</tr>
<tr>
<td>Food supplementation</td>
<td>Food supplementation</td>
<td>0.05</td>
<td>-0.33</td>
<td>0.43</td>
<td>-0.14</td>
</tr>
<tr>
<td>Nestling age</td>
<td>Nestling age</td>
<td>-0.09</td>
<td>-0.23</td>
<td>0.04</td>
<td>-0.01</td>
</tr>
<tr>
<td>N nestlings</td>
<td>N nestlings</td>
<td>0.07</td>
<td>-0.06</td>
<td>0.20</td>
<td>0.28</td>
</tr>
<tr>
<td>Distance to nest</td>
<td>Distance to nest</td>
<td>-0.11</td>
<td>-0.25</td>
<td>0.02</td>
<td>-0.15</td>
</tr>
<tr>
<td>Wind</td>
<td>Wind</td>
<td><strong>0.37</strong></td>
<td><strong>0.08</strong></td>
<td><strong>0.66</strong></td>
<td><strong>0.75</strong></td>
</tr>
<tr>
<td>Precipitation</td>
<td>Precipitation</td>
<td><strong>-0.16</strong></td>
<td><strong>-0.01</strong></td>
<td><strong>-0.31</strong></td>
<td>0.02</td>
</tr>
<tr>
<td>Temperature</td>
<td>Temperature</td>
<td>-0.04</td>
<td>-0.18</td>
<td>0.10</td>
<td><strong>-0.34</strong></td>
</tr>
<tr>
<td>Repetition</td>
<td>Repetition</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td><strong>-1.88</strong></td>
</tr>
<tr>
<td>Proximity to trees</td>
<td>Proximity to trees</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td><strong>-0.94</strong></td>
</tr>
<tr>
<td>Disturbance</td>
<td>Disturbance</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td><strong>-0.93</strong></td>
</tr>
<tr>
<td>Food suppl.*rodent act.</td>
<td>Food suppl.*rodent act.</td>
<td><strong>-0.35</strong></td>
<td><strong>-0.67</strong></td>
<td><strong>-0.03</strong></td>
<td>–</td>
</tr>
<tr>
<td>Food suppl.*nestl. age</td>
<td>Food suppl.*nestl. age</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>0.78</td>
</tr>
<tr>
<td>Nestl. age*N nestlings</td>
<td>Nestl. age*N nestlings</td>
<td><strong>0.15</strong></td>
<td><strong>0.03</strong></td>
<td><strong>0.27</strong></td>
<td>–</td>
</tr>
</tbody>
</table>

Random effects: detection probability model: nest identity: sd = 0.510, date: sd = 0.020; capture probability model: nest identity: sd = 0.574, date: sd = 0.020.

**Figure legends**

**Fig. 1** Probability of the decoy predator being detected in relation to time after the start of the predator exposure trial (in minutes) for fed (grey lines) and unfed (black lines) red kite breeding pairs (a) in situations of low rodent activity (10 % quantile), and (b) in situations of high rodent activity (90 % quantile). Solid
lines represent means and dotted lines 95% confidence intervals of model predictions. All other variables of the cox model were set to their mean values. As we did not find differences between years, the figure is based on a model without year effect. All numerical variables were set to their mean values and wind (categorical variable) was set to zero.

**Fig. 2** Capture probability in relation to the time since detection of the decoy predator for fed (grey lines) and unfed (black lines) red kite breeding pairs with (a) young nestlings (10% quantile), and (b) old nestlings (90% quantile). Solid lines represent means and dotted lines 95% confidence intervals of model predictions. As we did not find differences between years, the figure is based on a model without year effect. The results are shown for first trials (no repetition) without disturbance, no wind, and no proximity to trees. All numerical variables were set to their mean values.

**Fig. 3** Capture probability in relation to the time since detection of the decoy predator for red kite breeding pairs with different brood sizes. Solid lines represent means and dotted lines 95% confidence intervals of model predictions. As we did not find differences between years, the figure is based on a model without year effect. The results are shown for first trials (no repetition) without disturbance, no wind, and no proximity to trees. All numerical variables were set to their mean values.

**Figures**

![Figure 1](image)
Figure 2
Figure 3

References


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