Dynamic parental roles revealed by fine-scale hunting behaviour with concurrent pair tracking in the wild

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Abstract

Parental cooperation in offspring care is essential for offspring survival in species with extended biparental care. Yet, the mechanisms through which each parent's foraging skills and performance shape both their own and their partner's contributions to offspring rearing, particularly in natural conditions, remain poorly understood. Using high-resolution GPS and accelerometer data, we simultaneously tracked male and female barn owls (*Tyto alba*) during chick-rearing to investigate parental roles in unprecedented detail. Our results reveal a spectrum of parental contributions, ranging from uniparental male care to balanced biparental effort, with individual hunting efficiency and environmental conditions considerably influencing each parent's provisioning behaviour. Notably, we found low repeatability of biparental cooperation (biparentality) within pairs across nights, indicating that investment is dynamically adjusted in response to the partner's contribution and environmental factors. Females increased their foraging effort when male hunting performance declined, or resources were likely scarce. Higher biparentality across pairs was associated with enhanced growth outcomes for the youngest chicks, underscoring the fitness benefits of cooperative parental investment. Using cutting-edge high-resolution tracking technology, this study reveals previously inaccessible insights into the flexible, context-dependent dynamics of biparental care. We demonstrate how parental roles adjust to partner contribution and behaviour under natural conditions, showcasing the potential of biologging tools to deepen our understanding of the complex and often synergistic behavioural and ecological influences on parental care.

Keywords: biologging, parental coordination, parental care, parental negotiation, barn owl, plasticity

Introduction

Extended biparental care is a cooperative effort that plays a crucial role in offspring survival in many species [1]. Parental cooperation is dynamic, fluctuating as individuals balance offspring care and their competing needs, including self-maintenance, future reproductive opportunities, and survival [2–6]. Such shifts in parental cooperation— whether through short-term adjustments [7, 8] or across different phases of the breeding season [9] — reveal the plasticity of biparental care systems, which remains underexplored in natural conditions [6, 10].

Despite extensive research on parental investment, a key knowledge gap exists regarding how each parent's foraging behaviour and success influence their own provisioning contributions and, consequently, their partner's level of cooperation in offspring rearing [11]. In socially monogamous species, the division of parental duties is rarely fixed, often shifting in response to both social dynamics and environmental variability [6, 10, 12–14]. New technologies, such as the combination of Global Positioning Systems (GPS) and triaxial accelerometers, can help us collect refined behavioural data about individuals [15–17] potentially highlighting short-term responses, and simultaneous tracking of parents can provide invaluable insights on cooperation in biparental care systems [**?**]. High-resolution and simultaneous tracking can be a powerful tool to investigate the parental response to social and environmental conditions that parents face when raising offspring.

Much of the current understanding of biparental care is based on indirect or experimental approaches [2, 18–20], which often provide limited insights into real-time parental decision-making and cooperation under natural conditions [6, 10, 11]. Flexibility in parental contributions — referred to as facultative biparental care [21] — permits parents to adjust their effort according to factors like partner behaviour, contingent brood needs, and environmental conditions such as food availability [6, 10, 21, 22]. Investigating these dynamic adjustments is essential for understanding the adaptive significance and the ecological drivers of parental cooperation.

In this study, we employed simultaneous GPS and accelerometer tracking of both male and female barn owls (*Tyto alba*) during chick provisioning to capture high-resolution data on parental behaviour. By concurrently tracking both parents, we measured individual and combined hunting effort, prey delivery rates, hunting efficiency, self-feeding patterns and most importantly a pair 'biparentality' metric– defined as the proportion of prey brought to the nest by the female over the total by both parents – across nights. Parents may modulate their feeding rates on a daily basis, responding to their own foraging success, their partner's behaviour, and various environmental cues [10]. Over the breeding season, these adjustments can lead to shifts along a continuum from uniparental to biparental care, reflecting each parent and pair's adaptive strategies for optimizing reproductive success [9]. Our concurrent tracking approach provides an unprecedented view into how each parent allocates effort, negotiates roles, and dynamically adjusts contributions based on environmental conditions and their partner's behaviour.

Our findings illuminate the flexible nature of biparental care and how species adjust their reproductive strategies to meet environmental challenges. These insights contribute to broader discussions on the evolution of parental care systems and the resilience of these systems in the face of environmental changes.

Results

We analyzed the hunting and provisioning behavior of 136 barn owls from 68 pairs, using GPS and accelerometer data collected over 333 nights, averaging 5.23 ± 0.52 nights per pair (range: 4 to 6 nights). Across all pairs, we documented 20,553 hunting attempts (13,746 by males and 6,807 by females), with a hunting success rate of 31% ± 12 for males and 27% ± 19 for females. Males completed 3,089 foraging trips, averaging 8.69 trips per night (range: 1 to 31), while females made 1,192 trips, with a mean of 3.35 trips per night (range: 0 to 14).

Variation in biparental care

Barn owl pairs exhibited a spectrum of parental care strategies, from male-only provisioning to fully biparental care, with a mean biparentality of 0.27 ± 0.17 – calculated as the proportion of prey brought back to the nest by the female over the total brought by both parents (Fig. 1A). Low repeatability of biparentality among nights ($R = 0.115$, 95%C.I. = [0.06, 0.15]) indicated that the division of parental effort was flexible within pairs (controlled for year and brood size). Female and male contributions to chick provisioning averaged 0.67 ± 0.52 and 1.86 ± 0.98 prey per chick per night, respectively, with a combined total of 2.53 ± 1.18 prey per chick per night (Fig. 1D-F).

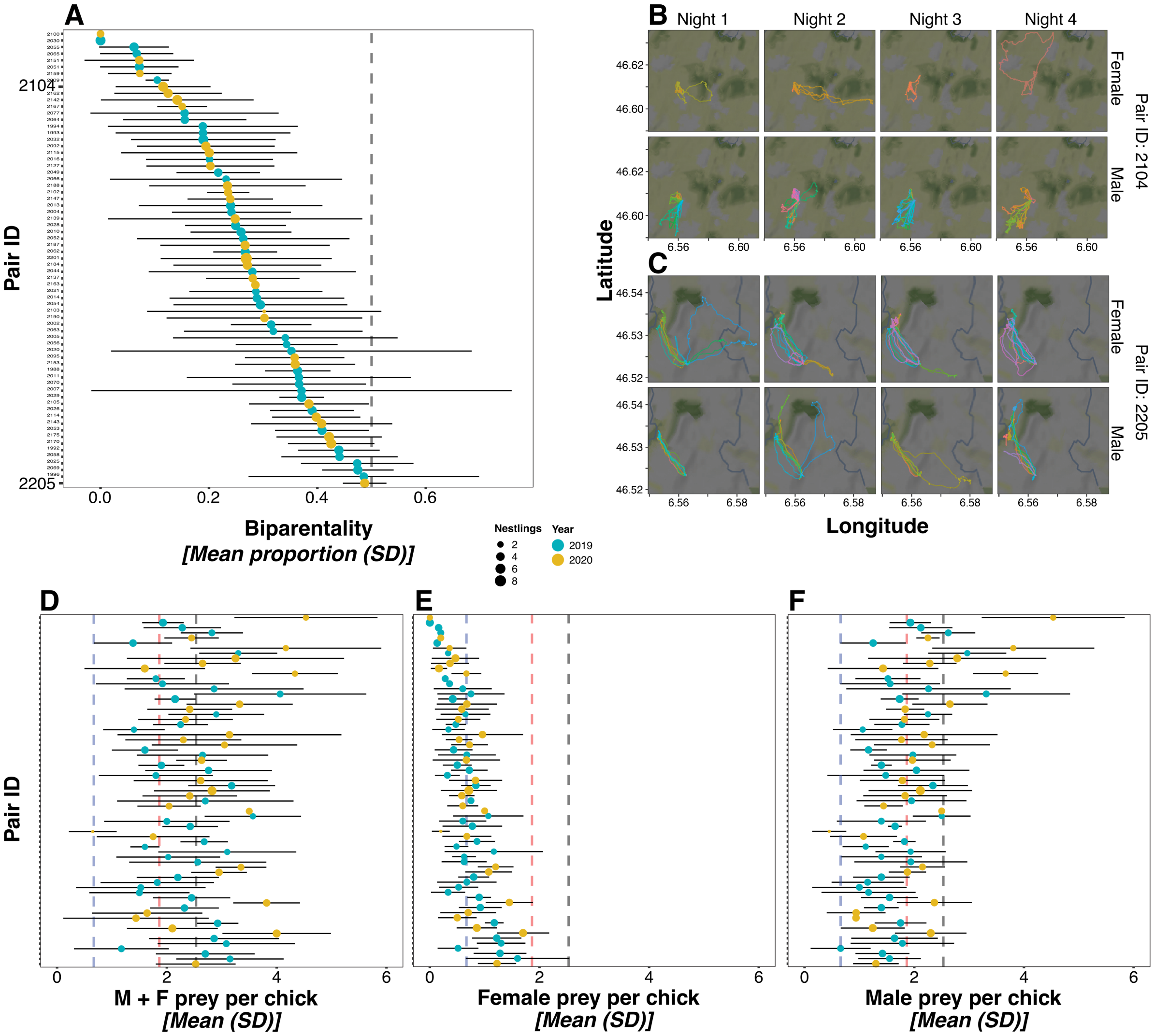

Figure 1: Flexible biparentality and relative chick provisioning by male and female barn owl parents. Summary values per pair of A) 'biparentality', the proportion of prey brought back to the nest by the female relative to the total brought by both parents, the dashed line highlights the equal investment from male and female parents; B) example of female (top row) and male (bottom row) tracks foraging for the brood in a pair with male contributing the most to the chick provisioning (different colours are different foraging trips); C) example of female (top row) and male (bottom row) tracks foraging for the brood in a pair with parents contributing almost equally to the chick provisioning (different colours are different foraging trips); D) prey items per chick by both parents combined; E) prey per chick by female parent, F) prey per chick by male parent. Dots are mean values; the range is the standard deviation. Dots are coloured by year, their size relative to the nestlings in the nest and they are arranged from top (uniparental pairs) to bottom (biparental pairs) by biparentality proportion, as displayed in A. Vertical dashed lines are mean prey items per chick by both parents (black), by male parent (red) and by female parent (blue).

The mean proportion biparentality per pair varied only slightly with brood size (Fig. S2). Pairwise comparisons revealed that broods with three or fewer chicks had lower biparentality than those with five chicks (estimate: -0.74, HPD: -1.40 to -0.08), while five-chick broods showed higher biparentality than six or more chicks broods (estimate: 0.98, HPD: 0.14 to 1.87). Other brood size comparisons did not show significant differences (Fig. S2; Table S2). Overall, biparentality generally increased with brood size, although the largest broods did not follow this pattern, possibly due to a small sample size (n = 6).

Predictors of flexible biparental care

On a nightly scale, biparentality proportion correlated positively with the relative provisioning – prey per chick – by females (ρ = 0.66, 95%Cr.I. = [0.60, 0.72], iterations = 10,000, Fig. S3) and negatively with the provisioning rate by males ($\rho = -0.39$, 95%Cr.I. = [-0.47, -0.29], iterations = 10,000, Fig. S4), suggesting that higher female contribution shifts the system toward biparental care. These relationships were consistent and slightly stronger when values were averaged across individuals (Fig. S5-S6).

To test if biparentality was influenced by environmental and/or social factors, we modelled biparentality proportion as a function of male and female foraging behaviour (hunting attempts, hunting success and self-feeding), year, preferred hunting habitat (wildflower strips area [23–25], Table S1), and chick loss during the tagging period (0 = no loss, 1 = at least one dead). Biparentality proportion increased with reductions in wildflower strip area and decreased with male hunting performance (attempts per night, success rate, and mean Vectorial Dynamic Body Acceleration – VeDBA), showing increases of 10%, 27%, 23%, and 11%, respectively (Fig. 2A, Table S3). Conversely, higher female hunting performance (attempts, success rate, and VeDBA) and reduced self-feeding (preys eaten over total hunted) were associated with increases in biparentality by 49%, 36%, 27%, and 33%, respectively (Fig. 2A, Table S3). Neither chick loss during tagging nor the year of tagging had meaningful effects on biparentality proportion.

Relative and combined parental chick provisioning

Pairs with more equal parental investment provided more food per chick, as their nightly biparentality proportion was positively related to prey delivery per chick by both parents combined (Fig. 2B, Table S4). Male hunting attempts showed the strongest positive effect on prey per chick, followed by male success rate and female hunting attempts (Fig. 2B, Table S4). Habitat, year, and other behavioural variables had weak or non-meaningful effects, while chick loss was negatively associated with food provisioning per chick (Fig. 2B, Table S4).

To investigate whether male behaviour influenced female provisioning, we modelled female prey delivery per chick as a function of male behavioural variables, wildflower strip area, year, and chick loss. Only the number of male hunting attempts per night positively related with female prey delivery, with a weak effect of wildflower strip area (Fig. 2C, Table S5). Similarly, we found that male provisioning was positively associated with female hunting attempts per night (Fig. 2D, Table S5). Wildflower strip area also showed a positive association, while chick loss had a minor negative effect (Fig. 2D, Table S5).

Temporal dynamics of foraging probability

Male foraging probability, defined as the likelihood of initiating a foraging trip as a function of time during the night (see Methods), consistently decreased regardless of biparentality proportion (Fig. 2F). Males in both uniparental and biparental pairs displayed similar probabilities of foraging throughout the night. In contrast, female foraging probability varied with their provisioning effort: females in pairs with low biparentality proportion reduced foraging probability by three-quarters within the first two hours of the night. In pairs with near-equal contributions, female foraging probability mirrored that of males (Fig. 2E). This finding emphasizes the greater flexibility in female behaviour and highlights the trade-offs between time, energy expenditure, and increased night-time foraging effort as biparentality proportion rises.

Contributions of specific parental behaviours to nestling survival

We further analysed nestling survival at logger recovery, incorporating individual parental behaviours (mean biparentality proportion, combined and single parental provisioning per chick), year, and wildflower strip area (see Fig. S7 and Table S19 in Supplementary Materials). Mean biparentality showed a weak positive trend (MPD = 0.17, 95% Cr.I. = [-0.08, 0.44]), as did the combined prey delivery by both parents (MPD = 0.17, 95% Cr.I. = [-0.08, 0.44]). When analysing single contributions by parent, female provisioning had a positive effect on nestling survival (MPD = 0.26, 95% Cr.I. = [0.01, 0.52]), whereas male provisioning showed no significant effect (MPD = 0.04, 95% Cr.I. = [-0.22, 0.31]). Additionally, male hunting attempts positively influenced nestling survival (MPD = 0.32, 95% Cr.I. = [0.04, 0.61]), while male hunting success rate had a negative effect (MPD = -0.24, 95% Cr.I. = [-0.49, -0.01]) and female success rate showed a positive trend (MPD = 0.23, 95% Cr.I. = [-0.02, 0.50]). Mean VeDBA, an energy expenditure proxy, was positively related to nestling survival for females (MPD = 0.25, 95% Cr.I. = [0.02, 0.49]) and showed a weaker association for males (MPD = 0.20, 95% Cr.I. = [-0.04, 0.44]).

Impact of flexible biparental care on chick growth

We assessed the effect of biparentality proportion on chick body condition by analysing chick weight and wing length as a function of biparentality proportion, measurement time

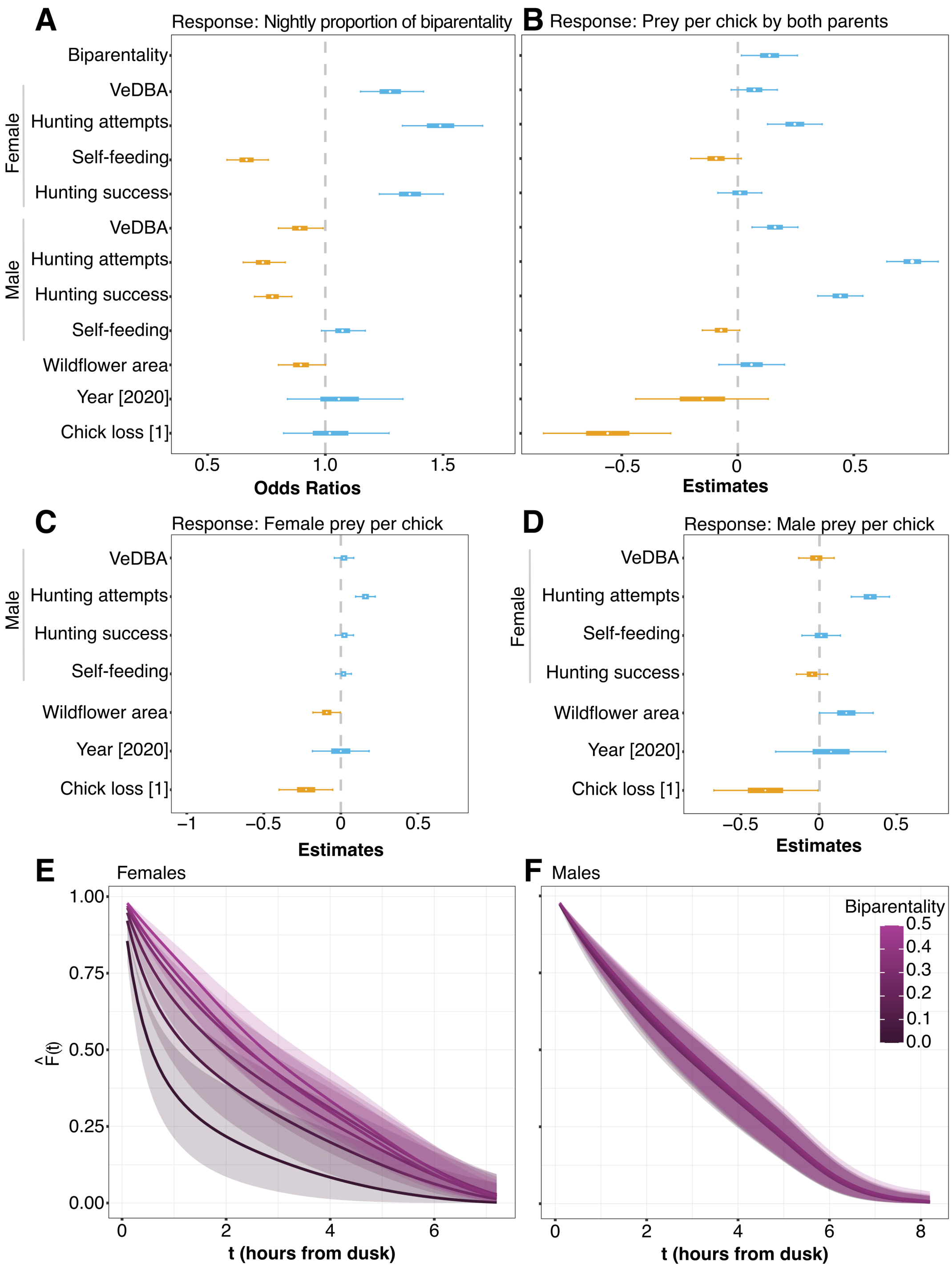

Figure 2: Predictors of flexible biparental care and temporal dynamics of foraging probability. Summary plots of the Bayesian Generalised and Linear mixed effect models showing the standardised effects of foraging performance and behaviours of parents, area of wildflower strips, year and brood size change on biparentality (A), on chick provisioning by both parents (B), on relative chick provisioning by female (C) and by male (D) (see Tables S3-S6). Standardised effects are expressed as posterior distributions (horizontal boxplots) with a mean (white dot), the 50% Credible Intervals (the box) and the 95% Credible Intervals limits (the whiskers). The categorical variables “Year” and “Chick loss” are showing the result of comparison between the group shown in squared brackets, [2020] and [1], and their reference level, [2019] and [0], respectively. The bottom panel shows the output of the time-to-event Piece-wise Exponential Additive Mixed Model (PAMM) as the probability of foraging (y-axis) with 95% confidence intervals (shaded areas) predicted at any time of the night (x-axis), expressed as hours from sunset, depending on biparentality proportion (purple-coloured lines and shaded 95% Confidence Intervals) for females (E) and males (F).

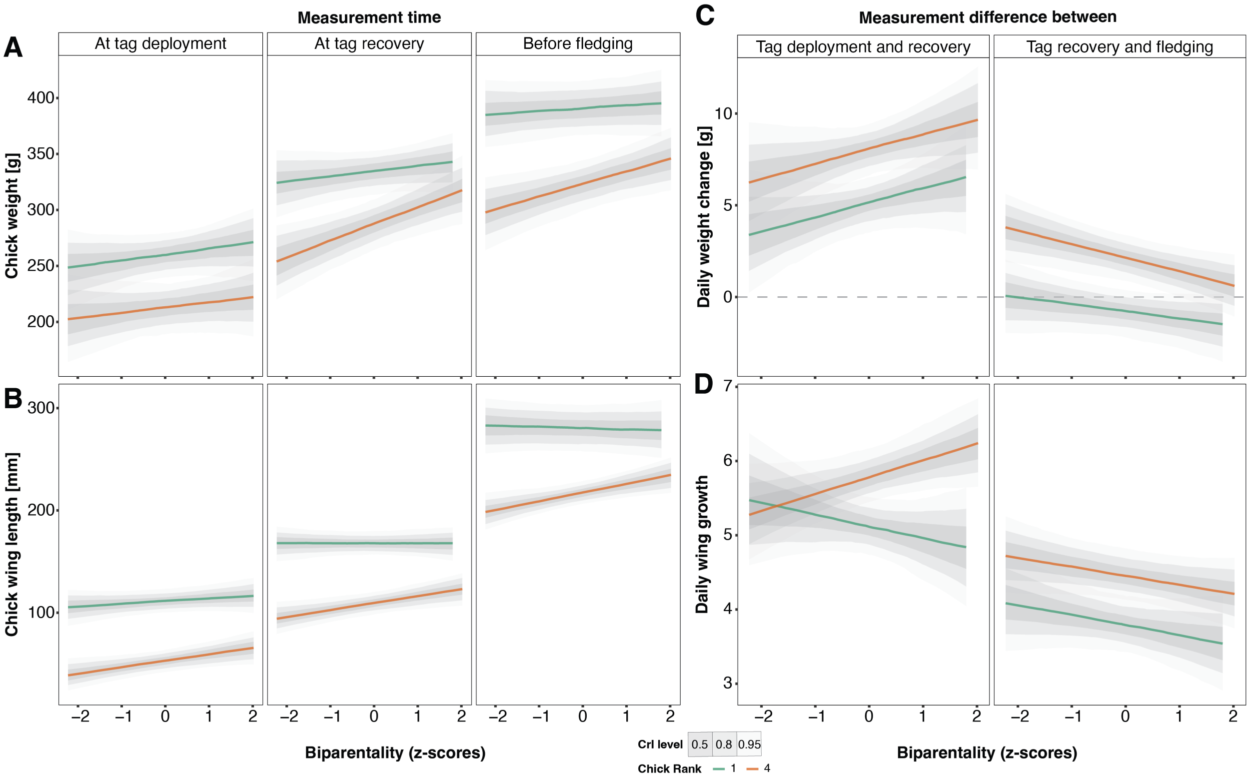

Figure 3: Relationships between mean pair biparentality and chick growth. Linear relationships between proxies of chick growth (y-axes in A, B, C and D) and standardised values of mean biparentality proportion (x-axes) in interaction with the chick rank (1 = oldest and 4 = born fourth or younger) divided per period of measurement (at tag deployment, tag recovery and before fledging). Dashed lines represent daily growth equal 0. For visualization purposes we show only the relationship in the first (green) and last chick rank (orange). Lines are the posterior means, and shaded areas are the predicted 50, 80 and 95% Credible Intervals. Details about the models and summary tables are in the Methods section and in Supplementary Materials Tables S7-S18.

(tag deployment, tag recovery, and pre-fledging), and chick rank (4-level factor: 1 = born first, 2 = second, 3 = third and 4 = born fourth or younger). We focused our analyses on the interaction terms between biparentality proportion with measurement time and chick rank, and on the slope differences (Fig. 3A, B). Chicks' weight was overall weakly positively related to biparentality (MPD = 5.79, 95%Cr.I. = [0.00, 11.50]; Table S7). Specifically, biparentality proportion had the strongest relationship with the youngest (rank 4) chicks' weight at tag recovery (MPD = 15.15, 95%Cr.I. = [4.35, 26.4]) and before fledging (MPD = 11.44, 95%Cr.I. = [2.29, 20.7]), but not before tag deployment (Fig. 3A, Table S8-S9). Wing length was also positively related to biparentality proportion in the youngest chicks for all three measurement times (Fig. 3B, Table S10-S12).

Daily weight gain also positively correlated with biparentality for all chick ranks (Fig. 3C; Table S13-15), while wing length growth increased with biparentality in younger chicks but remained stable or slightly negative for oldest (Fig. 3D, Table S16-18) in the period between tag deployment and recovery. In the following period, between tag recovery and fledging, wing and weight change were flat or slightly negative for all ranks, with average values higher in younger chicks (Fig. 3C-D, Table S13-18). These results underscore the benefit of flexible biparental care for younger chicks' growth and development.

Discussion

Using concurrent high-resolution movement data, our study highlights the complex dynamics of flexible biparental care and its implications for chick development in barn owls. Our findings show that both partner behaviour and environmental conditions influence the division of parental effort, with barn owl pairs dynamically adjusting between uniparental and biparental care based on male foraging success and habitat quality. This flexible allocation of parental duties suggests an adaptive strategy that enables pairs to optimize reproductive success in varying conditions[6, 10, 26].

Biologging offers an invaluable tool for examining complex, context-dependent adjustments in parental care that were previously challenging to capture in natural conditions[7, 15]. By combining GPS and accelerometer data, our approach provides unprecedented insights at a nightly scale into parental investment in response to partner performance. This high-resolution data allows for a nuanced view of how each parent's foraging effort, success, and temporal investment contribute to chick provisioning, advancing our understanding of biparental care as a dynamic and flexible trait[10]. The application of these novel methods aligns with recent calls for integrating detailed behavioural metrics to better capture interactive parental behaviors[11].

Our results indicate that females increase their foraging effort, energy expenditure, and chick provisioning in response to low male foraging efficiency or limited resources. This compensatory response by females in biparental pairs is consistent with the hypothesis that biparental care is more pronounced in challenging environments and when male provisioning is insufficient, supporting the adaptive value of flexible biparental roles in buffering environmental challenges[6, 10]. Such flexibility may be critical in species like barn owls, where biparental care varies in response to ecological pressures[9]. In this sense, we confirm the fundamental role of wildflower strips in deeply modified environments, such as agricultural and urban landscapes[23–25, 27].

The distinct expression of foraging behaviours observed in male and female parents, particularly in relation to biparentality, underscore the role of behavioural coordination in successful parental investment. Females in pairs with low biparentality, for example, cease foraging earlier in the night, while those in more balanced partnerships exhibit foraging probabilities akin to their male counterparts throughout the night. This difference in temporal foraging patterns illustrates the additional time and energy costs undertaken by females in cooperative pairs[28]. Observed associations between provisioning by one parent and hunting effort by the other confirm models suggesting that conditional cooperation helps managing the energetic demands of biparental care[29]. Also, parental effort (prey delivered per chick) of one sex was positively related to the hunting effort of the other. These results would support that partners providing more food to their offspring have higher behavioural similarity, defined as the tendency for two individuals to behave like each other. Behavioural similarity has been experimentally demonstrated to relate with higher reproductive success in monogamous species, such as cichlid fish[30] and birds[31–33]. In our study, greater biparentality and combined parental provisioning were weakly but positively linked to nestling survival, whereas increased female provisioning, higher hunting effort, and greater energy expenditure (VeDBA) by both parents had stronger positive effects. These findings underscore the importance of partial partner compensation and highlight how flexible parental roles can lead to tangible fitness benefits[10, 34].

Our study provides strong evidence that flexible biparental care benefits chick growth, especially for the last-born chicks in the brood, which often face higher mortality risks due to hatching asynchrony[35, 36]. Increased biparental provisioning was associated with enhanced growth outcomes in younger offspring, supporting the adaptive advantage of flexible parental roles in improving offspring survival[10, 34, 37]. In species like barn owls, where hatching asynchrony is pronounced[38], such flexibility appears to mitigate the competitive disadvantages experienced by later-hatched chicks, suggesting a selective benefit for adaptive parental strategies. One possible mechanism behind these observations is related to selective feeding by parents. For approximately the first 15 days after hatching, females remain in the nest, distributing the prey provided by the male to the chicks[39]. After this brooding period, females may choose to either join the male in chick provisioning, as shown in this study, or allow the male to provision alone[28]. In the latter case, the male's prey items may simply be left in the nest for the chicks to consume independently[40]. But when the female cooperates in provisioning, she may assist the younger chicks in feeding facilitating the ingestion of bigger prey items[41–43]. This interpretation does not preclude the possibility that highly efficient foraging males can adequately provision all chicks on their own when resources near the nest are abundant, as suggested by previous findings[44], irrespective of the level of female involvement.

Increased provisioning by females in biparental pairs incurs significant energetic costs, as reflected by elevated Vectorial Dynamic Body Acceleration (VeDBA) values and decreased self-feeding rates. These findings suggest that while biparental care enhances chick growth, it also places substantial physiological demands on the more active parent[45, 46]. The correlation between VeDBA, a proxy for movement-related metabolic power[47], and reproductive success highlights the importance of balancing provisioning effort with self-maintenance, underscoring the physiological trade-offs inherent in biparental care[48]. The observed reductions in self-feeding during intense provisioning periods may also confer indirect benefits, such as lower wing loading, which could reduce flight costs and potentially enhance foraging efficiency over time[49]. Decisions to nest closer to suitable foraging grounds or starting to nest earlier in the breeding season when food is more abundant may mitigate these costs[46].

Our study highlights the limitations of classic theoretical frameworks that model contributions to care as simple sex-specific traits and ignore behaviours taking place away from where offspring are fed. To further progress our understanding of parental care we need theory that incorporates newly measurable variables, such as hunting efficiency and effort, or self-feeding and energy expenditure. Parental care is a suite of integrated, flexible behaviours that vary according to environmental and social factors, and we urge further theoretical and empirical studies to address the drivers of parental flexibility, particularly how foraging performance, partner interactions, and ecological conditions influence parental care strategies, survival and fitness[50]. Accurate, high-resolution behavioural data can help refine or reformulate existing theories[11], and will be crucial for testing new theories that are more ecologically explicit[17]. A future comprehensive framework would perhaps bridge optimal foraging and parental negotiation models by incorporating both environmental and partner behaviour decision functions.

Finally, we show how biologging tools reveal previously inaccessible details of parental care dynamics, providing key insights into the adaptive strategies employed by a socially monogamous species in response to varying environmental and social pressures. As biologging technology continues to advance, our approach offers an empirical example for studying flexible parental care across species, contributing to a broader understanding of how ecological and social factors shape reproductive success in changing environments.

Materials and Methods

Study area, data collection and tag deployment

The study was conducted in the Western Swiss plateau, an area of 1,000 km^2 characterized by an open and largely intensive agricultural landscape, where a wild population of barn owls breeds in nest boxes [51, 52]. Between March and August in 2019 and 2020, 163 breeding barn owls (84 females, mean body mass: 322 ± 22.6 g; 79 males, mean body mass 281 ± 16.5 g) were equipped with data-loggers. We deployed 92 loggers in 2019 and 71 in 2020 (see [53]). Approximately 25 days after the first egg hatched, parent barn owls were captured using automatic sliding traps at their nest sites. AXY-Trek Mini loggers (Technosmart, Italy) were attached as backpacks using a Spectra tube harness (Bally Ribbon Mills, USA). The loggers recorded GPS data (1 Hz) from 30 minutes before sunset until 30 minutes after sunrise and accelerometer data (50 Hz) continuously (triaxial recording range ±16 g, 10-bit resolution). After 10 ± 2 days, loggers were recovered by recapturing the owls. The bio-loggers recorded data for 5 nights on average (± 1 night). Each device weighed on average 12.4 ± 0.1 g, which corresponds on average to 4% of the barn owl's total body mass (min = 3%, max = 5%), considered reasonable given the short period of deployment [53]. For this study we selected breeding partners with overlapping tracking periods (136 individuals in 68 pairs). Simultaneously, motion-sensitive camera traps (Reconyx HC500 hyperfire) positioned at the entrance of all nest boxes documented prey deliveries to the nest [53]. Barn owls were monitored from egg laying to fledging to gather data on their reproduction success. Number of eggs, nestlings, and body measurements were taken as part of annual monitoring of the species [51, 54]. Data handling, calculation of parameters, variables and statistical analyses were performed in the statistical environment R 4.3.2 [55] with RStudio as a graphic user interface [56].

Behavioural classification and variables

We classified barn owl behaviours (flight, landing, hunting strikes, self-feeding) using acceleration and GPS data [53]. Behaviours were summarized at one-second intervals and linked to the nearest GPS location in time. Behavioural classifications used the raw acceleration data, the vectorial dynamic body acceleration (VeDBA – a summary metric of body motion [**?**]), and body pitch angle (see details in [53]). Successful hunts were confirmed by nest box camera data and GPS records showing direct flights back to the nest after a hunting attempt or a self-feeding event. Unsuccessful strikes were inferred from hunting strikes followed by one or more other hunting strikes [53].

Biparental care was calculated as the proportion of prey brought by the female relative to the total prey brought by both parents per night (nightly biparentality) and over the tracking period (mean biparentality). A proportion of 0.5 indicates equal contribution, 0 indicates no contribution from the female (only paternal care), and 1 indicates all prey were provided by the female (only maternal care). We focused on the female's contribution owing to the greater variability in female provisioning behaviour.

We assessed several parameters at night and individual scale to understand parental provisioning contributions:

- Prey per chick: number of prey delivered per night divided by brood size at tag recovery by male (prey.per.chickM), female (prey.per.chickF) and both parents (prey.per.chick).
- Energy expenditure: measured by total hunting attempts (hunt.att.sumM and hunt.att.sumF), and average VeDBA (avg.vedbaM and avg.vedbaF).
- Hunting success rates: measured by dividing successful hunting attempts by total attempts (hunt.succ.rateM and hunt.succ.rateF) to assess hunting efficiency.
- Prey eaten (refuelling): we recorded the number of prey eaten per night and used it to calculate the proportion of prey eaten out of the total captured (prop.eaten.capturedF and prop.eaten.capturedM) to assess refuelling behaviour.

Environmental variables

To test if biparentality changed with different habitat features, we calculated the area and distance to several landscape features within a 1.5 km radius around the nest box, encompassing the local barn owl population's average home range (7 km^2) [25, 52, 57]. We extracted 11 habitat features, such as distance to road, distance to forest, distance to urban settlement, urban area, meadow area, hedgerow area, wildflower strips area, extensively used pasture area, extensive crop area, urban density (urban area divided by total building area), and crop diversity (number of different crops divided by total crops). Areas are expressed in km^2 and distances in meters. We focused on wildflower strips area, considered biodiversity promotion areas [23, 27], and positively selected by foraging barn owls during breeding [25] and wintering periods [24]. We confirmed the importance of wildflower strips as a key environmental feature by running univariate Bayesian Generalised Linear Models (GLMMs) estimated using MCMC sampling (3 chains of 20,000 iterations, 5,000 warmups; "brms" package in R [58]) for each environmental feature to test which best predicted biparentality proportion. Model comparison was done with leave-one-out cross-validation (function 'loo' from the "loo" package in R [59]) returning the difference of expected log predictive density (ELPD_diff) between the model with higher expected log predictive density (elpd) and the other models' elpds [59]. We then included the environmental variable from the best univariate model in multivariate models to test our predictions (see "Statistical Analysis" section).

Agricultural landscape features were provided by the "Direction Générale de l'Agriculture, de la Viticulture et des Affaires Vétérinaires" of the states of Vaud and Fribourg, and urban features were retrieved using the TLM3D catalog of the Swiss Federal Office (Swiss Topographic Landscape Model - `https://www.swisstopo.admin.ch/en/landscape-model-swisstlm3d`). Landscape features were calculated using the R package 'sf' [60].

We used year as an environmental factor in our analyses to control for annual variations in resource availability. Barn owl breeding performance is closely tied to prey abundance, particularly common voles (*Microtus arvalis*), which fluctuate annually [61, 62]. In our study area, 2019 was worse than 2020 in terms of clutches recorded (n = 62 and n = 104, respectively) and average prey (genus *Microtus*) found in nests (3.13 in 2019, 4.77 in 2020).

Statistical analysis

We tested repeatability in biparentality within pairs and across nights by running a mixed effect model using data at the night scale, with the PairID as a random effect, year and brood.size as fixed effects, using the package "rptR" with the function 'rpt' [63]. This allowed us to estimate the adjusted repeatability and its confidence intervals via parametric bootstrapping (nboost = 1000) [63].

To test if flexible biparentality was related to parent hunting behaviour, energy expenditure, and environmental conditions, we used Bayesian GLMMs estimated using MCMC sampling (3 chains of 20,000 iterations, 5,000 warmup). The nightly proportion of biparentality was predicted as a function of male and female hunting behaviours (sum of hunting attempts, hunting success proportion, refuelling proportion, mean VeDBA), area of favourite hunting ground (area_wildflower.zsqrt), year, and chick loss during the tagging period (brood.size.change01F). Pair ID was used as a random intercept. All continuous explanatory variables were standardized (z-scores). Bayesian modelling was performed using the "brms" package in R [58, 64]. Posterior means were used as estimates, with 2.5% and 97.5% quantiles as the upper and lower bounds of the 95% credible interval (CrI). Effects were considered meaningful when the 95% CrI did not contain 0.

Similarly, we analyzed female provisioning per chick (prey.per.chickF) as a function of male hunting behaviours, area of the favourite hunting ground, and year. The same model was used for prey.per.chickM as a function of female hunting behaviours. Also, we modeled the prey per chick provided by male and female combined (prey.per.chickMF) as a function of the biparentality proportion and parents' hunting behaviours. The combination of these four models reveals key relationships between parental investment and both social (partner) and environmental variables (area of the favourite hunting ground).

Furthermore, we evaluated the probability of foraging at each time point of the night by both male and female partners until the end of the nightly foraging activity (binomial variable: 1 as foraging trip and 0 as the termination of foraging activity each night), in relation to their flexible biparental system (biparentality proportion). We expected variation in both sexes, depending on partner effort, affecting the duration of their foraging during the night. To achieve this, we built a time-to-event Piece-wise Exponential Additive Mixed Model (PAMM) for each sex separately using the "pammtools" package in R [65]. This method combines the flexibility of Generalised Additive Mixed Models (GAMM) with Piece-wise Exponential Models (PEM) as an alternative to Cox models used in survival analysis. We estimated the probability of foraging at any given time point during the night and compared this probability within sexes by their biparentality proportion, and visually between sexes.

To test if mean biparentality affected chick growth, especially in larger broods where size differences among siblings are more pronounced, we ran Bayesian GLMMs as described above. These models assessed chick body weight and wing length as functions of measurement time (3-level factor: before tagging, after tagging, before fledging), chick rank (4-level factor: 1 = first-born, 2 = second, 3 = third, 4 = fourth or younger), mean biparentality, and the three-way interaction of these terms. By evaluating the interaction, we observed differences in chick sizes across ranks and time, along the biparentality gradient. Chick weight and wing length change were also modeled similarly, with the difference that the time factor included only two groups since the response variables reflected changes between two periods. We used the function 'emtrends' (estimated marginal means of linear trends) and 'pairs' from the R package "emmeans" [66] to interpret interaction effects. The summary shows the median of the posterior distribution (MPD) and highest posterior density (HPD) intervals.

Additionally, to test effects on nestling survival (nestlings counted at tag recovery divided by number of eggs), we constructed a series of Bayesian GLMs for each group of factors related to mean biparentality and chick provisioning, including year in all models. One model accounted for combined parental care using mean biparentality proportion, combined provisioning per chick, and wildflower strips area.

For each model, we reported MPD (median of the posterior distribution) and 95% CrI (95% credible interval), extracted with the "bayestestR" package in R [67]. Bayesian model checks were done visually using 'pp_check' (500 simulated draws) in the "bayesplot" package [68]. The GPS datasets analyzed are available in Movebank (`www.movebank.org`) under the project "Barn owl (*Tyto alba*)", ID 231741797 (`https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study231741797`). Processed tables and R scripts are available at `https://github.com/paolobecciu/flexbiparentality-barn-owls` [not public yet].

Author contribution

P.B.: Conceptualization, Data Curation, Formal Analysis, Investigation, Methodology, Visualization, Writing – Original Draft Preparation, Writing – Review & Editing. **K.S.**: Data Curation, Formal Analysis, Investigation, Methodology. **E.M.**: Formal Analysis, Investigation, Writing – Review & Editing. **J.L.S.**: Validation, Writing – Review & Editing. **An.R.**: Validation, Writing – Review & Editing. **B.A.**: Validation, Funding Acquisition, Resources, Writing – Review & Editing, Supervision. **Al.R.**: Funding Acquisition, Resources, Writing – Review & Editing, Supervision.

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References

[1] Clutton-Brock TH. The Evolution of Parental Care. Princeton University Press; 1991.

[2] Bijleveld AI, Mullers RHE. Reproductive effort in biparental care: An experimental study in long-lived

Cape gannets. Behavioral Ecology. 2009;20(4):736–744. doi:10.1093/beheco/arp054.

[3] Houston AI, Székely T, McNamara JM. Conflict between parents over care. Trends in Ecology and Evolution. 2005;20(1):33–38. doi:10.1016/j.tree.2004.10.008.

[4] Santos ESA, Nakagawa S. The costs of parental care: A meta-analysis of the trade-off between parental effort and survival in birds. Journal of Evolutionary Biology. 2012;25(9):1911–1917. doi:10.1111/j.1420-9101.2012.02569.x.

[5] Trivers RL. In: Campbell BG, editor. Parental Investment and Sexual Selection. 1st ed. New York: Routledge; 1972.

[6] Wojczulanis-Jakubas K. Being the Winner Is Being the Loser When Playing a Parental Tug-of-War – A New Framework on Stability of Biparental Care. Frontiers in Ecology and Evolution. 2021;9. doi:10.3389/fevo.2021.763075.

[7] Kavelaars MM, Baert JM, Van Malderen J, Stienen EWM, Shamoun-Baranes J, Lens L, et al. Simultaneous GPS-tracking of parents reveals a similar parental investment within pairs, but no immediate co-adjustment on a trip-to-trip basis. Movement Ecology. 2021;9(1):1–13. doi:10.1186/s40462-021-00279-1.

[8] McNamara JM, Gasson CE, Houston AI. Incorporating rules for responding into evolutionary games. Nature. 1999;401:368–371.

[9] Wang D, Zhang W, Yang S, Richter XYL. Sex differences in avian parental care patterns vary across the breeding cycle. Nature Communications. 2023;14(1). doi:10.1038/s41467-023-42767-5.

[10] Royle NJ, Russell AF, Wilson AJ. The evolution of flexible parenting. Science. 2014;345(6198):776–781. doi:10.1126/science.1253294.

[11] Savage JL, Hinde CA. What Can We Quantify About Carer Behavior? Frontiers in Ecology and Evolution. 2019;7. doi:10.3389/fevo.2019.00418.

[12] Griffith SC. Cooperation and Coordination in Socially Monogamous Birds: Moving Away From a Focus on Sexual Conflict. Frontiers in Ecology and Evolution. 2019;7. doi:10.3389/fevo.2019.00455.

[13] Johnstone RA, Hinde CA. Negotiation over offspring care - How should parents respond to each other's efforts? Behavioral Ecology. 2006;17(5):818–827. doi:10.1093/beheco/arl009.

[14] Vincze O, Kosztolányi A, Barta Z, Küpper C, Alrashidi M, Amat JA, et al. Parental cooperation in a changing climate: fluctuating environments predict shifts in care division. Global Ecology and Biogeography. 2017;26(3):347–358. doi:10.1111/geb.12540.

[15] Beltran RS, Kilpatrick AM, Picardi S, Abrahms B, Barrile GM, Oestreich WK, et al. Maximizing biological insights from instruments attached to animals. Trends in Ecology and Evolution. 2024;doi:10.1016/j.tree.2024.09.009.

[16] Nathan R, Monk CT, Arlinghaus R, Adam T, Alós J, Assaf M, et al. Big-data approaches lead to an increased understanding of the ecology of animal movement. Science. 2022;375(6582). doi:10.1126/science.abg1780.

[17] Patricelli GL. Behavioral ecology: New technology enables a more holistic view of complex animal behavior. PLoS Biology. 2023;21(8 August). doi:10.1371/journal.pbio.3002264.

[18] Paredes R, Jones IL, Boness DJ. Reduced parental care, compensatory behaviour and reproductive costs of thick-billed murres equipped with data loggers. Animal Behaviour. 2005;69(1):197–208. doi:10.1016/j.anbehav.2003.12.029.

[19] Pilakouta N, Hanlon EJH, Smiseth PT. Biparental care is more than the sum of its parts: experimental evidence for synergistic effects on offspring fitness. Proceedings of the Royal Society B: Biological Sciences. 2018;285(1884):20180875. doi:10.1098/rspb.2018.0875.

[20] Wiebe KL. Negotiation of parental care when the stakes are high: Experimental handicapping of one partner during incubation leads to short-term generosity. Journal of Animal Ecology. 2010;79(1):63–70. doi:10.1111/j.1365-2656.2009.01614.x.

[21] Smiseth PT. Behavioral dynamics between caring males and females in a beetle with facultative biparental care. Behavioral Ecology. 2004;15(4):621–628. doi:10.1093/beheco/arh053.

[22] Rehling A, Spiller I, Krause ET, Nager RG, Monaghan P, Trillmich F. Flexibility in the duration of parental care: zebra finch parents respond to offspring needs. Animal Behaviour. 2012;83(1):35–39. doi:10.1016/j.anbehav.2011.10.003.

[23] Arlettaz R, Krähenbühl M, Almasi B, Roulin A, Schaub M. Wildflower areas within revitalized agricultural matrices boost small mammal populations but not breeding Barn Owls. Journal of Ornithology. 2010;151(3):553–564. doi:10.1007/s10336-009-0485-0.

[24] Bühler R, Schalcher K, Séchaud R, Michler S, Apolloni N, Roulin A, et al. Influence of prey availability on

habitat selection during the non-breeding period in a resident bird of prey. Movement Ecology. 2023;11(1):14. doi:10.1186/s40462-023-00376-3.

[25] Séchaud R, Schalcher K, Machado AP, Almasi B, Massa C, Safi K, et al. Behaviour-specific habitat selection patterns of breeding barn owls. Movement Ecology. 2021;9(1):1–11. doi:10.1186/s40462-021-00258-6.

[26] Matysioková B, Remeš V. Evolution of parental activity at the nest is shaped by the risk of nest predation and ambient temperature across bird species. Evolution. 2018;72(10):2214–2224. doi:10.1111/evo.13580.

[27] Bretzel F, Vannucchi F, Romano D, Malorgio F, Benvenuti S, Pezzarossa B. Wildflowers: From conserving biodiversity to urban greening—A review. Urban Forestry and Urban Greening. 2016;20:428–436. doi:10.1016/j.ufug.2016.10.008.

[28] Becciu P, Séchaud R, Schalcher K, Plancherel C, Roulin A. Prospecting movements link phenotypic traits to female annual potential fitness in a nocturnal predator. Scientific Reports. 2023;13(1):5071.

[29] Johnstone RA, Manica A, Fayet AL, Stoddard MC, Rodriguez-Gironés MA, Hinde CA. Reciprocity and conditional cooperation between great tit parents. Behavioral Ecology. 2014;25(1):216–222. doi:10.1093/beheco/art109.

[30] Laubu C, Dechaume-Moncharmont FX, Motreuil S, Schweitzer C. Mismatched partners that achieve postpairing behavioral similarity improve their reproductive success. Science Advances. 2016;2(3). doi:10.1126/sciadv.1501013.

[31] Ihle M, Kempenaers B, Forstmeier W. Fitness Benefits of Mate Choice for Compatibility in a Socially Monogamous Species. PLOS Biology. 2015;13(9):e1002248. doi:10.1371/journal.pbio.1002248.

[32] Mariette MM, Griffith SC. Nest visit synchrony is high and correlates with reproductive success in the wild Zebra finch Taeniopygia guttata. Journal of Avian Biology. 2012;43(2):131–140. doi:10.1111/j.1600-048X.2012.05555.x.

[33] Spoon TR, Millam JR, Owings DH. The importance of mate behavioural compatibility in parenting and reproductive success by cockatiels, Nymphicus hollandicus. Animal Behaviour. 2006;71(2):315–326. doi:10.1016/j.anbehav.2005.03.034.

[34] McNamara JM, Houston AI, Barta Z, Osorno JL. Should young ever be better off with one parent than with two? Behavioral Ecology. 2003;14(3):301–310. doi:10.1093/beheco/14.3.301.

[35] Viñuela J. Opposing selective pressures on hatching asynchrony: egg viability, brood reduction, and nestling growth. Behavioral Ecology and Sociobiology. 2000;(48):333–343.

[36] Węgrzyn E, Węgrzyn W, Leniowski K. Hatching asynchrony as a parental reproductive strategy in birds: a review of causes and consequences. Journal of Ornithology. 2023;164(3):477–497. doi:10.1007/s10336-023-02066-8.

[37] Royle NJ, Smiseth PT, Kolliker M. The evolution of parental care. Oxford University Press; 2012.

[38] Roulin A. Short- and long-term fitness correlates of rearing conditions in Barn Owls Tyto alba. Ardea. 2002;90:259–267.

[39] Durant JM, Gendner JP, Handrich Y. Should I brood or should I hunt: A female barn owl's dilemma. Canadian Journal of Zoology. 2004;82(7):1011–1016. doi:10.1139/Z04-078.

[40] Ducouret P, Romano A, Dreiss AN, Marmaroli P, Falourd X, Bincteux M, et al. Elder Barn Owl Nestlings Flexibly Redistribute Parental Food according to Siblings' Need or in Return for Allopreening. The American Naturalist. 2020;196(2):257–269. doi:10.1086/709106.

[41] Roulin A. Offspring Desertion by Double-Brooded Female Barn Owls (Tyto Alba). The Auk. 2002;119(2).

[42] Sonerud GA, Steen R, Løw LM, Røed LT, Skar K, Selås V, et al. Evolution of parental roles in raptors: prey type determines role asymmetry in the Eurasian kestrel. Animal Behaviour. 2014;96:31–38. doi:10.1016/j.anbehav.2014.07.011.

[43] Sonerud GA, Steen R, Selås V, Aanonsen OM, Aasen GH, Fagerland KL, et al. Evolution of parental roles in provisioning birds: diet determines role asymmetry in raptors. Behavioral Ecology. 2014;25(4):762–772. doi:10.1093/beheco/aru053.

[44] Séchaud R, Schalcher K, Almasi B, Bühler R, Safi K, Romano A, et al. Home range size and habitat quality affect breeding success but not parental investment in barn owl males. Scientific Reports. 2022;12(1):6516. doi:10.1038/s41598-022-10324-7.

[45] Grunst AS, Grunst ML, Grémillet D, Chastel O, Cruz-Flores M, Gentès S, et al. Environment-dependent relationships between corticosterone and energy expenditure during reproduction: Insights from seabirds in the context of climate change. Functional Ecology. 2024;doi:10.1111/1365-2435.14630.

[46] Williams TD. Physiology, activity and costs of parental care in birds. Journal of Experimental Biology. 2018;221(17). doi:10.1242/jeb.169433.

[47] Wilson RP, Börger L, Holton MD, Scantlebury DM, Gómez-Laich A, Quintana F, et al. Estimates for energy expenditure in free-living animals using acceleration proxies: A reappraisal. Journal of Animal Ecology. 2019;(November 2018):1–12. doi:10.1111/1365-2656.13040.

[48] Grémillet D, Lescroël A, Ballard G, Dugger KM, Massaro M, Porzig EL, et al. Energetic fitness: Field metabolic rates assessed via 3D accelerometry complement conventional fitness metrics. Functional Ecology. 2018;32(5):1203–1213. doi:10.1111/1365-2435.13074.

[49] Norberg RA. Temporary Weight Decrease in Breeding Birds May Result in More Fledged Young. The American Naturalist. 1981;118(6):838–850. doi:10.1086/283874.

[50] Weathers WW, Sullivan KA. Juvenile foraging proficiency, parental effort, and avian reproductive success. Ecological Monographs. 1989;59(3).

[51] Frey C, Sonnay C, Dreiss A, Roulin A. Habitat, breeding performance, diet and individual age in Swiss Barn Owls (Tyto alba). Journal of Ornithology. 2011;152(2):279–290. doi:10.1007/s10336-010-0579-8.

[52] Milliet E, Schalcher K, Grangier-Bijou A, Almasi B, Butera F, Roulin A. The effects of land use changes on site occupancy and breeding success of the barn owl (Tyto alba) from 1993 to 2020. Global Ecology and Conservation. 2024;52. doi:10.1016/j.gecco.2024.e02988.

[53] Schalcher K, Milliet E, Séchaud R, Bühler R, Almasi B, Potier S, et al. Landing force reveals new form of motion-induced sound camouflage in a wild predator. eLife. 2024;12:RP87775. doi:https://doi.org/10.7554/eLife.87775.3.

[54] Roulin A. Barn Owls. Cambridge: Cambridge University Press; 2020.

[55] R Core Team. R: A Language and Environment for Statistical Computing; 2021. Available from: `https://www.R-project.org/`.

[56] RStudio Team. RStudio: Integrated Development Environment for R; 2020. Available from: `http://www.rstudio.com/`.

[57] Almasi B, Roulin A, Jenni L. Corticosterone shifts reproductive behaviour towards self-maintenance in the barn owl and is linked to melanin-based coloration in females. Hormones and Behavior. 2013;64(1):161–171. doi:10.1016/j.yhbeh.2013.03.001.

[58] Bürkner PC. Advanced Bayesian Multilevel Modeling with the R Package brms. The R Journal. 2018;10(1):395. doi:10.32614/RJ-2018-017.

[59] Vehtari A, Gelman A, Gabry J. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. Statistics and Computing. 2017;27(5):1413–1432. doi:10.1007/s11222-016-9696-4.

[60] Pebesma E. Simple Features for R: Standardized Support for Spatial Vector Data. The R Journal. 2018;10(1):439. doi:10.32614/RJ-2018-009.

[61] Klok C, de Roos AM. Effects of vole fluctuations on the population dynamics of the barn owl Tyto alba. Acta Biotheoretica. 2007;55(3):227–241. doi:10.1007/s10441-007-9013-x.

[62] Pavluvčík P, Poprach K, Machar I, Losík J, Gouveia A, Tkadlec E. Barn Owl Productivity Response to Variability of Vole Populations. PLOS ONE. 2015;10(12):e0145851. doi:10.1371/journal.pone.0145851.

[63] Stoffel MA, Nakagawa S, Schielzeth H. rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. Methods in Ecology and Evolution. 2017;8(11):1639–1644. doi:10.1111/2041-210X.12797.

[64] Bürkner PC. brms: An R Package for Bayesian Multilevel Models Using Stan. Journal of Statistical Software. 2017;80(1). doi:10.18637/jss.v080.i01.

[65] Bender A, Groll A, Scheipl F. A generalized additive model approach to time-to-event analysis. Statistical Modelling. 2018;18(3–4):299–321. doi:10.1177/1471082X17748083.

[66] Lenth R. emmeans: Estimated Marginal Means, aka Least-Squares Means. 2024;(R package version 1.10.0).

[67] Makowski D, Ben-Shachar M, Lüdecke D. bayestestR: Describing Effects and their Uncertainty, Existence and Significance within the Bayesian Framework. Journal of Open Source Software. 2019;4(40):1541. doi:10.21105/joss.01541.

[68] Gabry J, Simpson D, Vehtari A, Betancourt M, Gelman A. Visualization in Bayesian Workflow. Journal of the Royal Statistical Society Series A: Statistics in Society. 2019;182(2):389–402. doi:10.1111/rssa.12378.