

JOURNAL OF AVIAN BIOLOGY

Research article

Food availability affects parental anti-predator behaviour in red kites

Samuel Sieder^{1,2}, Patrick Scherler^{1,3}, Stephanie Witzak^{1,3}, Matthias Tschumi¹, Tobias Mühlemann^{1,4} and Martin U. Grüebler^{✉1}

¹Swiss Ornithological Institute, Sempach, Switzerland

²BOKU University of Natural Resources and Life Sciences, Vienna, Austria

³Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Switzerland

⁴ZHAW Life Sciences und Facility Management, Wädenswil, Switzerland

Correspondence: Martin U. Grüebler (martin.gruebler@vogelwarte.ch)

Journal of Avian Biology

2025: e03475

doi: [10.1002/jav.03475](https://doi.org/10.1002/jav.03475)

Subject Editor: Simon Griffith

Editor-in-Chief: Jan-Åke Nilsson

Accepted 18 June 2025



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 contribution 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 a decoy nest predator to trigger anti-predator behaviour. We used capture probability and time-to-capture in mist nets mounted next to the decoy predator as a 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 is shaped by both offspring vulnerability and offspring reproductive value, with changing contributions in relation to offspring age. Thus, parental predator responses are dynamically adjusted to the current environmental conditions affecting vulnerability and reproductive values of offspring as well as parental predation risks.

Keywords: food supplementation, harm-to-offspring, *Milvus milvus*, mobbing behaviour, parental investment, reproductive value



www.avianbiology.org

© 2025 The Author(s). Journal of Avian Biology published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

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 and for the continuation of providing care (Andersson et al. 1980, Montgomerie and Weatherhead 1988, Lind and Cresswell 2005, Ajie et al. 2007), 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 (Sordahl 1990, King 1999, Mo 2017). 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 (Dale et al. 1996, Swaisgood et al. 2003). 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 in terms of risk-taking 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). While both hypotheses are supposed to apply in most systems, their relative importance can vary. Previous studies investigated these hypotheses by quantifying mobbing intensity or risk-taking in relation to offspring age where the hypotheses make contrasting predictions; however, results are equivocal, providing support for either, or both hypotheses (Tryjanowski and Golawski 2004, Fernandez and Llambias 2013, Crisologo et al. 2017).

The reason for this might be twofold. First, if the two hypotheses are both contributing to the behavioural variation, the outcome of the relationship between anti-predator behaviour and offspring age depends on the shapes and slopes of the two separate functions, which are expected to be species-specific. Second, the relationships might change with

breeding conditions such as differential food availability or spells of bad weather (for theoretical details, see Dale et al. 1996). Thus, parental investment can be driven simultaneously by reproductive value and offspring vulnerability, but breeding conditions might shift the balance in favour of one or the other hypothesis. While adjustments of mobbing behaviour and risk-taking to different predators or different levels of predation risk were supported in many studies (Patterson et al. 1980, Curio 1983, Dassow et al. 2012, Mahr et al. 2015, Carlson et al. 2017), only few empirical tests exist examining the effect of breeding conditions on the relative importance of the two hypotheses (but see Hakkarainen and Korpimäki 1994, Listoen 2000), and the predictions of the effect of breeding conditions on anti-predator behaviour in relation to offspring age remain untested.

In many birds, including raptors, high food availability is associated with a high offspring survival rate and reduced harm during periods of parental absence (Martin 1987, Fuller 2012, Wellicome et al. 2013, Perrig et al. 2014, Gruebler et al. 2018, Nägeli et al. 2022). Under such conditions, the importance of the brood's reproductive value for parental investment is high, and parents should invest more into protecting old than young broods (Dale et al. 1996). In contrast, under poor food conditions, the dominant 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). However, studying the effect of food conditions on parental investment in the wild remains difficult because natural food conditions are intercorrelated with various factors potentially affecting parental behaviour. Thus, manipulating food availability through supplementary feeding experiments could be a suitable approach to test these predictions of food condition-dependent mobbing behaviour in birds (Fig. 1).

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, Zuberogitia et al. 2008). During capture events, predator placement therefore can also be used for the investigation of mobbing behaviour (Tolonen and Korpimäki 1995, Arroyo et al. 2001, Sternalski and Bretagnolle 2010, Carlson et al. 2017). 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 (Catty et al. 2013, Pfeiffer and Meyburg 2015, Staggenborg et al. 2017, Gruebler et al. 2018), 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

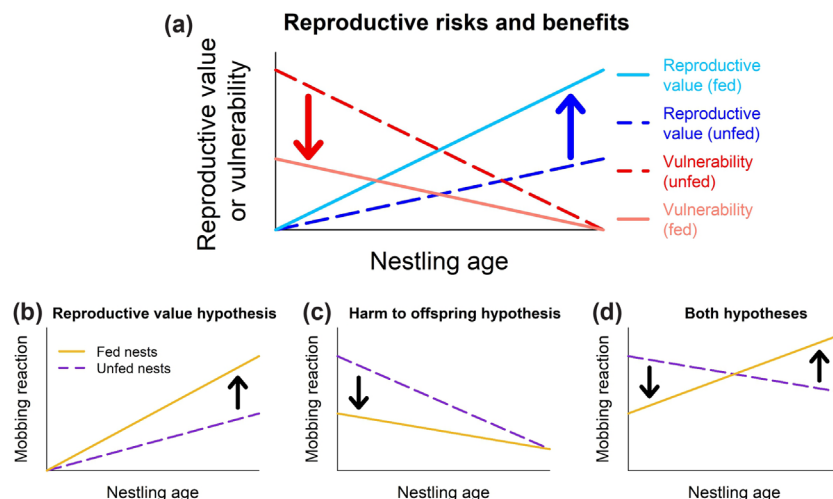


Figure 1. Effect of food supplementation on vulnerability and reproductive value of offspring in the course of the nestling period, and predictions of the outcome of the supplementation experiment on the intensity of anti-predator behaviour under different hypotheses. (a) With increasing age, the reproductive value of nestlings increases while the vulnerability of nestlings decreases. Experimental food supplementation is expected to result in a steeper increase in reproductive value (higher reproductive value of nestlings at the end of the nestling period) and in a flatter decline in vulnerability (lower vulnerability of nestlings at the beginning of the nestling period). Assuming that the mobbing reaction is associated either to the reproductive value of the nestlings, to the vulnerability of nestlings or to both, predictions of mobbing patterns in the course of the nestling period differ. (b) According to the ‘reproductive value’ hypothesis we predict an increase in parental mobbing intensity in the course of the nestling period, being more pronounced in food supplemented broods. (c) According to the ‘harm-to-offspring’ hypothesis, we predict a decreasing parental mobbing intensity in the course of the nestling period, starting at lower intensities in food supplemented broods. (d) In case of considerable contribution of both hypotheses, the mobbing intensity might not show a clear trend in the course of the nestling period, but experimental food supplementation is expected to decrease mobbing intensity at the beginning of the nestling period and increase mobbing intensity at the end of the nestling period.

of mobbing behaviour during capture events in relation to offspring age for pairs provided with and without supplementary food, 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 live eagle owl *Bubo bubo* as a measure of mobbing intensity while considering the time-to-detection of the predator to avoid biased time-to-capture. Experimentally increasing the reproductive value of the brood and simultaneously reducing the vulnerability of the brood by food supplementation allowed for 1) investigating anti-predator behaviour throughout the nestling period under different food conditions, and 2) differentiating whether the two hypotheses mainly act separately or in conjunction (Fig. 1). Under the sole contribution of the reproductive value hypothesis, we expect that food supplementation results in an additional increase in mobbing intensity towards the end of the nestling period, i.e. in a steeper positive slope of the increasing mobbing intensity curve (Fig. 1b). Under the sole contribution of the ‘harm-to-offspring’ hypothesis, we expect that food supplementation results in a reduced mobbing intensity at the beginning of the nestling period, i.e. in a reduced negative slope of the decreasing mobbing intensity curve (Fig. 1c). Under a joint contribution of the hypotheses, we expect that food supplementation results in both a reduced mobbing intensity at the beginning and an increased mobbing intensity at the end of the nestling period, i.e. in a rotation of the relationship towards increased slopes

irrespective of the baseline (Fig. 1d). This study contributes to a more holistic understanding of parental anti-predator investment under different environmental conditions.

Material and methods

Study area and study species

The study was conducted within the red kite breeding period (March–July), during the years 2016–2018 in the cantons of Fribourg and Bern, Switzerland (46°5′N, 7°15′E). The study area has an extent of approximately 17.5 × 22.5 km (ca 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. Agriculture is dominated by dairy farming and meat production, resulting in large areas dominated by grassland (Welti et al. 2020, Nägeli et al. 2022, Scherler et al. 2023b). The red kite is a facultatively scavenging European raptor species showing only small sexual dimorphism. It profits from anthropogenic feeding (Orros and Fellowes 2015, Cereghetti et al. 2019) 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 ca 30 pairs per 100 km² (Aebischer and Scherler 2021), but nesting territories are defended against conspecifics. 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, while eagle owls are the main predator of adult birds (Scherler et al. 2023a). Both individuals of a pair contribute to nest defence.

Supplementary feeding experiment

Supplementary feeding started before or during incubation and ended around fledging at a brood age of ca 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 × 0.6 m wooden board on a 2 m post. Every second day, we placed five dead individuals of one-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 (Davis and Davis 1981, Andereggen 2020). 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 methods and results of the rodent activity index, see Nägeli et al. 2022).

Predator exposure trials

Predator exposure trials were carried out from early May to mid-July of the years 2016–2018, during the rearing season of the nestlings. To trigger mobbing reactions in the breeding pairs, a human-habituated eagle owl was used as a decoy predator. The eagle owl was set on a perch at forest edges in close vicinity of the focal red kite nests within the defended nesting territory to ensure that neighbouring pairs do not show mobbing reactions. 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 six days to avoid disturbance during the very early nestling period. Exposure trials were carried out between 6:00 and 21:00 h. The trial generally ended no later than 100 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 proximity to the forest edge due to limited manoeuvrability. This was recorded as a binary variable denoted as 'proximity to trees' (decoy predator closer than 5 meters to the forest edge). At the beginning of every exposure trial, we measured the ambient temperature and, as a binary variable, the wind conditions (low vs high). No wind or just a small breeze indicated low wind conditions, while swaying small trees and leaves indicated high wind conditions (above Beaufort scale value 4). In stormy conditions (above Beaufort scale value 6), trials were not possible.

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 and time-to-capture as measures of mobbing intensity. To test the validity of the relationships between mobbing intensity and capture outcomes, we recorded the number of swoops after detection of the decoy until capture in a subset of trials. Since red kite breeding pairs are not permanently guarding the nest, but moving around, the time-to-detection of the eagle owl varied between the trials. Earlier analyses showed that time-to-detection is driven by food availability, age and size of the brood, weather variables, and breeding density (Sieder 2018, Sieder et al. unpubl.). After the detection of the decoy predator, normally, both members of the pair started mobbing. 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 or the end of the trial; see Fig. 2). The first warning call, the start of circling over the decoy, or first indications of slight swooping behaviour, were reliable signs of detection by the breeding pair after setting up the decoy predator and thus, defined as the timepoint of detection. The first reaction of the red kite parents had to be directly related to the predator. Just flying by and ignoring the predator was not interpreted as the first reaction, because it was no immediate response to the decoy predator, and thus, no evidence of detection. Since no individual identification of the parents was possible, this study quantifies the mobbing behaviour of breeding pairs. After capture, we measured body mass and wing length of each individual (Witczak et al. 2024) and calculated a body condition index by dividing body mass by wing length.

Statistical analysis

Data analysis was done in R, ver. 3.4.0 (www.r-project.org). The validity of the capture outcomes (capture success and time-to-capture) as a proxy for mobbing intensity is key for this study. We approached this issue in four steps by using the limited data set of swooping behaviour of the years 2017 and 2018. First, as swooping did not occur in all predator exposure trials (n = 271 out of 371 trials without swooping behaviour), but represented a requirement for capture, we used a

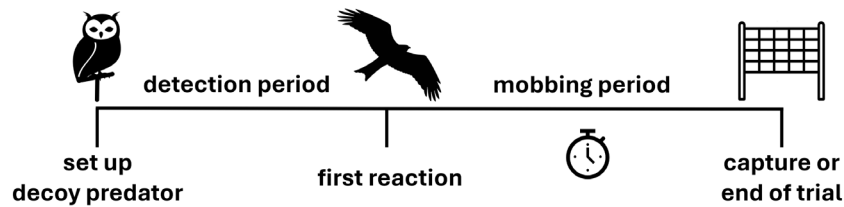


Figure 2. Schematic figure of the sequence of predator exposure-trials. After setup of the decoy predator, the trials were divided into two parts – the detection period, during which the decoy predator was not detected by the red kite parents, and the mobbing period, where the anti-predator behaviour was shown. The detection period ended with the first reaction of the breeding pair directly related to the decoy predator (warning call, start of circling, signs of upcoming swoops). After the start of the mobbing period, the time was measured until capture of a parent or termination of the predator exposure trial without capture. The trial ended latest 100 minutes after the setup of the decoy predator.

Chi-squared test to investigate the relationship between occurrence of swoops (yes/no) and capture success (yes/no). Second, as a refinement, we tested whether the time from the detection of the predator to the first swoop (or to the end of the trial if no swoop occurred) was associated with capture success (GLM, binomial error distribution). Third, we tested the relationship between the number of swoops per time unit and the time-to-capture (LM; with log-transformed capture time) for the subset of captured birds, assuming that higher swooping intensity results in shorter time-to-capture. Finally, we analysed whether the number of swoops was related to capture success while controlling for the effect of exposure time from detection to capture or the end of the trial.

To analyse the factors affecting mobbing intensity, we used a mixed effects cox-proportional hazard model with both a binary capture success variable and a time-to-capture variable as response, and date-ID and nest-ID as random effects (*coxme* function, R package ‘coxme’; Therneau 2018). 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 the model. Mean daily precipitation (source: MeteoSchweiz), ambient temperature, wind, distance between decoy predator and red kite nest, year (categorical), proximity to trees, disturbance, and whether repeated trials on the same nest within the same season had been performed (denoted as ‘repetition’) entered as fixed control variables. All numeric explanatory variables were centred and scaled before including them in the analyses. The initial model 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% confidence intervals (CI) overlapping zero were excluded by backward elimination, while all main effects remained in the model. To investigate the effect of body condition on mobbing intensity, we modelled time-to-capture of captured birds in relation to body condition using a linear model (LM; with log-transformed capture time).

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 \pm SD = 34.7 ± 16.5 days, $n = 371$). The broods contained between 1 and 3 nestlings (mean \pm 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 $20.6 \pm 4.3^\circ\text{C}$ (min = 7°C , max = 32.5°C , $n = 371$), and the distance between the eagle owl and red kite nests was 47.3 ± 29 m ($n = 371$). The mean rodent activity index varied between the years from 1.83 ± 0.69 in 2016 ($n = 51$), to 3.92 ± 1.8 in 2017 ($n = 149$) and 2.67 ± 0.5 in 2018 ($n = 171$). The monthly rodent activity index ranged from 1.42 to 6.50 (mean \pm SD = 3.05 ± 1.43 , $n = 371$). Red kite breeding pairs detected the decoy predator after 9.8 ± 14.5 SD minutes from the start of the trial ($n = 340$ trials). In the remaining 31 trials the predator was not detected at all. The mean body condition index of captured birds was 1.90 ± 0.14 SD and did not differ between fed and unfed parents (fed: 1.87 ± 0.07 SD, $n = 10$ individuals; unfed: 1.91 ± 0.15 SD, $n = 56$ individuals).

Correlation between mobbing behaviour and capture outcome

Capture success was clearly associated with the occurrence of swoops ($\chi^2 = 233.38$, $df = 1$, $p < 0.001$, $n = 371$) indicating that swooping behaviour was important for capturing. Capture success was also highly associated with the time from detection to the first swoop (GLM; estimate: -0.11 , 95% credible intervals (CrI): -0.15 to -0.08 ; Mac Fadden’s $R^2 = 0.36$, CrI: 0.34 to 0.37; $n = 293$ trials with detection), suggesting that a quick swooping response increased capture

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.

	Year	n attempts	n captured red kites
Unfed pairs	2016	42	16
	2017	101	18
	2018	162	27
Fed pairs	2016	9	5
	2017	48	4
	2018	9	1
Total		371	71

Table 2. Results of the mixed cox-proportional hazard model investigating factors affecting capture probability (and time-to-capture; $n=371$ trials at 248 nests). Effects with 95% CI not overlapping zero are printed in bold. Random effects: nest identity: $SD=0.574$, date: $SD=0.020$.

Variable	Estimate	95% CI	
		Lower	Upper
Year 2017	-0.16	-1.08	0.77
Year 2018	-0.26	-1.31	0.79
Rodent activity	0.07	-0.30	0.43
Food supplementation	-0.14	-0.92	0.66
Nestling age	-0.01	-0.33	0.31
n nestlings	0.28	0.01	0.56
Distance to nest	-0.15	-0.43	0.13
Wind	-0.75	-1.46	-0.04
Precipitation	0.02	-0.28	0.33
Temperature	-0.34	-0.61	-0.07
Repetition	-1.88	-2.88	-0.87
Proximity to trees	-0.94	-1.60	-0.28
Disturbance	-0.93	-1.77	-0.09
Food suppl. \times nestl. age	0.78	0.03	1.54

probability. The time-to-capture (only in trials with captures) was associated with the number of swoops per time unit (i.e. with the swooping rate; LM; estimate: -0.95 , 95% CrI: -1.24 to -0.67 ; adjusted $R^2=0.47$, 95% CrI: 0.30 to 0.59; $n=50$ trials with capture), showing that high swooping intensity reduced the time-to-capture. Finally, when controlling for exposure time, capture success was associated with the number of swoops (GLM; estimate: 0.33, 95% CrI: 0.23 to 0.44; Mac Fadden's $R^2=0.45$, 95% Credible Interval: 0.43 to 0.46; $n=293$ trials with detection), showing that swooping intensity also influenced capture success.

Drivers of mobbing behaviour

The overall capture probability of birds that detected the decoy predator was 0.21 ($SE=0.022$, $n=340$ trials) and the time-to-capture of captured birds was 19.5 ± 20.2 SD minutes ($n=71$ trials). The interaction between supplementary feeding and age of nestlings strongly affected capture probability and time-to-capture, our measure of mobbing intensity (cox-proportional hazard model; Table 2, Fig. 3). Non-supplemented parents showed a constant capture probability (and time-to-capture) throughout the nestling period, supporting neither a separate 'reproductive value' hypothesis nor a separate 'harm-to-offspring' hypothesis. Food supplementation resulted in a clearly reduced capture probability (and prolonged time-to-capture) in parents with young nestlings and in a slightly increased capture probability (and shortened time-to-capture) in parents with old nestlings. Together, this resulted in a considerably higher capture probability (and shorter time-to-capture) in old than young nestlings (Fig. 3). Capture probability was higher and time-to-capture shorter in parents with large than small broods (Table 2, Fig. 4). Control variables also affected the capture probability. Disturbance by bycatch, repeated capturing attempts at the same brood, and a decoy predator positioned close to the forest edge decreased capture probability (and

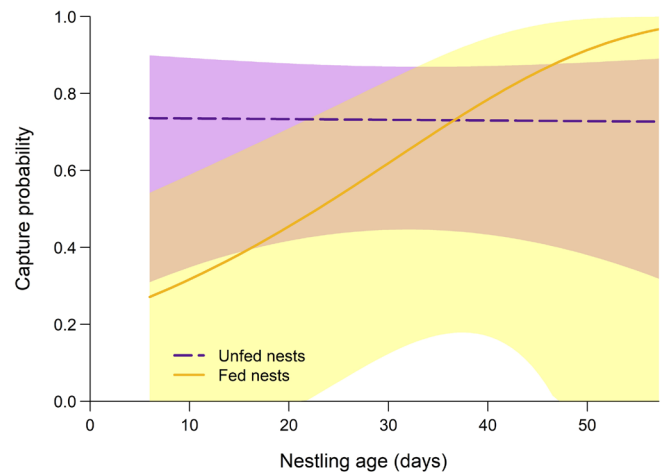


Figure 3. Capture probability in relation to the nestling age in days for unsupplemented red kite parents (unfed, purple dashed line) and food supplemented parents (fed, orange line). Lines represent means and shadings represent 95% confidence intervals of model predictions. The results are shown for first trials (no repetition) without disturbance, no wind, and no proximity to trees. All numerical variables were set to their mean values.

increased time-to-capture; Table 2). Also, weather variables affected the outcome of the capture trial. Windy conditions and high temperatures decreased capture probability and increased time-to-capture (Table 2). In addition, we found no evidence for body condition affecting time-to-capture (estimate body condition = 0.35, 95% CI = -1.75 to 2.47).

Discussion

This experimental study investigates the effect of food availability on the relative contribution of two hypotheses explaining variation in the intensity of parental anti-predator behaviour during the nestling period, the 'reproductive value of offspring' hypothesis, and the 'harm-to-offspring' hypothesis. We found that in red kites, the intensity of parental anti-predator behaviour did not change with increasing age of nestlings in the untreated control group, supporting none of the separate hypotheses. Under experimentally enhanced food conditions, the intensity of anti-predator behaviour decreased in parents with young nestlings and increased in parents with old nestlings compared to the unsupplemented group. This resulted in an overall increase in anti-predator behaviour throughout the nestling period. This pattern of experimental results indicates that under unsupplemented conditions, the contribution of the 'harm-to-offspring' hypothesis at the beginning of the nestling period is counterbalanced by the contribution of the 'reproductive value of offspring' hypothesis at the end of the nestling period. Supplemental food reduced the vulnerability of nestlings and lowered the contribution of the 'harm-to-offspring' hypothesis at the beginning of the nestling period while it increased the reproductive value of nestlings and the contribution of the 'reproductive value of offspring' hypothesis at the end of

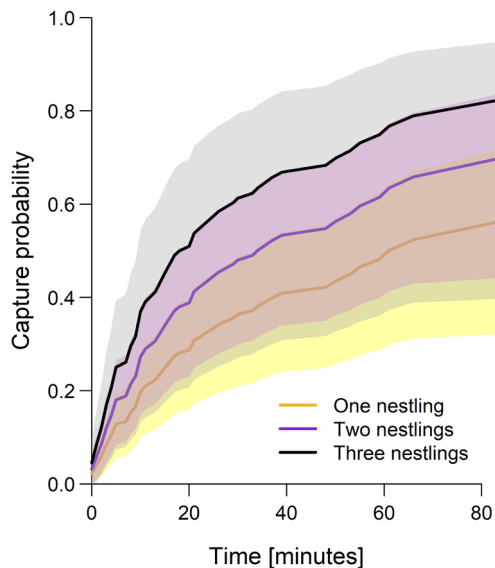


Figure 4. Capture probability in relation to the time since detection of the decoy predator for red kite breeding pairs with different brood sizes. Lines represent means and shadings represent 95% confidence intervals of model predictions. As we did not find differences between years, the figure is based 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.

the nestling period. Thus, the results support the previous theoretical prediction of Dale et al. (1996) that the ‘reproductive value of offspring’ hypothesis will have greater relevance under favourable breeding conditions, while the ‘harm-to-offspring’ hypothesis will become more relevant under poor breeding conditions. The study therefore provides strong evidence that food availability shapes not only the feeding rates and parental provisioning efforts but is also an important part of the dynamic adjustment of parental anti-predator investment during breeding.

Under a wide range of food conditions, food supplementation to parents might mainly affect parental condition rather than vulnerability and reproductive value of the brood (Boutin 1990, Ruffino 2014, Michel et al. 2022). An increased body condition of parents can also affect risk-taking behaviour. However, we did not find any indication for higher body condition of fed than unfed parents or for the expectation of increased parental condition resulting in an increased anti-predator behaviour (McNamara and Houston 1996). Instead, 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, Nägeli 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 improved access to food resources (Catitti et al. 2024) and thus, increased post-fledging survival probability of nestlings (Naef-Daenzer and Grüebler 2016).

To date, the two hypotheses were mainly tested using passerine birds as study systems and risk-taking in terms of time-to-enter the nest as response variable. However, our findings indicate that also large and long-lived species at high trophic positions dynamically adjust their own risks to both, the vulnerability and the reproductive value of their offspring to optimize their investment. Field observations during predator exposure trials support that, even in situations of low mobbing intensity, red kite parents invest time in supervising their brood and the predator; time that could otherwise be spent into food provisioning or self-maintenance (Martin and Briskie 2009, Ghaleb et al. 2013, Mutzel et al. 2013, Ibáñez-Álamo et al. 2015). 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 (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 particularly young nestlings have more urgent food requirements and are more susceptible to harm from starvation or developmental stress (Catitti et al. 2023), chasing away predators should expedite the return to foraging or brooding. 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 (Dewey and Kennedy 2001, Samelius and Alisauskas 2001, Catty et al. 2006, Rothenbach and Kelly 2012, Hu et al. 2017). We suggest that low-risk nest guarding and high-risk mobbing represent two different nest defence strategies that both reduce nest predation (Montgomerie and Weatherhead 1988, Caro 2005), but their cost-benefit ratio changes with food availability and other intrinsic and extrinsic factors (e.g. sex; see Wiebe and Tkaczyk 2024). Thus, parents of large species perform an adaptive predator response during breeding using a set of behavioural possibilities.

Not only nestling age and experimental treatment, but also brood size showed a clear effect on the intensity of 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 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, Nägeli 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 of 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 (Lazarus and Inglis 1986, Clutton-Brock 1991, Royle et al. 2012).

Finally, while we added weather variables mainly to account for potential biases, 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 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 mobbing intensity was decreased 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, our findings suggest that vulnerability and reproductive value of offspring both contribute to shape the parental anti-predator and risk-taking behaviour. The intensity of parental predator response can increase or decrease with offspring age depending on environmental conditions. Thus, future studies should refrain from discriminating the two hypotheses and develop study designs with a view of the multi-faceted dynamic nature of parental predator responses. Parental anti-predator investment seems to be adjusted to a multitude of factors associated with the brood, the parents, the environment, and the approaching predator. This study provides evidence that food availability affects anti-predator behaviour by altering the body condition of nestlings. The vulnerability of the offspring is suggested to be important for the choice of the nest defence strategy at the beginning of reproductive attempts. 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 (Nägeli et al. 2022). Ultimately, large-scale environmental factors affecting investment into nest defence may have significant demographic consequences.

Acknowledgements – We thank the members of the red kite research team for their essential participation in the field work: L. Achtnich, L. Anhäuser, M. Bachmann, C. Baucks, C. Blattner, B. Catitti, E. Cereghetti, D. Gilad, N. Guillod, M. Hertach, E. Jimenez, E. Meyrier, D. Nagl, M. Nägeli, J. Oymanns, V. van Bergen, and N. Welti. We acknowledge the great effort of the falconers M. and S. Schanze during

the capturing. We are grateful to F. Peissard for the housing of the eagle owls, to A. Aebischer for the administrative and field support, and to R. Graf for initial inputs. Open access publishing facilitated by Schweizerische Vogelwarte, as part of the Wiley – Schweizerische Vogelwarte agreement via the Consortium Of Swiss Academic Libraries. **Funding** – The study was supported by the Swiss National Science Foundation (grant no. 31003A_169668 to MUG).

Permits – All applicable institutional and national guidelines for the care and use of animals were followed. Research activities for this study were approved by the Scientific Committee of the Swiss Ornithological Institute. Capturing of red kites for ringing and tagging was done under the licence of the “Amt für Lebensmittelsicherheit und Veterinärwesen (LSVW)” of the Canton of Fribourg (permit no. 2017_29_FR) and the Federal Office for the Environment (FOEN).

Author contributions

Samuel Sieder: Data curation (equal); Formal analysis (lead); Investigation (equal); Methodology (equal); Visualization (equal); Writing – original draft (lead); Writing – review and editing (equal). **Patrick Scherler:** Conceptualization (equal); Investigation (supporting); Methodology (equal); Project administration (equal); Supervision (equal); Writing – original draft (supporting); Writing – review and editing (equal). **Stephanie Witczak:** Investigation (equal); Methodology (equal); Project administration (equal); Supervision (equal); Writing – original draft (supporting); Writing – review and editing (equal). **Matthias Tschumi:** Formal analysis (supporting); Visualization (equal); Writing – review and editing (equal). **Tobias Mühlemann:** Data curation (equal); Formal analysis (supporting); Investigation (equal); Methodology (equal); Writing – review and editing (equal). **Martin U. Grüebler:** Conceptualization (equal); Formal analysis (supporting); Funding acquisition (lead); Methodology (equal); Supervision (equal); Writing – original draft (supporting); Writing – review and editing (equal).

Transparent peer review

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/jav.03475>.

Data availability statement

Data are available from vogelwarte.ch Open Repository and Archive: <https://doi.org/10.5281/zenodo.15023237> (Sieder et al. 2025).

References

- Aebischer, A. and Scherler, P. 2021. Der Rotmilan - ein Greifvogel im Aufwind. – Haupt.
- Ajje, B. C., Pintor, L. M., Watters, J., Kerby, J. L., Hammond, J. I. and Sih, A. 2007. A framework for determining the fitness consequences of antipredator behavior. – *Behav. Ecol.* 18: 267–270.
- Andereggen, M. 2020. Prey delivery rate and diet composition of red kites (*Milvus milvus*) in Switzerland. – MSc thesis, Univ. Basel.

- Andersson, M., Wiklund, C. G. and Rundgren, H. 1980. Parental defence of offspring: a model and an example. – *Anim. Behav.* 28: 536–542.
- Apolloni, N., Gruebler, M. U., Arlettaz, R., Gottschalk, T. K. and Naef-Daenzer, B. 2018. Habitat selection and range use of little owls in relation to habitat patterns at three spatial scales. – *Anim. Conserv.* 21: 65–75.
- Arroyo, B. E., Mougeot, F. and Bretagnolle, V. 2001. Colonial breeding and nest defence in Montagu's harrier (*Circus pygargus*). – *Behav. Ecol. Sociobiol.* 50: 109–115.
- Bloom, P. H., Henckel, J. L., Henckel, E. H., Schmutz, J. K., Woodbridge, B., Bryan, J. R., Anderson, R. L., Detrich, P. J., Maechtle, T. L., McKinlea, J. O., McCrary, M. D., Titus, K. and Schempf, P. F. 1992. The Dho-Gaza with great horned owl lure: an analysis of its effectiveness in capturing raptors. – *J. Raptor Res.* 26: 167–178.
- Bloom, P. H., Clark, W. S. and Kidd, J. W. 2007. Capture techniques. – In: Bird, D. M. and Bildstein, K. L. (eds), *Raptor research and management techniques*. – Hancock House Publishers, pp. 193–220.
- Boutin, S. 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. – *Can. J. Zool.* 68: 203–220.
- Carlson, N. V., Healy, S. D. and Templeton, C. N. 2017. Hoo are you? Tits do not respond to novel predators as threats. – *Anim. Behav.* 128: 79–84.
- Caro, T. M. 2005. Antipredator defenses in birds and mammals. Interspecific interactions. – Univ. Chicago Press.
- Catitti, B., Gruebler, M. U., Kormann, U. G., Scherler, P., Witczak, S., van Bergen, V. S. and Jenni-Eiermann, S. 2022. Hungry or angry? Experimental evidence for the effects of food availability on two measures of stress in developing wild raptor nestlings. – *J. Exp. Biol.* 225: jeb244102.
- Catitti, B., Kormann, U. G. and Gruebler, M. U. 2023. Turning tables: food availability shapes dynamic aggression behaviour among asynchronously hatching siblings. – *R. Soc. Open Sci.* 10: 230328.
- Catitti, B., Gruebler, M. U., Farine, D. R. and Kormann, U. G. 2024. Natal legacies cause social and spatial marginalization during dispersal. – *Ecol. Lett.* 27: e14366.
- Catry, P., Phillips, R. A., Forcada, J. and Croxall, J. P. 2006. Factors affecting the solution of a parental dilemma in albatrosses: at what age should chicks be left unattended? – *Anim. Behav.* 72: 383–391.
- Catry, I., Franco, A. M. A., Rocha, P., Alcazar, R., Reis, S., Cordeiro, A., Ventim, R., Teodósio, J. and Moreira, F. 2013. Foraging habitat quality constrains effectiveness of artificial nest-site provisioning in reversing population declines in a colonial cavity nester. – *PLoS One* 8: e58320.
- Cereghetti, E., Scherler, P., Fattebert, J. and Gruebler, M. U. 2019. Quantification of anthropogenic food subsidies to an avian facultative scavenger in urban and rural habitats. – *Landsc. Urban Plan.* 190: 103606.
- Clutton-Brock, T. H. 1991. *The evolution of parental care*. – Princeton Univ. Press.
- Crisologo, T. L., Bonter, D. N. and Koenig, W. 2017. Defending the weak: parental defense peaks when chick vulnerability is greatest in the herring gull (*Larus argentatus*). – *Ethology* 123: 113–122.
- Curio, E. 1978. The adaptive significance of avian mobbing: I. Teleonomic hypotheses and predictions. – *Ethology* 48: 175–183.
- Curio, E. 1983. Why do young birds reproduce less well? – *Ibis* 125: 400–404.
- Dale, S., Gustavsen, R. and Slagsvold, T. 1996. Risk taking during parental care: a test of three hypotheses applied to the pied flycatcher. – *Behav. Ecol. Sociobiol.* 39: 31–42.
- Dassow, J. A., Eichholz, M. W., Stafford, J. D. and Weatherhead, P. J. 2012. Increased nest defence of upland-nesting ducks in response to experimentally reduced risk of nest predation. – *J. Avian Biol.* 43: 61–67.
- Davis, P. E. and Davis, J. E. 1981. The food of the red kite in Wales. – *Bird Study* 28: 33–40.
- Dewey, S. R. and Kennedy, P. L. 2001. Effects of supplemental food on parental-care strategies and juvenile survival of northern goshawks. – *Auk* 118: 352–365.
- Dugatkin, L. A. and Godin, J.-G. 1992. Prey approaching predators: a cost-benefit perspective. – *Ann. Zool. Fenn.* 29: 233–252.
- Fernandez, G. J. and Llambías, P. E. 2013. Parental risk-taking behaviour and nest defence during the nestling rearing stage in northern house wrens *Troglodytes aedon*. – *Acta Ornithol.* 48: 55–63.
- Fisher, R. J., Poulin, R. G., Todd, L. D. and Brigham, R. M. 2004. Nest stage, wind speed, and air temperature affect the nest defence behaviours of burrowing owls. – *Can. J. Zool.* 82: 707–713.
- Fuller, R. J. 2012. *Birds and habitat - relationships in changing landscapes*. – Cambridge Univ. Press.
- Ghalambor, C. K., Peluc, S. I. and Martin, T. E. 2013. Plasticity of parental care under the risk of predation: how much should parents reduce care? – *Biol. Lett.* 9: 20130154.
- Greig-Smith, P. W. 1980. Parental investment in nest defence by stonechats (*Saxicola torquata*). – *Anim. Behav.* 28: 604–619.
- Gruebler, M. U., Müller, M., Michel, V. T., Perrig, M., Keil, H., Naef-Daenzer, B. and Korner-Nievergelt, F. 2018. Brood provisioning and reproductive benefits in relation to habitat quality: a food supplementation experiment. – *Anim. Behav.* 141: 45–55.
- Hakkarainen, H. and Korpimäki, E. 1994. Nest defence of Tengmalm's owls reflects offspring survival prospects under fluctuating food conditions. – *Anim. Behav.* 48: 843–849.
- Hu, Y.-B., Zhao, Q.-S., Lou, Y.-Q., Chen, L.-J., González, M. A. and Sun, Y.-H. 2017. Parental attendance of chestnut thrush reduces nest predation during the incubation period: compensation for low nest concealment? – *J. Ornithol.* 158: 1111–1117.
- Ibáñez-Álamo, J. D., Magrath, R. D., Oteyza, J. C., Chalfoun, A. D., Haff, T. M., Schmidt, K. A., Thomson, R. L. and Martin, T. E. 2015. Nest predation research: recent findings and future perspectives. – *J. Ornithol.* 156: 247–262.
- King, D. I. 1999. Mortality of an adult veery incurred during the defense of nestlings. – *Wilson Bull.* 111: 576–577.
- Komdeur, J. 1999. Predation risk affects trade-off between nest guarding and foraging in Seychelles warblers. – *Behav. Ecol.* 10: 648–658.
- Lazarus, J. and Inglis, I. R. 1986. Shared and unshared parental investment, parent-offspring conflict and brood size. – *Anim. Behav.* 34: 1791–1804.
- Lind, J. and Cresswell, W. 2005. Determining the fitness consequences of antipredation behavior. – *Behav. Ecol.* 16: 945–956.
- Listoen, C. 2000. Risk taking during parental care: A test of the harm-to-offspring hypothesis. – *Behav. Ecol.* 11: 40–43.
- Mahr, K., Riegler, G. and Hoi, H. 2015. Parental risk management in relation to offspring defence: bad news for kids. – *Proc. Biol. Sci.* 282: 20141670.

- Martin, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. – *Annu. Rev. Ecol. Syst.* 18: 453–487.
- Martin, T. E. and Briskie, J. V. 2009. Predation on dependent offspring: a review of the consequences for mean expression and phenotypic plasticity in avian life history traits. – *Ann. N.Y. Acad. Sci.* 1168: 201–217.
- McNamara, J. M. and Houston, A. I. 1996. State-dependent life histories. – *Nature* 380: 215–221.
- Michel, V. T., Tschumi, M., Naef-Daenzer, B., Keil, H. and Gruebler, M. U. 2022. Reduced habitat quality increases intrinsic but not ecological costs of reproduction. – *Ecol. Evol.* 12: e8859.
- Mo, M. 2017. Killing of a mobbing crested pigeon *Ocyphaps lophotes* by an Australian raven *Corvus coronoides*. – *Aust. Field Ornithol.* 34: 35–36.
- Montgomerie, R. D. and Weatherhead, P. J. 1988. Risks and rewards of nest defence by parent birds. – *Q. Rev. Biol.* 63: 167–187.
- Mutzel, A., Blom, M. P. K., Spagopoulou, F., Wright, J., Dingemanse, N. J. and Kempenaers, B. 2013. Temporal trade-offs between nestling provisioning and defence against nest predators in blue tits. – *Anim. Behav.* 85: 1459–1469.
- Naef-Daenzer, B. and Gruebler, M. U. 2016. Post-fledging survival of altricial birds: ecological determinants and adaptation. – *J. Field Ornithol.* 87: 227–250.
- Nägeli, M., Scherler, P., Witczak, S., Catitti, B., Aebischer, A., van Bergen, V., Kormann, U. and Gruebler, M. U. 2022. Weather and food availability additively affect reproductive output in an expanding raptor population. – *Oecologia* 198: 125–138.
- Orros, M. E. and Fellowes, M. D. E. 2015. Widespread supplementary feeding in domestic gardens explains the return of reintroduced red kites *Milvus milvus* to an urban area. – *Ibis* 157: 230–238.
- Patterson, T. L., Petrinovich, L. and James, D. K. 1980. Reproductive value and appropriateness of response to predators by white-crowned sparrows. – *Behav. Ecol. Sociobiol.* 7: 227–231.
- Perrig, M., Gruebler, M. U., Keil, H. and Naef-Daenzer, B. 2014. Experimental food supplementation affects the physical development, behaviour and survival of little owl *Athene noctua* nestlings. – *Ibis* 156: 755–767.
- Pfeiffer, T. and Meyburg, B.-U. 2015. GPS tracking of red kites (*Milvus milvus*) reveals fledging number is negatively correlated with home range size. – *J. Ornithol.* 156: 963–975.
- Rothenbach, C. A. and Kelly, J. P. 2012. The parental dilemma under variable predation pressure: adaptive variation in nest attendance by great egrets. – *Condor* 114: 90–99.
- Royle, N. J., Smiseth, P. T. and Kölliker, M. 2012. The evolution of parental care. – Oxford Univ. Press.
- Ruffino, L., Salo, P., Koivisto, E., Banks, P. B. and Korpimäki, E. 2014. Reproductive responses of birds to experimental food supplementation: a meta-analysis. – *Front. Zool.* 11: 80.
- Samelius, G. and Alisauskas, R. T. 2001. Deterring arctic fox predation: the role of parental nest attendance by lesser snow geese. – *Can. J. Zool.* 79: 861–866.
- Sapir, N., Wikelski, M., McCue, M. D., Pinshow, B. and Nathan, R. 2010. Flight modes in migrating European bee-eaters: heart rate may indicate low metabolic rate during soaring and gliding. – *PLoS One* 5: e13956.
- Scherler, P., van Bergen, V. S., Catitti, B., Kormann, U. G., Witczak, S., Anderegg, M., Herzog, J. S., Aebischer, A., Roth, N. and Gruebler, M. U. 2023a. Brutbiologie des Rotmilans *Milvus milvus* in den Westschweizer Voralpen. – *Ornithol. Beob.* 120: 276–292.
- Scherler, P., Witczak, S., Aebischer, A., van Bergen, V., Catitti, B. and Gruebler, M. U. 2023b. Determinants of departure to natal dispersal across an elevational gradient in a long-lived raptor species. – *Ecol. Evol.* 13: e9603.
- Shepard, E. L. C., Wilson, R. P., Rees, W. G., Grundy, E., Lambertucci, S. A. and Vosper, S. B. 2013. Energy landscapes shape animal movement ecology. – *Am. Nat.* 182: 298–312.
- Shepard, E. L. C., Williamson, C. and Windsor, S. P. 2016. Fine-scale flight strategies of gulls in urban airflows indicate risk and reward in city living. – *Phil. Trans. R. Soc. B* 371: 20150394.
- Shepard, E. L. C., Cole, E.-L., Neate, A., Lempidakis, E. and Ross, A. 2019. Wind prevents cliff-breeding birds from accessing nests through loss of flight control. – *eLife* 8: e43842.
- Sieder, S. 2018. Fast food, slow birds - a trade-off between foraging and nest attendance modulates parental mobbing in a long-lived raptor. – MSc thesis, University of Natural Resources and Life Sciences.
- Sieder, S., Scherler, P., Witczak, S., Tschumi, M., Mühlemann, T. and Gruebler, M. U. 2025. Supplementary material for "Food availability affects parental anti-predator behaviour in red kites". – Vogelwarte.ch, Open Repository and Archive, <https://doi.org/10.5281/zenodo.15023237>.
- Sordahl, T. A. 1990. The risks of avian mobbing and distraction behaviour: an anecdotal review. – *Willson Bull.* 102: 349–352.
- Staggenborg, J., Schaefer, H. M., Stange, C., Naef-Daenzer, B. and Gruebler, M. U. 2017. Time and travelling costs during chick-rearing in relation to habitat quality in little owls *Athene noctua*. – *Ibis* 159: 519–531.
- Stearns, S. C. 1992. The evolution of life histories. – Oxford Univ. Press.
- Sternalski, A. and Bretagnolle, V. 2010. Experimental evidence of specialised phenotypic roles in a mobbing raptor. – *Behav. Ecol. Sociobiol.* 64: 1351–1361.
- Swaigood, R. R., Rowe, M. P. and Owings, D. H. 2003. Anti-predator responses of California ground squirrels to rattlesnakes and rattling sounds: the roles of sex, reproductive parity, and offspring age in assessment and decision-making rules. – *Behav. Ecol. Sociobiol.* 55: 22–31.
- Therneau, T. M. 2018. coxme: mixed effects cox models. – R package ver. 2.2-10, <https://CRAN.R-project.org/package=coxme>
- Tolonen, P. and Korpimäki, E. 1995. Parental effort of kestrels (*Falco tinnunculus*) in nest defense: effects of laying time, brood size, and varying survival prospects of offspring. – *Behav. Ecol.* 6: 435–441.
- Tryjanowski, P. and Golawski, A. 2004. Sex differences in nest defence by the red-backed shrike *Lanius collurio*: effects of offspring age, brood size, and stage of breeding season. – *J. Ethol.* 22: 13–16.
- Wellicome, T. I., Danielle Todd, L., Poulin, R. G., Holroyd, G. L. and Fisher, R. J. 2013. Comparing food limitation among three stages of nesting: supplementation experiments with the burrowing owl. – *Ecol. Evol.* 3: 2684–2695.
- Welti, N., Scherler, P. and Gruebler, M. U. 2020. Carcass predictability but not domestic pet introduction affects functional response of scavenger assemblage in urbanized habitats. – *Funct. Ecol.* 34: 265–275.
- Wiebe, K. L. and Tkaczyk, S. P. 2024. Risk-taking in bluebirds after exposure to a nest predator relates to parental roles and

- shows little cooperation between partners. – *Ethology* 131: e13531.
- Witczak, S., Kormann, U., Schaub, M., Oppel, S. and Gruebler, M. U. 2024. Sex and size shape the ontogeny of partial migration. – *J. Anim. Ecol.* 93: 406–416.
- Zuberogoitia, I., Martínez, J. E., Martínez, J. A., Zabala, J., Calvo, J. F., Azkona, A. and Pagan, I. 2008. The Dho-gaza and mist net with Eurasian eagle-owl (*Bubo bubo*) lure: effectiveness in capturing thirteen species of European raptors. – *J. Raptor Res.* 42: 48–51.