

Food supplementation reduces early-stage nest attendance under adverse weather conditions in Red Kites

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Parental care strategies have evolved to ensure optimal offspring rearing under varying environmental conditions. Nest attendance is a fundamental behaviour providing protection against predators and adverse weather, but it is traded against time spent foraging. Investigating environmental factors acting on this trade-off is crucial for understanding the ecological mechanisms underlying population-level reproductive output. We therefore experimentally increased the food available to breeding pairs of a long-lived raptor, the Red Kite *Milvus milvus*, and monitored parental nest attendance in food-supplemented ($N = 37$) and non-supplemented ($N = 58$) broods in two breeding seasons. As food supplementation has recently been shown to increase nestling body condition, we hypothesized that supplementary food would allow parents to reduce their investment in foraging and instead increase nest attendance. Nest attendance was highest early in the nestling phase and increased with rainfall in control nests. However, contrary to what was expected under our hypothesis, nest attendance did not increase in food-supplemented pairs, neither in dry nor in rainy weather conditions. This suggests that the extra time gained through supplementary feeding is not invested in additional nest attendance but is likely to be allocated to other parental or self-maintenance activities, such as predator vigilance, self-foraging or territory defence. Our study emphasizes the cost of nest attendance, particularly early in the nestling-rearing phase, and suggests that regulating these costs is a key mechanism by which environmental conditions shape the trade-off between parental self-maintenance and current reproduction.

Keywords: brooding, food availability, nest attentiveness, parental care, raptor.

The rearing of offspring is a crucial part of the reproductive cycle of most birds (Clutton-Brock 1991). This phase involves a multitude of parental care behaviours, requiring a delicate balance in the allocation of energy resources (Clutton-Brock 1991, Dale *et al.* 1996, Listøen *et al.* 2000, Rishworth *et al.* 2014). During nestling rearing, parents of altricial birds often spend a significant amount of time on the nest. This nest attendance behaviour serves the fundamental function of protection against predators (Redondo 1989, Hu *et al.* 2017) and against

adverse weather conditions during the nestlings' vulnerable period during which they lack self-thermoregulation and develop feathers (Visser 1998, Brodin *et al.* 2003). Nest attendance is, after food provisioning, probably the most essential parental behaviour during this phase (Redondo 1989, Brodin *et al.* 2003, Hu *et al.* 2017). Nest attendance is usually traded against foraging activities (the 'parental dilemma', Rothenbach & Kelly 2012). This requires parents to navigate the trade-off between minimizing the risk of brood predation or failure and ensuring adequate food provisioning (Varpe *et al.* 2004, Catry *et al.* 2006, Fontaine & Martin 2006, Rehling *et al.* 2012). The optimal solution in the trade-off between nestling demands and parental

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self-maintenance activities changes throughout the nestling period, leading to different patterns of parental nest attendance over time (Palmer *et al.* 2001). Indeed, altricial nestlings gain full thermoregulatory abilities within the first half of the developmental period (Jovani & Tella 2004, Katzenberger *et al.* 2015) after which a significant drop in nest attendance is observed (Royle *et al.* 2012). Further, depending on the species size and the local predator community, predation pressure may be stronger early in the growth period and decreases as the nestlings increase in size (Catry *et al.* 2009). As nestlings grow, their nutritional demand also increases, prompting parents to forage for more food and, consequently, to reduce nest attendance (Dijkstra *et al.* 1990, Brodin *et al.* 2003). Altogether, the relative value of these time-dependent functions shapes the well-known patterns of high nest attendance early in the nestling phase, followed by a decrease with age (Newton 1979).

Patterns of nest attendance emerge as a result of the dynamic interplay between environmental conditions, and parent and offspring state through the nestling period. Variation in nest attendance patterns has often been detected within and between species (Bassi *et al.* 2017) and is likely to have long-term consequences on offspring performance (Rensel *et al.* 2010). Environmental conditions occurring during the nestling phase can affect parental trade-offs associated with nest attendance in different ways. First, favourable food resources can affect the trade-off between parental nestling protection and parental food provisioning (Regehr & Montevecchi 1997, Rastogi *et al.* 2006), with increased food availability being associated with an increased proportion of time spent at the nest (Soler & Soler 1996, Dawson & Bortolotti 2002). Second, increased food availability can additionally affect the trade-off between investment into current reproduction and self-maintenance, with long-lived species investing more in self-maintenance than short-lived species (Roff 1992, Stearns 1992). Thus, parents under favourable food conditions may invest more time in self-maintenance (Spencer & Bryant 2002, Brodin *et al.* 2003, Varpe *et al.* 2004) instead of nest attendance. Third, adverse weather events can intensify the need for nest attendance due to the increased vulnerability of nestlings (Radford *et al.* 2001), but the extent of this intensification might differ in poor or good food conditions (Sieder *et al.* 2025). Despite the

abundance of studies investigating the proximate effect of environmental factors on patterns of nest attendance (Elkins 1983, Hu *et al.* 2017, Behrens *et al.* 2019), experimental studies investigating how the interaction of environmental factors act throughout development to form distinct nest attendance patterns are largely lacking (Dewey & Kennedy 2001).

Here, we examine whether the extra time gained by parents under favourable food conditions is invested into parental nest attendance or other behaviours away from the nest throughout the nestling-rearing period in a wild population of Red Kites *Milvus milvus*. To this end, we provided breeding pairs with supplementary food during the nestling-rearing period and applied extensive camera-trap monitoring at the nests to record parental nest attendance. In this species, nest attendance is initially almost exclusively carried out by the female, while the male brings most of the prey. After the first 3 weeks of the nestling-rearing period, both parents bring food items, which are placed in the nest to allow the nestlings to feed themselves (Carter 2001). While adult Red Kites face relatively low predation pressure, nestlings in our population encounter consistent threats throughout their growth stages (Aebischer & Scherler 2021, Scherler *et al.* 2023): Carrion Crow *Corvus corone* only at younger age, then Pine Marten *Martes martes*, Eurasian Goshawk *Accipiter gentilis* and Eurasian Eagle-Owl *Bubo bubo* at all ages. Further, nestling Red Kites reach thermoregulation within the first 2 weeks of age, a stage where they also start developing their feathers. Such physiological and environmental constraints create a trade-off between the parental need to stay at the nest and the need to leave to forage, and the food demand grows with age and brood size. This trade-off is expected to manifest in an increase in nest attendance as weather conditions deteriorate, and decreases as nestlings age and in large broods, respectively. Further, an increase in food availability is expected to reduce the overall time allocated to foraging throughout the nestling period (Uttley *et al.* 1994), influencing the trade-off that shapes nest attendance patterns. We hypothesize that the time gained from the foraging time budget is re-invested in nest attendance (Fig. 1). Consequently, in food-supplemented broods, parents should exhibit higher nest attendance compared to non-supplemented broods. This effect is expected to be greater in conditions

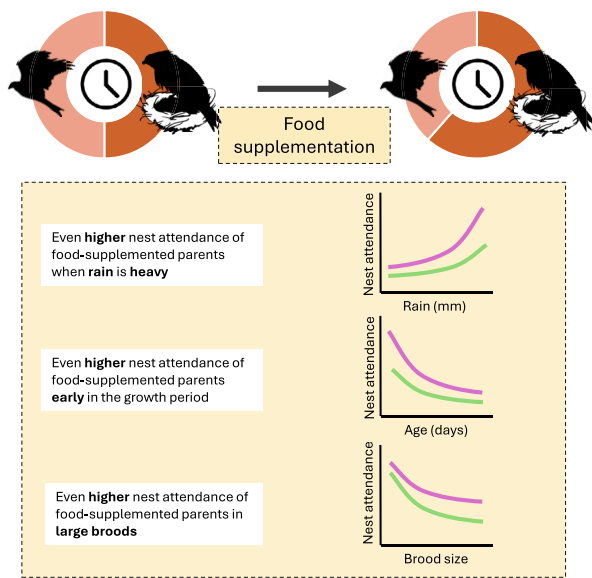


Figure 1. Conceptual representation of the hypothesis for the effect of supplementary feeding on parental nest attendance in relation to rainfall experienced during the nestling phase, nestling age and brood size. Food-supplemented parents (purple) reduce the time allocated to searching for food compared to non-supplemented ones (green line). We hypothesize that the time saved from foraging is reallocated to nest attendance, especially when the nestlings are most vulnerable, that is in heavy rainfall conditions and early in the nestling phase, and in large broods.

that increase the vulnerability of nestlings, such as in heavy rain, during early developmental stages and particularly in large broods, where parents typically spend more time foraging.

METHODS

Study population and nest attendance

The study was conducted in Western Switzerland, in the Sensebezirk region (cantons of Bern and Fribourg). The study area covers 387 km² over an elevational gradient from 482 to 1763 m (see Nägeli *et al.* 2021, for details of the study site). The region harbours one of the highest known densities of Red Kites globally (Knaus *et al.* 2018), and the study population is part of a long-term study (Scherler *et al.* 2023). Red Kite nests were observed by telescope from a safe distance to determine whether there were nestlings and to estimate their age (see Nägeli *et al.* 2021, for details on the monitoring protocols). After identifying nestlings, we determined nest attendance

using camera traps (Reconyx HC500/PC900, RECONYX Inc., Holmen, WI, USA) installed at the nest (Fig. 2). We monitored 95 active Red Kite nests during the nestling period in the years 2016 ($N = 29$) and 2017 ($N = 66$), for a total number of 1829 observed brood-days (369 in 2016 and 1460 in 2017). To avoid brood abandonment, cameras were mounted during good weather conditions after the oldest nestling was estimated to be at least 10 days. By this age, we assumed that thermoregulation abilities were sufficiently developed in the event that parents left the nest unattended for some hours due to the nest-climbing event. The exact age of the brood was determined by using the length of the eighth primary feather of the most developed nestling, measured at the time the nest was climbed to mount the camera (Nägeli *et al.* 2021). We set the cameras to take pictures at a fixed interval of 1 min (time-lapse function) during daytime from 03:00 h until 23:00 h local time. Camera traps were placed in the nesting tree or a neighbouring tree at relatively close distance (mean = 116 cm $\pm$ 48 cm; range = 56–397 cm; Fig. 2b and c). For every picture, we determined whether an adult was present on the nest, spanning a nestling age range of 10–65 days, although most observations were below 50 days (95th percentile = 48 days). At Day 51, the oldest nestling usually stopped spending the night on the nest and could then be considered fully fledged (Scherler *et al.* 2023). We considered an adult to be attending the nest if it was on the nest rim or near the centre. When the adult was on a branch near the nest, it was not considered to be attending the nest. When attending the nest, most time was usually spent on the rim without interaction with the nestlings or protecting them against adverse weather (Scherler *et al.* 2023). For data analysis, we restricted observations to the active daily period to minimize the confounding effect of nest attendance during the inactive period. Based on patterns of nest attendance (Fig. S1), we defined the active period as 06:00 h to 17:00 h.

Feeding experiment

To experimentally assess the effect of food availability on parental nest attendance, we performed a feeding experiment. Supplementary food was provided at 37 nests ($N = 9$ in 2016; $N = 28$ in



Figure 2. Example of the field methods used in this study: (a) feeding platform with a Red Kite swooping overhead, (b) camera trap installed at a nest and (c) photograph of a nest taken by one of the nest cameras.

2017) by using platforms (60 × 60 cm) elevated 2 m above the ground, placed within 200 m of the nest-site (Fig. 2). Supplementary food consisted of dead day-old chicken chicks (mean weight per chick = 38 ± 2.3 g). For most nests ($N = 21$), we started the feeding treatment after laying of the first egg, but for 10 nests, we started before egg-laying and for six nests after nestlings hatched. Thus, the period of supplementary feeding ranged from 18 days before egg-laying until 66 days after egg-laying. However, at the time when nest attendance recordings started, all nests with feeding treatment were being fed. The platforms were filled every second day in 2017 and every 1–5 days in 2016, initially with five day-old chicks per nestling per day, and with 10 day-old chicks per nestling per day after 10 days of age. Additionally, five day-old chicks per adult (i.e. 10 chicks) were provided at the same rates for the entire period of feeding treatment. When other scavengers such as Common Buzzard *Buteo buteo*, Black Kite *Milvus migrans* or neighbouring Red Kites were observed using the platform, 10 extra day-old chicks per feeding event were added to reduce the effect of interspecific competition on food availability. The maximum number of day-old chicks provided per feeding was 90.

Weather data

We obtained hourly cumulative precipitation data from three weather stations located within the study region (Fribourg Poiseux, Mühleberg and Plaffeien; Federal Office of Meteorology and

Climatology, MeteoSwiss). These stations form a triangular configuration encompassing most of the monitored nests (Fig. S2). For each nest, we extracted from the closest weather station the cumulative rainfall over a 4-h period including the 2 h before each hour of camera trap observation, the focal hour and the hour after it, to capture precipitation affecting nest conditions before and during observation hours while accounting for short temporal mismatches between biological observations and meteorological records. Correlations among stations confirmed substantial spatial variability in rainfall at the hourly scale (pairwise $r < 0.4$), consistent with the localized nature of precipitation events, while correlations increased over longer time windows (reaching ~ 0.7 at 5 h; Fig. S3).

Statistical analysis

To test the effect of supplementary feeding on nest attendance of Red Kite parents accounting for the size of the brood, age of the nestlings and different rain conditions, we used a beta-binomial regression model implemented in the package *brms* in R (Bürkner 2017). For each hour of camera trap observation, we modelled the number of minutes an adult was present at the nest relative to the total number of observed minutes using a binomial response. We only retained hours where the camera trap recorded at least 50 min of the hour (99% of the total dataset). This led to data from $N = 1\,297\,568$ images recorded each minute being summarized as 21 163 h of data. As

explanatory variables, we used the feeding treatment (0 = control; 1 = treatment), 4-h precipitation sum (mm), brood size (1, 2, 3) and age of the first hatched nestling (days). To test the predictions outlined in Figure 1, we fitted interactions between feeding treatment, nestling age and rainfall, as well as an interaction between feeding treatment and brood size. Year was also added as a fixed covariate to account for differences in the feeding schedule and environmental variation between 2016 and 2017. We included hatching date of each brood as a fixed covariate to account for potential variation in nest attendance patterns arising from parental quality (with early breeders potentially representing higher quality parents) and seasonal effects, such as increased attendance under cooler temperature conditions. We added the identity of the brood as a random intercept and accounted for the temporal non-independence of the data by adding the time sequence for each brood as a random slope. We followed a full model approach: all the explanatory variables were kept in the model, but interactions with negligible effect sizes were excluded when the 95% credible interval (95% CrI) overlapped zero. All continuous variables were standardized to have a mean of 0 and a standard deviation of 1 prior to being entered in the model. In a preliminary exploration, we fitted the final model under a range of weakly informative to more strongly regularizing priors for the intercept, fixed effects and dispersion parameter (ϕ). Across all specifications, posterior estimates, conditional effects and predictive performance were highly consistent, with no meaningful differences detected using leave-one-out (LOO) cross-validation. Given this robustness, we report results based on the most regularizing prior specification as a conservative choice. Full details of the prior sets tested, and LOO comparisons are provided in Table S1. The final model was estimated using four Markov chains with default settings for warm-up and sampling iterations. Convergence diagnostics, including R-hat values (all ~ 1), effective sample sizes (all bulk ESS > 700) and trace plots, were all checked to confirm model reliability. All model fits were assessed via visual inspection of the posterior predictive checks of both the replicated data and the standard deviation obtained by the posterior predictive distribution (Fig. S4). To indicate support for a given effect, we report for each model parameter the posterior probability (PP), defined

as the probability that an estimated parameter is positive or negative, with values closer to 1 indicating greater certainty about the effect's direction (Korner-Nievergelt *et al.* 2015).

Despite our experiment mimicking an 'ad libitum' food condition, parents differed in the amount of supplementary food brought onto the nest due to variation in acceptance of this food source or competition with other species using the same feeding platform. To ensure that the observed effect of food supplementation was not biased by the broods with low acceptance of the feeding treatment, we conducted a suite of validation analyses. First, we applied the same model to a subset containing all non-supplementary fed broods ($N = 58$) and broods confirmed through camera observations to be intensively using the feeding platforms (delivering more than three chicken chicks to the nest per day throughout the nestling period; $N = 20$), which yielded qualitatively the same results (Table S2; Fig. S5). Then, we ran additional models, one accounting for the intensity of feeding and the other accounting for the time when feeding started at each brood, showing no effect of those two parameters on the nest attendance patterns (Tables S3 & S4). Additionally, we performed a sensitivity analysis on the rainfall covariate by summing it over multiple temporal windows ranging from 1 to 5 h. This analysis confirmed that our qualitative conclusions were robust to the choice of temporal resolution (Fig. S6).

All analyses were performed in R version 4.5.2 (R Core Team 2023).

RESULTS

The proportion of hourly nest attendance declined strongly with nestling age, with the magnitude of decline depending on rainfall and supplementary feeding (Table 1; Fig. 3). When there was no rain, predicted attendance probability at 10 days of age was high and similar in both treatment groups (estimated proportion of hourly nest attendance for food supplemented and non-supplemented, respectively = 0.60 [95% CrI: 0.45–0.73]; 0.65 [95% CrI: 0.53–0.76]), whereas by 25 days, it had declined to intermediate values (median and 95% CrI: 0.25 [0.19–0.32]; 0.30 [0.23–0.36]), and by 42 days, attendance was low (median and 95% CrI = 0.06 [0.05–0.09]; 0.08 [0.06–0.10]). However, under heavy rainfall, the difference in nest

Table 1. Parameter estimates from the Bayesian beta-binomial mixed-effects model examining factors associated with parental nest attendance in Red Kites. The estimates represent the mean of each parameter's posterior distribution, with the corresponding 95% credible interval (CrI) provided. Fixed effects with CrI that do not cross 0 are highlighted in bold. The column PP reports the posterior probability for a given effect (i.e. the probability that the effect is strictly positive or negative as estimated by the model).

Fixed effects parameters	Estimate	2.5%	97.5%	PP
(Intercept)	−1.535	−1.804	−1.266	1
Age	−0.982	−1.153	−0.806	1
Feeding treatment	−0.224	−0.462	0.024	0.965
Rainfall (4-h sum)	0.163	0.122	0.204	1
Brood size [2]	−0.064	−0.27	0.14	0.734
Brood size [3]	−0.163	−0.427	0.091	0.887
Year [2017]	−0.076	−0.361	0.203	0.693
Hatching date	−0.251	−0.384	−0.12	1
Age × Feeding treatment	0.059	−0.199	0.315	0.674
Age × Rainfall (4-h sum)	−0.217	−0.286	−0.153	1
Feeding treatment × Rainfall (4-h sum)	−0.13	−0.19	−0.072	1
Age × Feeding treatment × Rainfall (4-h sum)	0.198	0.117	0.281	1
Random effects parameters	SD	2.5%	97.5%	
Brood_ID (Intercept)	0.558	0.45	0.682	
time_num_(Intercept)	0.866	0.699	1.054	
Brood_ID:time_num	0.371	0.135	0.572	

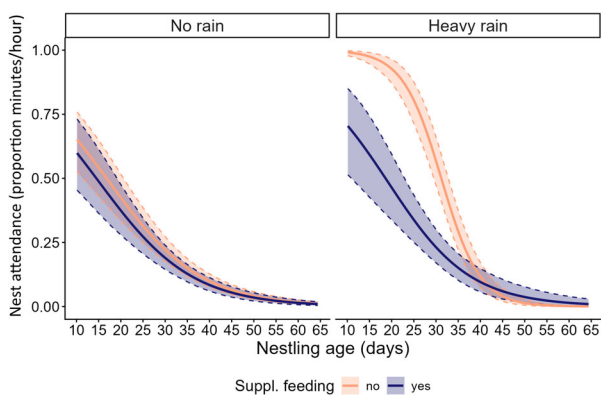


Figure 3. Proportion of hourly nest attendance by Red Kite parents in relation to nestling age for two rain conditions (no rain and 95th percentile of rain values) in Red Kites ($N = 37$ food supplemented, $N = 58$ non-supplemented). Thick lines and shaded areas correspond to the median and 95% credible intervals (95% CrI) from the posterior distribution of a Bayesian beta-binomial regression model.

attendance between food-supplemented and non-supplemented broods was markedly stronger, especially early in the nestling phase (Fig. 3). While parents in control broods substantially increased their attendance in adverse weather conditions when the nestlings were young (i.e. 10 days; median and 95% CrI: 0.83 [0.74–0.90]), this was not the case in the food-supplemented broods (median and 95% CrI at 10 days old: 0.63 [0.47–0.76]). This difference decreased as nestlings grew older (median and 95% CrI for food-supplemented and non-supplemented broods at 25 days, respectively: 0.27 [0.20–0.34]; 0.40 [0.33–0.48]) and was not present at fledging age (median and 95% CrI for food-supplemented and non-supplemented broods at 42 days, respectively: 0.07 [0.05–0.09]). Feeding treatment did not affect nest attendance across broods of different sizes (mean effect and 95% CrI for the interaction with brood size: size 2 = 0.12 [−0.24 to 0.47]; size 3 = 0.01 [−0.45 to 0.46]). Consequently, this interaction was excluded from the final model. There was a tendency for parents in large broods (three nestlings) to attend the nest less than parents with single nestlings, but the effect had low certainty (PP = 0.73). Nest attendance did not differ on average between the two monitored years, but it was higher in pairs that started breeding early than those breeding late in the season (Table 1).

DISCUSSION

By experimentally manipulating food availability for the parents, we demonstrated that increased food availability was associated with decreased nest attendance under conditions in which the nestlings were most vulnerable, such as early developmental stages during heavy rainfall. These findings contradict the hypothesis that increased food supplementation would lead to parents spending more time at the nest. Instead, our results suggest that the increased food availability releases time from foraging, which is reallocated to other parental activities than nest attendance.

We see three non-mutually exclusive possibilities to explain reduced nest attendance by food-supplemented parents. First, parents may re-direct their efforts into other off-nest parental activities. The widely known positive relationship between food availability and nest attendance is explained by the idea that when food is abundant,

the greatest benefit comes from staying at the nest, as increased nest attendance can reduce predation rates (Davis *et al.* 2005, Rastogi *et al.* 2006). However, defence against predation is not solely dependent on nest attendance. For example, in Bald Eagles *Haliaeetus leucocephalus*, most nest guarding during the nestling phase occurs from perches in adjacent trees (Turrin & Watts 2015). By staying close to the nest, adults can monitor the needs of their offspring by assessing their behaviour (Quillfeldt & Masello 2004), while proactively deterring potential intruders and predators (Komdeur & Kats 1999). This strategy is likely to be more effective than guarding from the nest itself, especially for Red Kites, whose nests are typically located in the dense crowns of coniferous or deciduous trees (Scherler *et al.* 2023). An increase in food availability near the nest, as mimicked by our food supplementation experiment, enables parents to forage while maintaining the ability to defend the nest (Martindale 1982, Vafidis *et al.* 2018). Red Kites, being skilled flyers, can effectively target enemies in flight when they have a clear view. Therefore, food-supplemented parents may be, on average, in closer proximity to the nest because they do not need to travel far to get food and can additionally use the time gained from efficient foraging to perch near the nest, where they may best fulfil nest-defence duties. Our food supplementation experiment was indeed associated with higher survival rates of last-hatched nestlings, which are typically the most disadvantaged within broods due to reduced access to food (Nägeli *et al.* 2021, Catitti *et al.* 2023). Although speculative, this increase in survival may partly result from enhanced nest defence by food-supplemented parents, providing indirect support for our hypothesis that increased local food availability allows parents to better balance foraging and nest defence.

Under adverse weather conditions or when the nestlings are young, time spent off the nest is usually limited, but under food-rich conditions, nestlings are in better condition (Nägeli *et al.* 2021) and are more likely to withstand prolonged time periods without the parents directly at the nest. Therefore, food availability may mediate the time allocated to alternative parental care strategies, especially in periods of maximum vulnerability of the nestlings. Indeed, in a parallel study, we showed that food-supplemented Red Kite parents detected a decoy predator earlier than non-supplemented parents when natural food

availability was low (Sieder *et al.* 2018). The current study complements these findings, suggesting that with favourable food conditions, parents might be less 'tethered' to the nest and gain the flexibility to maximize their nest-guarding duties from a distance.

A second possible explanation for reduced nest attendance by food-supplemented parents is that it allows self-maintenance activities, such as preening and resting. The degree of parental investment arises from a trade-off between the needs of the offspring and the survival of the adults (Catry *et al.* 2006, Tieleman *et al.* 2008). Red Kites have an estimated average reproductive lifespan of 10.7 years, making it a long-lived bird species (BirdLife International 2020). In long-lived bird species, the trade-off favouring parental survival is particularly important, as lifetime fitness is accrued over many years, and excessive energy expenditure in a single breeding attempt can incur substantial fitness costs. In such species, the decision to breed in a given year is non-trivial (the 'prudent parent hypothesis', Drent & Daan 2002), and it is not uncommon for parents to skip breeding altogether in years of adverse environmental conditions (Erikstad *et al.* 1998, Reed *et al.* 2015). Therefore, breeding birds should seek an optimum condition in which parental investment does not lead to physical or physiological exhaustion (Santos & Nakagawa 2012, Thys *et al.* 2019). Limited food availability in the surrounding environment often challenges such an optimum by obliging parents to increase their foraging efforts (Abrams 1991, Shaffer *et al.* 2001, Gladbach *et al.* 2009). However, how time is allocated under optimal food conditions is less clear. In species where food availability fluctuates significantly within a breeding season, parents may increase their foraging efforts when conditions are favourable as an investment for the future (Schifferli *et al.* 2014). Conversely, in species where food conditions are relatively stable, high food availability may reduce the pressure of food provisioning duties, allowing parents to focus on self-maintenance activities. Our results that food-supplemented parents reduce nest attendance under adverse weather conditions and in early nestling stages are in agreement with the latter scenario. By regularly supplying food, we may have created a stable, food-rich environment where parents could prioritize self-maintenance over nest attendance in periods that would otherwise require high parental investment.

Third, the lower nest attendance of supplemented parents during rainy periods early in the nestling stage may reflect the interaction between the constant availability of food at the feeding platform and the better condition of supplemented chicks. Because food is accessible even during rain, supplemented adults can continue foraging, whereas non-supplemented parents avoid costly foraging trips and instead remain at the nest (Baucks 2018). At the same time, nestlings in supplemented nests are fitter and better able to cope with the energetic demands of thermoregulation. Typically, under adverse weather conditions, parents increase nest attendance to shield their offspring, which may not have fully developed their final plumage (Barras *et al.* 2021). However, nestlings in better body condition can more easily meet the energetic demands of thermoregulation under such conditions (O'Connor 1984, Kirkley & Gessaman 1990). Because the youngest nestlings observed in our study were already 10 days old, they probably had at least partly developed thermoregulation abilities. It is expected that nestlings of supplementary fed nests reach this state earlier (Robb *et al.* 2008, Ruffino *et al.* 2014). Consequently, the combination of continuous food access and improved chick condition may enable supplemented parents to leave the nest more readily during rainy periods, while non-supplemented parents remain to protect their more vulnerable young.

Patterns of parental nest attendance are driven by the interaction of multiple factors, such as perceived predation risk and value of the offspring, which are then traded against parental survival (Lima 2009). Our results highlight that the quantity and distribution of food resources around the nest can influence such trade-offs and result in shifts in nest attendance in favour of other parental activities such as nest guarding and territory defence from strategic off-nest locations. However, there could be other activities in which Red Kite parents engage when they are released from the need to attend the nest which call for further investigation. For instance, the time saved from foraging can be reinvested in other activities that can ensure long-term fitness benefits. Indeed, the density of Red Kites in our study area is among the highest recorded for the species worldwide (Aebischer & Scherler 2021), and birds experience fierce competition for breeding territories. Thus, as with other long-lived species, Red Kites may use the time off the nest to visit neighbouring territories to assess success rates and

potential vacancies to inform future breeding decisions. This extraterritorial prospecting during breeding may play a role in ensuring the stability of the future reproductive output.

Overall, our findings suggest that some of the costs of parental care for breeding Red Kites can be alleviated by favourable food conditions during the nestling period. This can occur by reducing the cost of foraging and of leaving the nest unattended during adverse weather, particularly during periods when nestlings are most vulnerable. Time spent off the nest may help reduce predation risk, thereby increasing offspring survival, while also benefiting the self-maintenance of the adults. Consequently, our study highlights the costs associated with nest attendance, and that the regulation of these costs acts as a key mechanism by which environmental conditions influence the trade-off between parental self-maintenance and brood care during breeding.

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AUTHOR CONTRIBUTIONS

Martin Urs Grüebler: Conceptualization; funding acquisition; writing – original draft; methodology;

writing – review and editing; project administration; supervision; resources. **Urs Gabriel Kormann:** Writing – review and editing; supervision; project administration; conceptualization; methodology. **Valentijn Serge van Bergen:** Conceptualization; investigation; writing – original draft; methodology; visualization; writing – review and editing; formal analysis; data curation. **Benedetta Catitti:** Conceptualization; investigation; writing – original draft; methodology; validation; visualization; writing – review and editing; software; formal analysis; supervision; data curation.

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CONFLICT OF INTEREST

The authors declare to have no conflicts of interest.

ETHICAL NOTE

None.

Data Availability Statement

Data and code required to replicate the study's results are available in the Zenodo repository at <https://doi.org/10.5281/zenodo.21133063>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Proportion of nest attendance in relation the hour of the day for three age-classes. Red dashed lines indicate the time threshold (6 AM and 5 PM local time) we used to subset our data to capture parental nest attendance during hours of activity.

Figure S2. Plot of the study region extent showing the locations of the three weather stations (Fribourg Poiseux, Mühleberg and Plaffeien; red crossed circles) and the monitored Red Kite nests (points). Nest colours indicate the closest weather

station from which the rainfall data have been extracted.

Figure S3. Correlation of rainfall between weather stations across different time intervals. Correlation matrices show the pairwise Pearson correlation coefficients of rainfall measured at multiple weather stations. Separate matrices are shown for cumulative rainfall intervals of 1–5 h. Colours indicate the strength and direction of the correlation, with blue representing strong negative correlations, white indicating no correlation and red representing strong positive correlations. Values inside each cell correspond to the numeric correlation coefficients.

Figure S4. Posterior predictive checks for the beta-binomial model of nest attendance. The left panel shows the distribution of the observed response (dark line) overlaid with replicated data drawn from the posterior predictive distribution (light lines), illustrating that the model accurately captures the strong peak at zero and the upper tail of the distribution. The right panel shows the posterior predictive distribution of the standard deviation (light bars) compared with the observed standard deviation (vertical line), indicating that the model slightly overestimates variability and therefore conservatively accounts for extra-binomial variation.

Figure S5. Parental nest attendance probability in relation to nestling age for two rain conditions in Red Kites. Thick lines and shaded areas correspond to the median and 95% credible intervals (95% CrI) from the posterior distribution of a Bayesian mixed-effect beta-binomial regression model. The used dataset was a subset of the original, with a selection of broods where feeding platforms were used intensively ($N = 20$), and the non-supplemented group ($N = 58$).

Figure S6. Coefficient estimates from the beta-binomial model of the hourly proportion of time spent on the nest, shown for cumulative rainfall aggregated over different temporal windows. Each panel corresponds to a distinct rainfall accumulation interval (1–5 h). The 2-h window includes the hour of observation and the immediately preceding hour; the 3-h window includes the hour preceding the observation, the observation hour and the subsequent hour; the 4-h window includes the 2 h preceding the observation, the observation hour and the subsequent hour; and the 5-h window includes the 2 h preceding the observation,

the observation hour and the two subsequent hours.

Table S1. Prior sensitivity analysis and leave-one-out cross-validation (LOO) results for the fitted models. The table reports the prior distributions tested for the intercept and fixed effects (specified on the logit scale) and for the dispersion parameter (ϕ), along with model comparison metrics based on LOO. *Elpd_diff* denotes the expected log predictive density difference relative to the best-performing model, and *Se_diff* is the associated standard error. In all cases, the absolute differences in expected log predictive density are smaller than their corresponding standard errors, indicating that the models are statistically indistinguishable in terms of out-of-sample predictive performance. Consequently, we retained the model with tighter priors for subsequent analyses.

Table S2. Parameter estimates (posterior means) and 95% credible intervals (CrI) from models fitted to the subset of broods confirmed by camera observations to be intensively using the feeding platforms ($N = 20$), compared to control broods ($N = 58$). Fixed effects whose 95% CrI do not cross 0 are in bold. The column PP reports the posterior probability for a given effect (i.e. the probability that the effect is strictly positive or negative as estimated by the model).

Table S3. Parameter estimates (posterior means) and 95% credible intervals (CrI) from models including the intensity of feeding (number of chicks delivered per day) as a covariate. The analysis was only performed on supplementary fed broods ($N = 37$). Fixed effects whose 95% CrI do not cross 0 are in bold. The column PP reports the posterior probability for a given effect (i.e. the probability that the effect is strictly positive or negative as estimated by the model). The feeding intensity had no effect on nest attendance patterns found on the complete dataset.

Table S4. Parameter estimates (posterior means) and 95% credible intervals (CrI) from models including the onset of feeding (timing of supplementation relative to brood age) as a covariate. Due to incomplete egg-laying data, this model is based on a subset of the food-supplemented broods ($N = 33$). Fixed effects whose 95% CrI do not cross 0 are in bold. The column PP reports the posterior probability for a given effect (i.e. the probability that the effect is strictly positive or negative as estimated by the model). The timing of feeding initiation had no effect on nest attendance patterns found on the complete dataset.