

Research

Benefits of extra food to reproduction depend on maternal condition

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The amount of food resources available to upper-level consumers can show marked variations in time and space, potentially resulting in food limitation. The availability of food resources during reproduction is a key factor modulating variation in reproductive success and life-history tradeoffs, including patterns of resource allocation to reproduction versus self-maintenance, ultimately impacting on population dynamics. Food provisioning experiments constitute a popular approach to assess the importance of food limitation for vertebrate reproduction. In this study of a mesopredatory avian species, the lesser kestrel *Falco naumanni*, we provided extra food to breeding individuals from egg laying to early nestling rearing. Extra food did not significantly affect adult body condition or oxidative status. However, it increased the allocation of resources to flight feathers moult and induced females to lay heavier eggs. Concomitantly, it alleviated the costs of laying heavier eggs for females in poor body condition, and reduced their chances of nest desertion (implying complete reproductive failure). Extra food provisioning improved early nestling growth (body mass and feather development). Moreover, extra food significantly reduced the negative effects of ectoparasites on nestling body mass, while fostering forearm (a flight apparatus trait) growth among highly parasitized nestlings. Our results indicate that lesser kestrels invested the extra food mainly to improve current reproduction, suggesting that population growth in this species can be limited by food availability during the breeding season. In addition, extra food provisioning reduced the costs of the moult–breeding overlap and affected early growth tradeoffs by mitigating detrimental ectoparasite effects on growth and enhancing development of the flight apparatus with high levels of parasitism. Importantly, our findings suggest that maternal condition is a major trait modulating the benefits of extra food to reproduction, whereby such benefits mostly accrue to low-quality females with poor body condition.

Keywords: body condition, egg size, food limitation, food provisioning, income breeding, moult–breeding overlap, offspring, oxidative status, sex allocation



Introduction

Seasonal or stochastic fluctuations of ecological conditions often result in limited availability of food resources for upper-level consumers. Variation in food availability is one of the key factors modulating variation in life-history traits related to reproduction among individuals, ultimately affecting population dynamics (Lack 1954). Food availability is commonly exploited by individuals as a cue to adjust reproductive decisions to contingent ecological conditions, providing 'biological information' (sensu Wagner and Danchin 2010) on when and where best to breed and how much resources to invest in producing and raising offspring to maximise fitness (Martin 1987). Whenever breeding individuals are exposed to poor environmental conditions, resulting in food limitation, parents are expected to trade self-maintenance against reproduction and offspring provisioning, with major implications for their survival and breeding success (Lack 1966, Martin 1987).

The relevance of food limitation during reproduction for population dynamics can be assessed by analysing the effects of resource availability on breeding success, or via experimental manipulation (removal or addition) of food resources. The most widespread experimental approach to investigate the extent to which reproduction is limited by food resources, and to highlight the resulting life-history trade-offs, is to provide extra food to breeders, while concomitantly assessing variation in reproductive investment and output of individuals receiving the extra food compared to unsupplemented controls (reviewed by Martin 1987, Boutin 1990). Among vertebrates, birds have been the favourite subject of food supplementation experiments during breeding (Martin 1987, Boutin 1990, Ruffino et al. 2014). In spite of broad differences in food provisioning protocols and of the heterogeneity of effects among studies, which may be partly due to variable background ecological conditions (in terms of e.g. food availability) during the experiments (Ruffino et al. 2014), individuals receiving extra food generally achieved reproductive benefits relative to control. These include advancing egg laying (Meijer and Drent 1999, Aparicio and Bonal 2002), laying heavier eggs and/or larger clutches (Wiebe and Bortolotti 1995, Korpimäki and Wiehn 1998, Karell et al. 2008, Saino et al. 2010), and enjoying improved nestling growth and survival (Dewey and Kennedy 2001, Hipkiss et al. 2002). Hence, most bird populations appear limited by food availability during the highly energy-demanding reproductive phase of the life cycle (Martin 1987, Boutin 1990, Ruffino et al. 2014).

Besides breeding output, extra food could affect parental condition. Food-supplemented parents may indeed spare energy resources that are otherwise required for self-maintenance and offspring provisioning, or directly use extra food to enhance their own survival prospects. Extra food may improve parental body condition (Garcia et al. 1993, Schoech 1996, Cucco and Malacarne 1997, Dewey and Kennedy 2001) and physiological state, in terms of e.g.

immune system functioning or oxidative status (Karell et al. 2008, Alan and McWilliams 2013, Fletcher et al. 2013, Giordano et al. 2015). For instance, extra food may lower oxidative damage by reducing physical activity for self-provisioning (Giordano et al. 2015). Moreover, food provisioning may affect the timing and extent of feather moult, a highly energy-demanding process in the avian life cycle (Murphy 1996), and a reduction of the costs of the overlap between moult and competing activities, such as reproduction and migration (Siikamäki 1998, Danner et al. 2014).

In general, it may be expected that the advantages provided by extra food vary according to the resource allocation and consumption decisions that parents adopt during the breeding season (Roff 1992, Stearns 1992). For instance, breeding success of 'capital breeders' (whose reproduction relies on energy stored in advance of breeding; Jönsson 1997) may show limited sensitivity to extra food provisioning during the reproductive period, whereas that of 'income breeders' (which do not accumulate reserves prior to breeding and fuel reproduction with concurrent energy intake) should be more positively affected (Meijer and Drent 1999). Similarly, the behavioural responses to food supplementation by parents may vary between species, populations or individuals, depending on which strategy maximises lifetime reproductive success under specific environmental contexts (e.g. high or low background prey availability) or physiological constraints (Kacelnik and Cuthill 1990, Ydenberg 1994, Markman et al. 2002). On the one hand, providing parents with extra food may reduce the amount of resources delivered to the progeny, reducing reproductive costs and enhancing parental residual reproductive value, while offspring quality and breeding success are unaltered (Dawson and Bortolotti 2002). On the other hand, extra food may not reduce offspring provisioning rates with natural food items, markedly increasing fledging success (Gonzalez et al. 2006).

Finally, whenever sexes differ in their susceptibility to harsh rearing environments, parents may adaptively tune the sex ratio of their offspring in relation to extrinsic conditions (West et al. 2000, West and Sheldon 2002). Indeed, nutritional constraints may affect avian sex allocation (Wiebe and Bortolotti 1992, Korpimäki et al. 2000, Saino et al. 2010), with mothers biasing the sex ratio of their clutches towards the larger sex, which is more susceptible to harsh rearing environments, when food resources are abundant (Wiebe and Bortolotti 1992, Nager et al. 1999, Korpimäki et al. 2000).

In this study of the lesser kestrel *Falco naumanni*, a small (ca 120 g), sexually dimorphic, cavity-nesting diurnal raptor with biparental care of the progeny (Cramp 1998), we provided extra food to breeders from the onset of egg laying to the early nestling rearing stage, and assessed the effects of food supplementation on different short-term fitness components, such as: 1) parental body condition and oxidative status (in terms of plasma non-enzymatic total antioxidant capacity, TAC and total oxidant status, TOS; Erel 2004, 2005); 2) moult timing and extent (lesser kestrels may initiate the annual moult of primary feathers during reproduction; Cramp 1998,

Zuberogoitia et al. 2018); 3) breeding performance, including egg and clutch characteristics (egg mass, clutch size, hatching success, duration of the incubation period), biparental nest desertion (i.e. the abandonment of eggs and/or nestlings by both parents, leading to reproductive failure for the current breeding season; Székely et al. 1996), offspring growth and mortality; 4) patterns of primary sex allocation and sex-biased offspring mortality. We expected: 1) an overall positive effect of food supplementation on parental condition and oxidative status (increased TAC and/or decreased TOS); 2) earlier onset of annual moult and/or faster primary feathers growth among food-supplemented individuals compared to controls; 3) extra food to have an overall positive effect on breeding performance (Ruffino et al. 2014) and to shorten incubation (Sanz 1996), because reduced self-provisioning needs of food-supplemented parents may induce them to spend more time incubating eggs compared to controls. In the sexually-size dimorphic lesser kestrel (males are ca 15% lighter than females; Donazar et al. 1992, Cramp 1998), we might also expect 4) food-supplemented females to lay female-biased clutches and/or raise female-biased broods (Korpimäki et al. 2000; but see Aparicio and Cordero 2001).

Importantly, we investigated whether female body condition modulated the effects of extra food on breeding performance. To our knowledge, no previous study has investigated whether individual quality modulates the fitness benefits of extra food provisioning. We expected low-quality, poor condition females to obtain greater fitness benefits from extra food provisioning compared to high-quality, better condition females.

Material and methods

Study species, study area and general field procedures

The lesser kestrel is a long-distance Afro-palearctic migrant (Cramp 1998). European breeding populations spend the non-breeding period mainly in the Sahel and reach the breeding areas in March–April (Cramp 1998). Egg laying takes place in late April–early May, and a previous food provisioning experiment beginning before egg laying revealed that food-supplemented females advanced first egg laying date by ca one week compared to control ones (Aparicio and Bonal 2002), suggesting that egg laying may be food-limited. Females lay clutches of 3–5 eggs with a 2–3 days laying interval between consecutive eggs. Eggs are incubated for ca 30 days by both parents. Altricial nestlings hatch asynchronously, generating strong size hierarchies among nestmates, with last-hatched, low-ranking nestlings often dying when resources are insufficient (Aparicio 1997). Fledging occurs at ca 40 days post-hatching. Lesser kestrels feed mainly on invertebrates (Orthoptera, Coleoptera), lizards (chiefly *Podarcis siculus*) and small rodents (voles, *Microtus* spp.) (Cramp 1998, Rodríguez et al. 2010, Catty et al. 2016, Di Maggio et al. 2018) that are captured in open farmland or grassland

areas surrounding breeding colonies (Morganti et al. 2016, Cecere et al. 2018). Both parents contribute to rearing nestlings (Cramp 1998). During breeding, some adults initiate their complete annual moult by shedding a few primary feathers (usually between 1 and 3 feathers, mostly P4–P6; primaries numbered descendantly) (Cramp 1998; see also Zuberogoitia et al. 2018).

The study was carried out during April–July 2016 at the Matera (southern Italy; 40°67'N, 16°60'E) colony (ca 1000 pairs, La Gioia et al. 2017). In this colony, many pairs breed in specially designed concrete nestboxes (external size: 30 cm height × 30 cm width × 37 cm length; entrance hole diameter 65 mm) with wooden front and rear panels (Podofillini et al. 2018 for further details of nestboxes). For the present study, we relied on 209 nestboxes that were checked three times a week during the entire breeding season (late April–end July) to determine the onset of egg laying, egg hatching, duration of the incubation period, nestling body mass, morphology and mortality. Eggs were weighed using a digital scale (accuracy 0.1 g) and individually marked using a non-toxic black marker to record the laying sequence. In those cases when two (or more) eggs were found in a same nestbox during the same monitoring session, we coded each egg using their mean laying order value (e.g. in the case of uncertainty between the fourth and the fifth egg, we coded both eggs as 4.5). Duration of the incubation period was expressed as the difference (in days) between the day of hatching of the first egg and the day of laying of the first egg in a clutch (laying date hereafter).

After hatching of the first egg, each nestbox was checked five times to assess nestling growth. Over this period, nestbox monitoring sessions occurred at an average of 0.8 (range 0–3), 3.0 (2–5), 5.3 (4–9), 7.9 (7–11) and 16.0 (14–18) days after hatching of the first egg. We did not check nestboxes after the fifth session because nestlings may start wandering outside nestboxes when ca 15 days old, making monitoring difficult and increasing the risk of inducing premature fledging (Podofillini et al. 2018). Nestling body mass was recorded during all monitoring sessions, tarsus and forearm length (the latter measured from the front of the folded wrist to the proximal end of the ulna) were recorded at the fourth monitoring session, and the length of primary feather P8 (a measure of nestling feather growth) was recorded at the fifth monitoring session (it could not be accurately recorded at earlier sessions). Nestlings were ranked according to hatch order, or to body mass (assigning the higher rank to the heavier nestling) when two or more newly hatched nestlings were found on the same monitoring session (Podofillini et al. 2018). The first hatched nestling was assigned the highest rank (i.e. rank 1). During the first four monitoring sessions, we recorded the intensity of infestation by *Carnus hemapterus*, a common blood-sucking dipteran ectoparasite of cavity-nesting birds (Capelle and Whitworth 1973). Ectoparasite infestation was assessed on each nestling for three body regions (interclavicular depression and right and left underwings) on a 0–3 scale (0: no ectoparasites, 1: 1–3 flies, 2: 4–6 flies and 3: >6 flies). Nestling ectoparasite load was expressed as the

mean value of ectoparasite infestation across the three body regions (Podofillini et al. 2018). At the fourth monitoring session, a small (ca 200 µl) blood sample was collected in capillary tubes by puncturing the brachial vein with a sterile needle. Blood was kept at -20°C and later used to molecularly determine sex (according to Griffiths et al. 1998).

A nest was considered as deserted if no eggs from a complete clutch hatched (clutch desertion) or if all nestlings were found dead from one session to the next (brood desertion) (Székely et al. 1996), leading to complete reproductive failure for the current breeding season (lesser kestrels are single-brooded; Cramp 1998). Although in our case nest desertion occurs because both parents abandon the clutch/brood (biparental desertion, Székely et al. 1996), the process likely begins with desertion by one parent (the female in other raptor species with a similar breeding ecology; Newton and Marquiss 1984, Kelly and Kennedy 1993), rapidly followed by desertion of the other parent because the costs of reproduction for the remaining parent would be unsustainable (Székely et al. 1996).

Starting from ca 10–15 days before the expected time of hatching, adults were captured opportunistically by hand in the nestbox or by nestbox traps while brooding their eggs or feeding newly hatched nestlings. We captured ca 80% of the adults breeding in experimental nestboxes. Upon capture, birds were individually marked, and body mass (0.1 g) and keel length (using a dial calliper, accuracy 0.1 mm) were recorded. As an index of body condition, we used the scaled mass index (SMI hereafter), which standardizes body mass at a fixed value of a linear body measurement (keel length in our case) based on the scaling relationship between mass and length (Peig and Green 2009, 2010). Body mass and keel length were moderately positively correlated in both sexes; females: $r = 0.27$, $p = 0.016$, $n = 82$; males: $r = 0.33$, $p = 0.004$, $n = 74$). As the scaling exponent significantly differed between the sexes (Supplementary material Appendix 1 Table A1), SMI was computed for each sex separately.

We recorded moult status by inspecting flight feathers of the right wing (moult was mostly symmetrical; our unpubl.). When growing/newly grown primary feathers were found, we measured their length using a ruler (accuracy 1 mm); in case of a shed primary feather with no signs of quill growth, we recorded a value of 0. Moult status was expressed as moult initiation (i.e. whether an individual had begun moulting, including the presence of shed feathers, or not) and total moult investment. Total moult investment was assumed to reflect the total amount of resources invested in the synthesis of new feathers. It was expressed as the sum of the length of all growing feathers (in mm), and was assigned a value of 0 if no sign of moult was detected or if feathers were shed but had not yet grown (i.e. no resources allocated yet to new feather synthesis). Finally, for each individual we collected ca 500 µl of blood into microhematocrit capillary tubes by puncturing the brachial vein using a sterile needle. To separate plasma from blood cells, two capillary tubes per individual were centrifuged (11 500 rpm \times 10 min)

within 4 h of sampling. Plasma was then stored at -20°C for later biochemical assays.

Food supplementation

We alternately assigned each nestbox where an egg was found to a food supplementation or a control treatment. Food-supplemented pairs were provided with commercial white laboratory mice (*Mus musculus*, ca 20 g each) placed within the nestbox (at the rear end). We provided three mice every two days during egg laying and after hatching, and one mouse every two days during incubation (visits were reduced during incubation to limit disturbance to brooding adults). In the vast majority of cases, mice disappeared between consecutive monitoring sessions. Although we could not directly assess mice consumption by the target breeding pair, the consumption of extra food was confirmed by regularly observing regurgitated pellets containing white fur within nestboxes where mice were placed. Food supplementation ceased when nestlings were ca eight days old (i.e. at the fourth monitoring session) because by the time of the subsequent nest visit (14–18 days old) they may have started wandering outside nestboxes, where they are fed by parents, and we could not provide food outside nestboxes (as we could not control whether it was actually consumed by the target individuals or by other birds). Overall, each food-supplemented pair received ca 40 mice (ca 800 g of extra food). To standardize disturbance, control nestboxes were inspected in exactly the same way and with the same frequency as those receiving the extra food, simulating mice insertion into the nestbox. The lesser kestrel performs intensive mate-feeding (Donazar et al. 1992, Cramp 1998): before and during egg laying/incubation, the male feeds its partner, and deposits prey within the nest cavity for later consumption by the female if mate is absent (Podofillini et al. unpubl.; Cramp 1998). Hence, placing extra food within the nestbox mimicked a natural condition and assured that only the target breeding female received most of the extra food, at least during egg laying and early incubation, avoiding common pitfalls of food provisioning experiments (where target individuals may not actually consume the extra food; Ruffino et al. 2014). During nestling rearing, parents may have used the extra food both to feed themselves or to provision their nestlings.

Oxidative status of breeding adults

The oxidative status reflects the balance between circulating antioxidants and pro-oxidants (e.g. free radicals), deriving from normal physiological activity, pathological states or the external environment (Halliwell and Gutteridge 2007). Pro-oxidants may cause oxidative damage to biomolecules, cells and tissues, impairing organismal functions (Halliwell and Gutteridge 2007). Oxidative stress arises whenever an organism's antioxidant defences are insufficient to counteract oxidative damage (Halliwell and Gutteridge 2007). High levels of antioxidants and low levels of pro-oxidants are regarded as

indicators of good health state and positively predict fitness (e.g. survival; Bize et al. 2008, Saino et al. 2011). Food is a major source of antioxidants such as vitamins and carotenoids, as well as of substances (e.g. proteins) that do not have direct antioxidant activity, but may affect an organism's resistance to oxidative stress (Halliwell and Gutteridge 2007, Costantini 2014). Moreover, high food availability might reduce the oxidative costs of foraging for self and offspring provisioning (Costantini 2014, Giordano et al. 2015). Hence, extra food may positively affect oxidative status through different mechanisms, leading to high levels of antioxidants/low levels of pro-oxidants. As proxies of the oxidative status of breeding adults, we measured TAC through a global test of blood non-enzymatic antioxidant capacity, and TOS, reflecting the overall concentration of circulating pro-oxidants in the blood flow. High TAC indicates high antioxidant capacity, while high TOS indicate high levels of circulating pro-oxidants and an increased risk of oxidative damage.

TAC was measured according to Erel (2004), with some modifications. Briefly, 7 μ l of plasma were added to 230 μ l of the 2,2'-azinobis-(3-ethylbenzothiazoline-6-sulfonic acid) radical cation (ABTS^{•+}) solution, which bleaches depending on the concentration of non-enzymatic antioxidants in the sample. The reaction was monitored at an absorbance of $\lambda = 750$ nm by a spectrophotometer. The final absorbance is inversely related to TAC of samples. The reaction was calibrated by drawing a standard curve with serial dilution of Trolox and the results were expressed as μ M Trolox equivalent.

TOS was measured according to Erel (2005). Briefly, 20 μ l of plasma were added to 237 μ l of a ferrous ion-*o*-dianisidine and Xylenol Orange solution. Oxidant molecules oxidise the ferrous ion to the ferric ion, which reacts with Xylenol Orange to give a coloured (blue) complex. Colour intensity was measured by a spectrophotometer at an absorbance of $\lambda = 535$ nm and it is proportional to the total amount of oxidant agents in the plasma. The assay was calibrated by drawing a standard curve with serial dilution of hydrogen peroxide (H₂O₂) and the results were expressed as nM H₂O₂ equivalent ml⁻¹.

The mean intra- and inter-plate coefficients of variation of TAC, measured on a pool of plasma assayed twice in all plates, were 2.7 (0.5 SD) % and 5.3 (0.7 SD) %, while the same figures for TOS were 2.9 (0.9 SD) % and 4.8 (1.1 SD) %, respectively. We measured TAC for all available plasma samples, while TOS could be only measured for a subsample of these because of plasma amount limitations.

Statistical analyses

To investigate the effects of food supplementation (0 = control, 1 = food-supplemented) on response variables, we relied on generalized linear, linear mixed or generalized linear mixed models (GLMs, LMMs or GLMMs, respectively), as summarized in Table 1. Below we provide details on reasons for including specific predictors in models and on coding of dichotomous variables.

To control for intra-seasonal variation in SMI, oxidative and moult status (birds were captured over 38 days, during both incubation and nestling-rearing stages), in GLMs of these variables we included either breeding stage (0 = incubation, 1 = nestling rearing) or sampling date (Julian date; day 1 = January 1) as predictors, choosing the one which better fitted the data (Supplementary material Appendix 1 Table A2) (selected predictors are shown in Table 1). Due to sex differences in body mass (mean body mass: females = 155 g (11 SD), males = 135 g (10 SD), $n = 82$ and 76 , respectively; $t_{156} = 12.1$, $p < 0.001$; see also Donazar et al. 1992), and consequently in SMI, in GLMs where SMI was included as a predictor together with sex (0 = female, 1 = male), we centred SMI within each sex category to eliminate the possibility of spurious SMI/sex effects on dependent variables (Lewin and Mitchell 1999). In GLMs of SMI and oxidative status we included total moult investment among predictors, as moult might affect physiological state (Hemborg and Lundberg 1998, Rubolini et al. 2002, Costantini 2014). Although adults were food-supplemented for a variable number of days before sampling (mean value = 27 days (SD 7)), there was no evidence that such variation affected food supplementation effects on SMI, oxidative and moult status (Supplementary material Appendix 1 Table A3).

Owing to the intrinsic association between laying order and clutch size (only large clutches can have large values of laying order), in mod of egg mass and hatching success (0 = egg not hatched, 1 = egg hatched) we coded laying order as relative laying order, assigning value 1 to the first egg and 3 to the last one. Intermediate eggs were assigned values between 1 and 3 according to clutch size (e.g. eggs from a 3-egg clutch were coded 1, 2 and 3; eggs from a 5-egg clutch were coded 1, 1.5, 2, 2.5 and 3). In the egg mass LMMs we included the squared term of relative laying order because the change in egg mass along the laying sequence was best described by a quadratic function of relative laying order (Supplementary material Appendix 1 Table A4). Because food supplementation began after laying of the first egg, the mass of the first egg could not be affected by food supplementation. The effect of food supplementation on egg mass was therefore evaluated as the food supplementation \times relative laying order interaction.

The GLM of nest desertion (0 = nest not deserted, 1 = nest deserted) was fitted by including both female and male SMI as a predictor (in separate models by sex): although desertion in related species is always initiated by females, we cannot rule out the possibility that it was initiated by males and depended on male (rather than female) condition.

Primary sex ratio (PSR) was expressed as the ratio between number of sons and brood size, computed for the subset of nests where all eggs hatched. To investigate whether sex allocation varied along the laying sequence according to food supplementation, we fitted a binomial GLMM of nestling sex and tested the food supplementation \times rank interaction.

Table 1. Summary of the generalized linear (mixed) models fitted to the data to investigate the effects of food supplementation on different fitness components. For consistency, the same sequence of analyses is followed in the 'Results' section. All models included the main effect of food supplementation (0 = control, 1 = food supplemented). Initial models included all two-way interactions between food supplementation and each additional predictor (see 'Statistical analyses' for further details). Non-significant ($p > 0.05$) interactions were removed from initial models in a single step. The final models reported in Table 2–5 thus included all main fixed effects and any statistically significant interaction. Random intercept effects were included in LMMs/GLMMs in order to account for non-independence of data belonging to the same clutch/brood and for repeated sampling of the same individual (in the nestling body mass model).

Dependent variable	Additional predictors (confounding variables)	Random intercept effects	Error distribution	Details of fitted model	Notes
Effects of food supplementation on body condition, oxidative and moult status					
Body condition (SMI)	sex, breeding stage, total moult investment	–	Gaussian	Table 2	
Total antioxidant status (TAC)	sex, sampling date, SMI, total moult investment	–	Gaussian	Table 2	
Total oxidant status (TOC)	sex, sampling date, SMI, total moult investment	–	Gaussian	Table 2	
Moult initiation	sex, sampling date, SMI	–	Binomial	Table 2	
Total moult investment	sex, sampling date, SMI	–	Gaussian	Table 2	skewed residuals
Effects of food supplementation on egg mass and hatching success					
Egg mass	relative laying order, (relative laying order) ² , laying date, clutch size, female SMI	clutch identity	Gaussian	Table 3	
Egg hatching success	relative laying order, laying date, clutch size, female SMI	clutch identity	Binomial	Table 3	deserted nests excluded
Effects of food supplementation on clutch size, duration of the incubation period and nest desertion					
Clutch size	laying date, female SMI	–	Gaussian	Table 4	skewed residuals
Duration of the incubation period	laying date, clutch size, female SMI	–	Gaussian	Table 4	skewed residuals
Nest desertion	laying date, clutch size, female or male SMI	–	Binomial	Table 4	
Effects of food supplementation on sex allocation					
Primary sex ratio (PSR)	laying date, clutch size, female SMI	clutch identity	Binomial	Table 4	
Nestling sex	rank, laying date	brood identity	Binomial	Table 4	
Effects of food supplementation on nestling body mass, morphology and mortality					
Body mass	age, rank, laying date, brood size, ectoparasite load	brood identity, nestling identity	Gaussian	Table 5	
Tarsus length	age, rank, laying date, brood size, ectoparasite load	brood identity	Gaussian	Table 5	
Forearm length	age, rank, laying date, brood size, ectoparasite load	brood identity	Gaussian	Table 5	
Feather length	age, rank, laying date, brood size, ectoparasite load	brood identity	Gaussian	Table 5	
Mortality	rank, laying date, brood size, ectoparasite load	brood identity	Binomial	Table 5	

Because we could not assign most of the nestlings to their egg of origin, we assumed that laying order was closely reflected by nestling rank, an assumption supported by the strong correlation between these variables (for nestlings from eggs with known laying order; $r = 0.86$, $n = 49$).

In LMMs of nestling body mass (recorded at four monitoring sessions) and morphology (tarsus, forearm and feather length recorded at a single session), we included ectoparasite load among predictors. Age effects were controlled for by including the linear term of age, as growth is mostly linear during the sampled age range (Podofillini et al. 2018). Nestling mortality was evaluated as a nestling being alive (0) or dead (1) by the fifth monitoring session. Nestlings that disappeared before they were able to move outside nestboxes

were assumed to be dead, even if no remains were found (likely removed/eaten by parents/nestmates). In tarsus, forearm and feather length LMMs, and in the mortality GLMM, brood size and ectoparasite load were the maximum values recorded across all monitoring sessions (Podofillini et al. 2018).

Due to weak sex differences in body size (Supplementary material Appendix 1 Table A5; Podofillini et al. 2018), we did not consider sex in the analyses of nestling body mass, morphology and mortality to ensure the largest possible sample size (some nestlings could not be sexed due to premature death/disappearance).

Differential effects of food supplementation on target traits according to other model predictors were tested by

including two-way interactions between food supplementation and additional predictors in initial models. In the nestling body mass LMM, we also included the rank \times age interaction (accounting for differential growth of nestlings according to rank; Podofillini et al. 2018). Final models included all main effects and significant interaction terms, while non-significant ($p > 0.05$) interactions were removed in a single step. Analyses were run in R ver. 3.3.3 (<www.r-project.org>). LMMs/GLMMs were fitted using the lme4 package (Bates et al. 2014). Non-Gaussian models were not overdispersed (dispersion parameter always < 1.25). GLMMs overdispersion was computed using the blmeo package (Korner-Nievergelt et al. 2015). When GLM residuals showed a highly skewed distribution, significance was calculated by randomization (Manly 1991) (permucopack; Frossard and Renaud 2018) (Table 1). For all models, we report R^2 as computed by the rsq (GLMs) and r2glmm (GLMMs) packages (Dabao 2017, Jaeger et al. 2017). To facilitate comparisons of food supplementation effects between different models, and to compare effects between different predictors, we report the absolute value of Pearson's r (obtained from the partial correlation/semi-partial R^2 values returned by the rsq and r2glmm packages).

We considered data from 100 nestboxes (50 food-supplemented, 50 controls), in which we found 423 eggs and captured 160 adults (80 food-supplemented (36 males, 44 females), 80 controls (42 males, 38 females)). To ensure the largest possible sample size in egg and clutch characteristics models, if SMI was not significant we reported results while excluding this variable. Twenty-two clutches/broods (out of 100) were deserted (13/50 controls, 9/50 food-supplemented). Among these, 16 were deserted at the clutch stage. We recorded data for 288 nestlings from 42 food-supplemented and 43 control broods. Sample size may vary between analyses because of missing information for some variables.

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.5db0168>> (Podofillini et al. 2019).

Results

Effects of food supplementation on body condition, oxidative and moult status

Extra food did not significantly affect adult body condition and oxidative status (TAC and TOS) (Table 2). Because of large sexual dimorphism in body mass, females had considerably larger SMI than males (Table 2). Moreover, antioxidant defences progressively improved during the breeding season and birds in better body condition had better antioxidant defences, as TAC significantly increased with both sampling date and SMI (Table 2, Fig. 1).

Food supplementation increased resource allocation to primary feather moult. Although the proportion of individuals initiating moult did not significantly differ between treatments (controls = 0.27 (19/70); food-supplemented = 0.38 (28/74), Table 2), the increase of total moult investment with sampling date was significantly larger for food-supplemented individuals (estimate = 4.17 (0.50 SE) mm day^{-1}) than controls (1.71 (0.43 SE) mm day^{-1}) (food supplementation \times sampling date interaction, Table 2, Fig. 2). Besides, females initiated moult much more frequently (0.52) than males (0.13) (Table 2), and the probability of initiating moult markedly increased with sampling date (Table 2). However, the total moult investment, after accounting for the strong sampling date effect, did not significantly differ between the sexes (Table 2).

Effects of food supplementation on egg mass and hatching success

Food supplementation significantly mitigated the (non-linear) decline in egg mass along the laying sequence observed in control clutches (food supplementation \times relative laying order interaction, Table 3), food-supplemented females producing larger last-laid eggs compared to controls (Fig. 3) (Supplementary material Appendix 1 Table A6 for details of egg mass models selection). The predicted egg mass among last eggs laid by food-supplemented females was 14.58 g, while it was 13.93 g among control females (Fig. 3). Egg mass peaked at relative laying order 0.96 among control (implying a continuous decline within the actual relative laying order values) and 1.54 among food-supplemented females, respectively (Fig. 3).

Extra food allowed females in poor body condition to lay heavier eggs compared to poor condition control females: egg mass significantly increased with SMI among control females (estimate: 0.032 (0.013 SE)), whereas no significant association emerged among food-supplemented ones (-0.011 (0.014 SE)) (food supplementation \times female SMI interaction, Table 3, Fig. 4). Finally, eggs belonging to larger clutches were significantly lighter than those belonging to smaller ones (Table 3). A similarly supported (according to the Akaike information criterion value) model of egg mass variation further revealed that food supplementation had stronger positive effects on egg mass among early-breeders than among late-breeders (Supplementary material Appendix 1 Table A7, Fig. A1; see also Supplementary material Appendix 1 Table A6 for more details about fitting of the egg mass models).

Hatching success was not significantly affected by food supplementation (Table 3): the proportion of hatched eggs was 0.82 (146/178) in control clutches and 0.84 (146/173) in food-supplemented ones. In addition, hatching success significantly decreased among late-laid eggs in the laying sequence (Table 3) (Supplementary material Appendix 1 Table A8 for further details about fitting of the egg hatching success model).

Table 2. Generalized linear models of the effects of food supplementation on body condition (scaled mass index, SMI), oxidative (TAC, TOS) and moult status (probability of initiating moult, total moult investment); the coding of the sex variable is 0=female, 1 =male; t-values are reported as test statistics for Gaussian models, Z-values for the binomial model of the probability of initiating moult.

Predictors	Estimate (SE)	t/Z	p	Effect size r
SMI (n = 144) ($R^2 = 0.43$)				
Food supplementation	2.86 (2.16)	1.32	0.19	0.11
Sex	-21.72 (2.21)	9.83	<0.001	0.64
Breeding stage	-3.66 (2.60)	1.41	0.16	0.12
Total moult investment	-0.02 (0.03)	0.58	0.56	0.05
TAC (n = 126) ($R^2 = 0.38$)				
Food supplementation	-65.62 (45.74)	1.43	0.15	0.13
Sex	5.30 (45.47)	0.12	0.91	0.01
Sampling date	18.52 (3.66)	5.04	<0.001	0.42
SMI ^a	9.06 (1.74)	5.20	<0.001	0.43
Total moult investment	0.23 (0.75)	0.31	0.76	0.03
TOS (n = 71) ($R^2 = 0.04$)				
Food supplementation	0.41 (0.42)	0.99	0.33	0.12
Sex	-0.123 (0.41)	0.32	0.75	0.04
Sampling date	-0.03 (0.04)	0.74	0.47	0.09
SMI ^a	-0.01 (0.02)	0.88	0.38	0.11
Total moult investment	0.003 (0.008)	0.34	0.74	0.04
Probability of initiating moult (n = 144) ^b ($R^2 = 0.30$)				
Food supplementation	0.64 (0.44)	1.46	0.15	0.14
Sex	-1.83 (0.45)	4.04	<0.001	0.35
Sampling date	0.13 (0.04)	3.71	<0.001	0.38
SMI ^a	-0.01 (0.02)	0.73	0.47	0.07
Total moult investment (n = 144) ^c ($R^2 = 0.43$)				
Food supplementation ^d	14.05 (4.61)	3.05	0.003	0.25
Sex	-7.35 (4.67)	1.57	0.12	0.13
Sampling date ^d	2.97 (0.34)	8.84	<0.001	0.60
SMI ^a	-0.28 (0.18)	1.57	0.12	0.13
Food supplementation × sampling date	2.46 (0.65)	3.76	<0.001	0.30

^a Variable group-centered within sex categories.

^b Binomial GLM.

^c p-values from randomization test.

^d Estimate for mean-centered covariate.

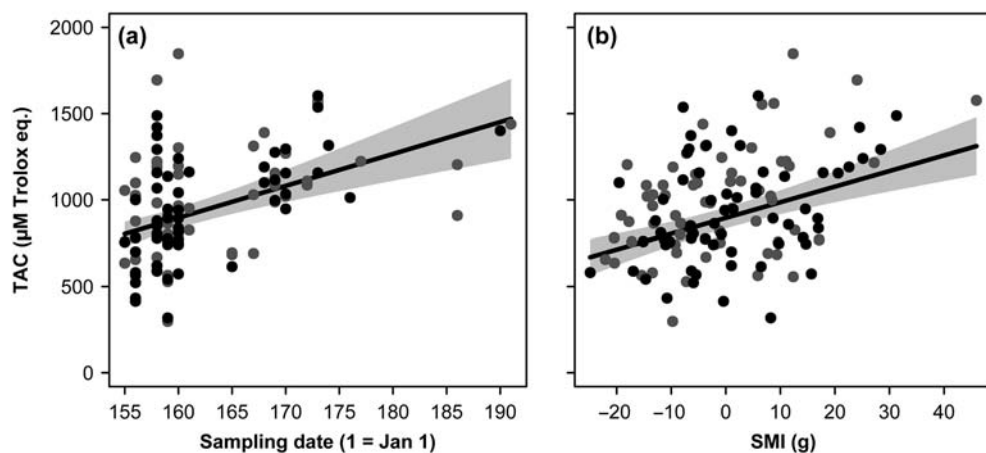


Figure 1. Plasma non-enzymatic total antioxidant capacity (TAC) of breeding adults markedly increased with (a) sampling date and (b) body condition (scaled mass index, SMI; values centered within each sex category), irrespective of food supplementation. Black dots: food-supplemented individuals; grey dots: control individuals. The fitted lines (with 95% confidence bands) are derived from the corresponding model reported in Table 2.

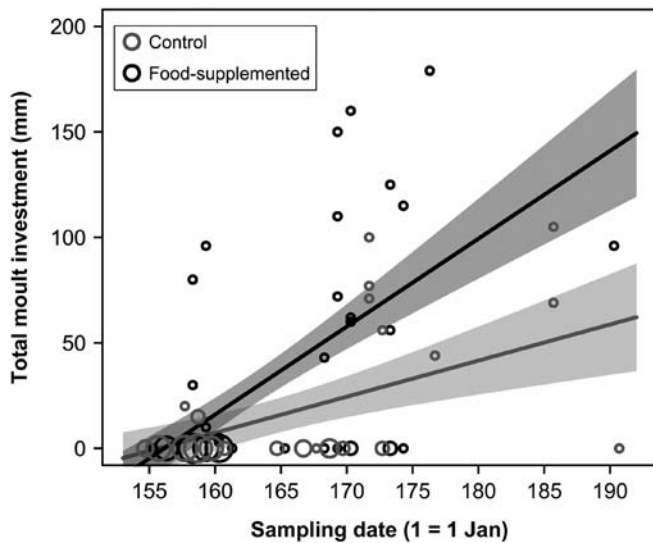


Figure 2. Food supplementation promoted the allocation of resources into renewal and growth of primary feathers (total moult investment) in breeding adults. Dot size is proportional to the number of overlapping datapoints, with the smallest dots corresponding to single data, and larger dots proportional to sample size according to the function: dot size = $1 + \ln(\text{sample size})$. The fitted lines (with 95% confidence bands) are derived from the corresponding model reported in Table 2. Black line and dots: food-supplemented individuals; grey line and dots: control individuals. Data from the two treatment groups were represented with slightly modified x-axis values to reduce overlap and improve clarity.

Effects of food supplementation on clutch size, duration of the incubation period and nest desertion

Extra food did not significantly affect clutch size (food-supplemented females = 4.3 (0.7 SD), controls = 4.2 (0.7 SD), $n = 50$ in both groups) and duration of the incubation period (food-supplemented clutches = 32.6 days (2.4 SD),

controls = 32.5 (2.3 SD), $n = 41$ and 43, respectively), the latter becoming significantly shorter in late-laid clutches compared to early-laid ones (Table 4).

Body condition significantly mediated the effects of food supplementation on the likelihood of nest desertion (food supplementation \times female SMI interaction, Table 4): control females in good body condition were less likely to abandon their nest than those in poor body condition (estimate = -0.147 (0.065 SE)), while this was not the case among food-supplemented females (estimate = 0.009 (0.044 SE)) (Fig. 5). Hence, in the food-supplemented group, females with low SMI were as likely to desert their nest as those with high SMI (Fig. 5). This analysis could not be performed by including male (instead of female) SMI because we could obtain male SMI data for five deserted nests only, all of which were controls. However, when restricting the analyses to control clutches/broods, female SMI significantly negatively predicted the probability of nest desertion, while male SMI did not (Supplementary material Appendix 1 Table A9).

Effects of food supplementation on sex allocation

PSR was slightly male-biased (0.57, $n = 72$ males and 54 females from 31 complete clutches) but did not significantly deviate from 0.5 (intercept-only binomial GLM, $Z = 1.60$, $p = 0.11$). Sex allocation was not significantly affected by food supplementation nor by other predictors (Table 4) (Supplementary material Appendix 1 Table A10 for additional details of PSR model fitting).

When considering the entire set of sexed nestlings, the proportion of males was 0.48 ($n = 123$ males and 130 females), again not significantly deviating from 0.5 (intercept-only binomial GLMM with brood identity as a random effect, $Z = 0.46$, $p = 0.64$). Food supplementation did not significantly affect sex allocation along the laying sequence (food supplementation \times nestling rank interaction, estimate = -0.31 (0.24 SE),

Table 3. Mixed models of the effects of food supplementation on egg mass and hatching success. Degrees of freedom for F-tests of the egg mass linear mixed model (LMM) were estimated according to the Kenward–Roger's approximation; Z-values are reported as test statistics for the egg hatching success binomial generalized linear mixed model.

Predictors	Estimate (SE)	F/Z	df	p	Effect size r
Egg mass ($n = 349$ eggs, $n = 82$ clutches) ($R^2 = 0.30$)					
Food supplementation ^a	0.19 (0.25)	0.59	1,76	0.45	0.08
Relative laying order ^a	0.72 (0.31)	5.21	1,265	0.023	0.06
(Relative laying order ²) ^a	-0.28 (0.08)	13.29	1,265	<0.001	0.10
Laying date	-0.01 (0.02)	0.31	1,77	0.58	0.05
Clutch size	-0.50 (0.18)	7.48	1,77	0.008	0.25
Female SMI ^a	0.01 (0.01)	0.76	1,76	0.39	0.09
Food supplementation \times relative laying order	0.33 (0.09)	13.12	1,264	<0.001	0.09
Food supplementation \times female SMI	-0.04 (0.02)	5.14	1,75	0.026	0.23
Egg hatching success ($n = 351$ eggs, $n = 83$ clutches) ^b ($R^2 = 0.03$)					
Food supplementation	0.12 (0.39)	0.31	–	0.76	<0.01
Relative laying order	-0.69 (0.23)	3.04	–	0.002	0.17
Laying date	0.01 (0.03)	0.30	–	0.77	<0.01
Clutch size	0.03 (0.30)	0.09	–	0.93	<0.01
Female SMI ^c	-0.01 (0.01)	0.39	–	0.69	<0.01

^a Estimate for mean-centered covariate.

^b Dispersion parameter = 0.88.

^c Estimate from a different model (sample size: $n = 302$ eggs, $n = 71$ clutches).

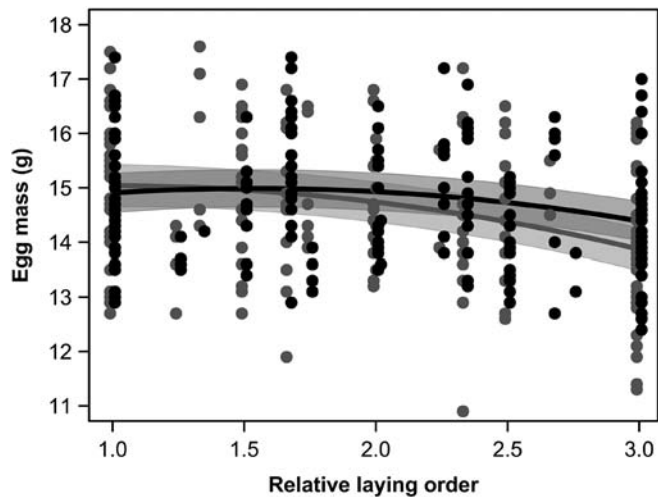


Figure 3. Egg mass significantly declined along the laying sequence (relative egg laying order) in a quadratic fashion in both control and food-supplemented females, but the quadratic function had significantly different peak values for eggs laid by control and food-supplemented females, resulting in heavier last-laid eggs among food-supplemented females compared to controls. The fitted lines (with 95% confidence bands) are derived from the corresponding model reported in Table 3. Black dots and black line: food-supplemented females; grey dots and grey line: control females. Data from the two treatment groups were represented with slightly modified x-axis values to reduce overlap and improve clarity.

$Z = -1.29$, $p = 0.20$). The final model disclosed a strong sex bias along the laying sequence (effect of rank, Table 4), with a female bias among high-ranking nestlings (hatched from first-laid eggs) and a male bias among low-ranking nestlings (hatched from last-laid eggs). A similar tendency also emerged when analysing those nestlings whose egg of origin was known (Supplementary material Appendix 1 Table A10). In this subset, there was no significant difference in mass between male

and female eggs, and no significant difference in mass allocation to male and female eggs according to food supplementation (Supplementary material Appendix 1 Table A11).

Effects of food supplementation on nestling body mass, morphology and mortality

Food supplementation significantly improved nestlings' body mass growth, and significantly mitigated body mass loss induced by haematophagous ectoparasites (Table 5, Fig. 6): the mass increase of food-supplemented nestlings was ca 10% greater than controls, a significant difference (food supplementation \times age interaction) (food supplemented: 7.17 (0.13 SE) g day^{-1} ; controls: 6.47 (0.12 SE) g day^{-1} ; Table 5), and body mass significantly decreased with parasite load among control nestlings (estimate: -2.62 (0.89 SE)), whereas this was not the case among food-supplemented ones (0.16 (0.85 SE)) (food supplementation \times ectoparasite load interaction, Table 5, Fig. 6). Besides, high ranking nestlings were significantly larger and grew faster than low ranking ones (Table 5), nestlings from late clutches were significantly lighter than those from early clutches, and those from larger clutches were lighter than those from smaller clutches (Table 5).

Skeletal growth was not significantly affected by food supplementation (Table 5). However, food supplementation enhanced forearm growth under highly parasitized conditions (significant food supplementation \times ectoparasite load interaction, Table 5): in control nestlings, forearm length did not significantly change with ectoparasite load (estimate: -0.71 (0.57 SE)), whereas it significantly increased with ectoparasite load among food-supplemented nestlings (1.11 (0.53 SE)) (Fig. 6). Both skeletal traits showed a tendency to be larger in nestlings from larger clutches, after accounting for age and rank effects (Table 5).

Food-supplemented nestlings grew significantly longer feathers than controls at 16 days of age, after accounting for age and rank effects (Table 5).

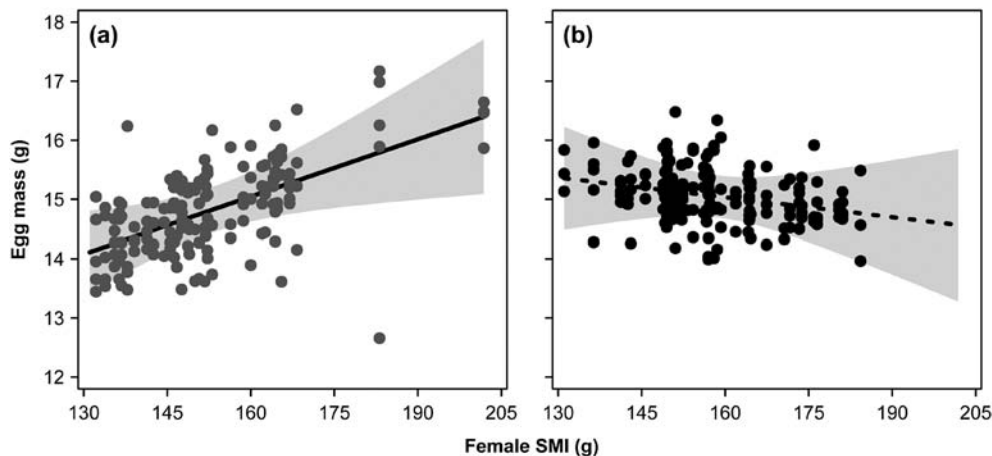


Figure 4. Egg mass significantly increased with body condition (scaled mass index, SMI) among control females (a), while no significant association emerged among food-supplemented females (b). Partial plots accounting for other model effects are shown. The fitted lines (with 95% confidence bands) are derived from the corresponding model reported in Table 3. Full line: significant slope; dotted line: non-significant slope.

Table 4. Generalized linear models (GLMs) of the effects of food supplementation on clutch size, duration of the incubation period, nest desertion and primary sex ratio (PSR, proportion of males in a brood), and binomial generalized mixed model (GLMM) of the probability of a nestling being male; t-values are reported as test statistics for Gaussian GLMs, Z-values for binomial models.

Predictors	Estimate (SE)	t/Z	p	Effect size r
Clutch size (n=100 clutches) ^a (R ² =0.01)				
Food supplementation	0.10 (0.14)	0.74	0.46	0.07
Laying date	-0.01 (0.01)	0.79	0.43	0.08
Female SMI ^b	-0.01 (0.01)	0.62	0.54	0.07
Duration of the incubation period (n=84 clutches) ^a (R ² =0.15)				
Food supplementation	0.07 (0.48)	0.14	0.89	0.02
Laying date	-0.11 (0.03)	3.40	0.001	0.36
Clutch size	0.53 (0.35)	1.50	0.14	0.17
Female SMI ^c	-0.01 (0.02)	0.23	0.82	0.03
Probability of nest desertion (n=82 clutches) (R ² =0.19)				
Food supplementation ^d	-0.04 (1.01)	0.04	0.97	0.03
Laying date	0.07 (0.05)	1.37	0.17	0.25
Clutch size	0.10 (0.57)	0.18	0.86	0.08
Female SMI ^d	-0.06 (0.04)	1.58	0.11	0.17
Food supplementation × female SMI	0.16 (0.08)	2.07	0.038	0.23
PSR (n=31 broods) ^e (R ² =0.06)				
Food supplementation	-0.36 (0.38)	0.95	0.34	0.16
Laying date	-0.01 (0.03)	0.37	0.71	0.07
Clutch size	-0.17 (0.27)	0.62	0.54	0.12
Female SMI ^f	0.01 (0.02)	0.18	0.86	0.02
Probability of a nestling being male (n=253 nestlings, n=80 broods) ^g (R ² =0.05)				
Food supplementation	-0.31 (0.27)	1.15	0.25	0.07
Rank	0.38 (0.12)	3.23	0.001	0.21
Laying date	-0.01 (0.02)	0.22	0.82	0.01

^a p-values are from a randomization test

^b Estimate from a different model with smaller sample size (n=82 clutches).

^c Estimate from a different model with smaller sample size (n=72 clutches).

^d Estimate for mean-centered covariate.

^e Dispersion parameter = 1.23; PSR expressed as n males/brood size.

^f Estimate from a different model with smaller sample size (n=25 broods).

^g Dispersion parameter = 1.15.

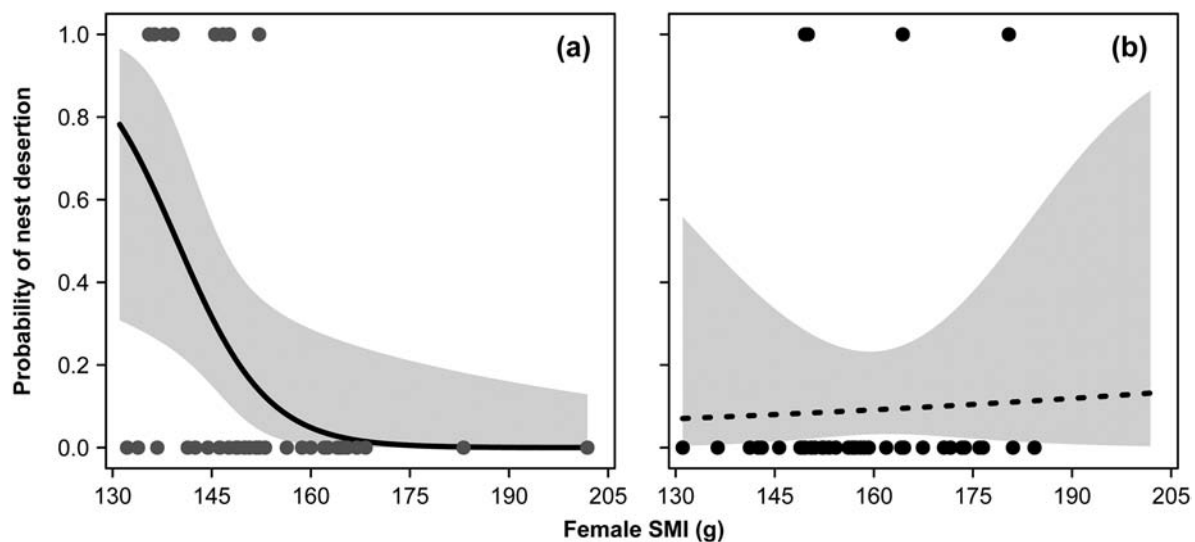


Figure 5. The probability of nest desertion significantly declined with female body condition (scaled mass index, SMI) among control females (a), but not among food-supplemented ones (b). The fitted lines (with 95% confidence bands) from the corresponding binomial model reported in Table 4 are shown (full line: significant slope; dotted line: non-significant slope). Dots represent original data.

Table 5. Mixed models of the effects of food supplementation on nestling body mass (g), morphology [tarsus, forearm and feather length (mm)], and mortality. Degrees of freedom for F-tests were estimated according to the Kenward–Roger's approximation.

Predictors	Estimate (SE)	F/Z	df	p	Effect size r
Body mass (n=288 nestlings, n=85 broods) ($R^2=0.87$)					
Food supplementation ^a	2.27 (1.22)	3.50	1, 79	0.07	0.16
Age ^a	6.47 (0.12)	5836.60	1, 767	<0.001	0.92
Rank ^a	−3.99 (0.33)	147.80	1, 238	<0.001	0.46
Laying date	−0.23 (0.08)	7.60	1, 95	0.007	0.18
Brood size	−1.38 (0.43)	10.30	1, 519	0.001	0.16
Ectoparasite load ^a	−1.20 (0.62)	3.70	1, 902	0.05	0.07
Food supplementation×age	0.69 (0.17)	16.30	1, 754	<0.001	0.12
Food supplementation×ectoparasite load	2.78 (1.22)	5.16	1, 901	0.023	0.09
Age×rank	−1.00 (0.08)	171.50	1, 806	<0.001	0.37
Tarsus length (n=249 nestlings, n=79 broods) ($R^2=0.66$)					
Food supplementation	0.62 (0.39)	2.56	1, 74	0.11	0.15
Age	1.54 (0.11)	179.32	1, 227	<0.001	0.70
Rank	−0.96 (0.12)	62.66	1, 214	<0.001	0.41
Laying date	−0.03 (0.03)	1.16	1, 81	0.28	0.10
Brood size	0.37 (0.19)	3.86	1, 95	0.052	0.16
Ectoparasite load	0.21 (0.24)	0.73	1, 238	0.39	0.06
Forearm length (n=250 nestlings, n=79 broods) ($R^2=0.70$)					
Food supplementation ^a	0.64 (0.54)	1.36	1, 72	0.24	0.09
Age	2.74 (0.19)	213.55	1, 197	<0.001	0.72
Rank	−1.64 (0.21)	58.31	1, 224	<0.001	0.42
Laying date	0.01 (0.04)	0.11	1, 83	0.74	0.03
Brood size	0.57 (0.28)	4.23	1, 102	0.042	0.15
Ectoparasite load ^a	0.26 (0.40)	0.41	1, 192	0.52	0.05
Food supplementation×ectoparasite load	1.82 (0.76)	5.61	1, 195	0.019	0.17
Feather length (n=186 nestlings, n=69 broods) ($R^2=0.61$)					
Food supplementation	2.10 (1.04)	4.05	1, 61	0.049	0.19
Age	4.60 (0.45)	103.59	1, 124	<0.001	0.66
Rank	−2.75 (0.40)	47.68	1, 150	<0.001	0.42
Laying date	−0.06 (0.09)	0.42	1, 77	0.52	0.06
Brood size	0.53 (0.51)	1.07	1, 82	0.30	0.09
Ectoparasite load	0.46 (0.79)	0.33	1, 154	0.57	0.05
Mortality (n=285 nestlings, n=85 broods) ^b ($R^2=0.17$)					
Food supplementation	−0.68 (0.54)	1.25	–	0.21	0.09
Rank	1.32 (0.24)	5.50	–	<0.001	0.37
Laying date	−0.02 (0.04)	0.47	–	0.64	0.04
Brood size	−0.61 (0.28)	2.19	–	0.029	0.18
Ectoparasite load	−0.63 (0.40)	1.56	–	0.12	0.10

^a Estimate for mean-centered covariate.

^b Dispersion parameter=0.83.

Overall, 31% (44/143) control nestlings and 23% (33/145) food-supplemented ones died by 16 days of age, a non-significant difference (Table 5). Mortality was considerably higher among low ranking nestlings (strong positive effect of rank on mortality) and among those growing in larger clutches (Table 5). Results were qualitatively similar if deserted broods were excluded (Supplementary material Appendix 1 Table A12).

Discussion

In this study of a mesopredatory avian species, we simulated favourable environmental conditions during reproduction by providing extra food to breeders, and assessed the consequences of food supplementation for adult conditions,

resource allocation to an energy-demanding process (flight feather moult) competing with breeding, breeding output and early offspring growth. Below we discuss the main findings.

Moult–breeding overlap and extra food provisioning

Although moult is mostly temporally separated from competing activities such as reproduction and migration (Jenni and Winkler 1994, Barta et al. 2008), in several species, including the migratory lesser kestrel, tight annual scheduling of the yearly cycle has promoted the evolution of moult–breeding overlap (Hemborg and Lundberg 1998, Hemborg 1999, Zuberogoitia et al. 2018). Similarly to other raptors, lesser kestrels start their annual flight feather moult when incubating, females being more likely to do so than males (reviewed

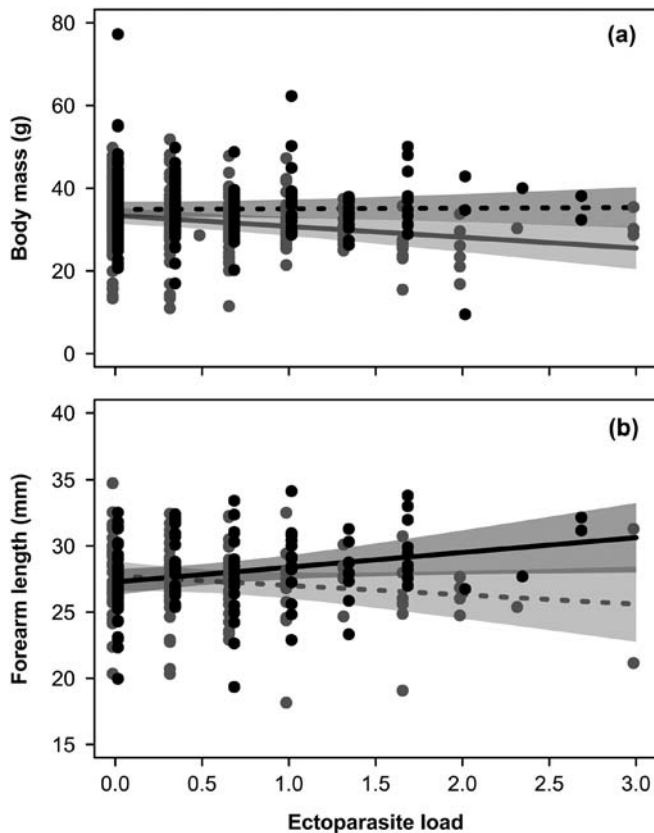


Figure 6. Variation of (a) body mass and (b) forearm length according to ectoparasite load in control and food-supplemented nestlings. Partial plots accounting for other model effects are shown. Black dots and black line: food-supplemented nestlings; grey dots and grey line: control nestlings. The fitted lines (with 95% confidence bands) are derived from the corresponding models reported in Table 5. Data from the two treatment groups were represented with slightly modified x-axis values to reduce overlap and improve clarity.

by Zuberogitia et al. 2018). Males, as in most falcons, are smaller, more agile, perform extensive mate-feeding and carry most of the prey to their progeny (Donazar et al. 1992, Krüger 2005): they are thus likely to pay a greater cost than females for the moult–breeding overlap (Espie et al. 1996). Extra food resulted however in greater moult investment in both sexes, after statistically controlling for seasonal effects on timing of moult. The positive effect of food supplementation on flight feather renewal supports the idea that moult–breeding overlap is costly (Hemborg and Lundberg 1998, Saino et al. 2014) and that favourable environmental conditions promote a greater allocation of resources to feather renewal (Espie et al. 1996, Siikamäki 1998, Danner et al. 2014). A greater resource allocation to moulting feathers may either be a direct consequence of food supplementation, with birds investing extra resources in new feathers' synthesis, or a consequence of lower mobility of fed individuals compared to controls, which may have reduced maintenance costs and promoted feather renewal.

Extra food effects on egg mass, nest desertion and nestling body mass and morphology

Females invested part of resources gained from the extra food in producing heavier last-laid eggs. This result is in line with evidence that egg size is a plastic trait that rapidly responds to the ecological conditions to which the mother is exposed to (Wiebe and Bortolotti 1995, Karell et al. 2008, Saino et al. 2010). Extra food led to a ca 4% increase in the mass of last-laid eggs compared to control eggs (Christians 2002). Although egg size is a critical trait for offspring fitness soon after hatching (Williams 1994), such a relatively minor increase in egg size did not produce any significant survival/growth advantage of last hatched (low ranking) food-supplemented nestlings compared to controls. The lack of detectable egg mass effects on offspring fitness could be due to the moderately favourable ecological conditions in the study year (in terms of food supplies and weather; Cecere et al. unpubl.), as the effects of extra food provisioning on fitness may vary according to contingent ecological conditions (Hipkiss et al. 2002, Karell et al. 2008, Ruffino et al. 2014).

Furthermore, extra food allowed poor-condition females to lay eggs that were as large as those laid by good condition ones. Among controls, ca 16% of the variation in mean egg mass of a clutch was explained by female body condition (correlation between mean egg mass and female SMI, $r = 0.40$), in line with previous studies (reviewed by Christians 2002). However, this correlation was heavily modified when females could consume extra food, with variance in egg mass explained by body condition dropping to 1.6% ($r = -0.13$). Overall, we conclude that food provisioning positively affected female egg production, and that the benefits of extra food in terms of egg size increase were greater for poor condition females.

A similar finding emerged for the likelihood of nest desertion, which was higher for poor condition control females compared to poor condition food-supplemented ones. Nest desertion is widespread in birds, especially among long-lived species (Székely et al. 1996). It occurs whenever the perceived costs of current reproduction for parents outweigh the expected fitness payoffs of future reproduction (Kelly and Kennedy 1993, Székely et al. 1996), which may be the case under harsh ecological conditions (Anderson et al. 1982, Hörnfeldt et al. 1990, Oppliger et al. 1994, Wiggins et al. 1994) or among low-quality parents with poor body condition (Kelly and Kennedy 1993, Wiggins et al. 1994, Yorio and Boersma 1994). It may also follow from mortality of one parent (Roche et al. 2010, Santema and Kempenaers 2018), which may dramatically increase the costs of current reproduction for the remaining parent in biparental species (Székely et al. 1996). Our results suggest that extra food alleviated the costs of reproduction for females of low phenotypic quality, reducing their probability of completely failing reproduction, in accordance with the hypothesis that nest desertion is the outcome of an adaptive life-history decision conditional on maternal state (Székely et al. 1996).

Among nestlings, extra food resulted in significantly higher mass gain and increased feather growth. Such an effect was most likely due to parents using the extra food to feed their nestlings, as by 10–15 days post hatching nestlings are not able to swallow or split to pieces a relatively large food item (mice) by themselves (Cramp 1998). It also suggests that parents did not markedly reduce nestling provisioning with natural prey items. Furthermore, extra food provisioning affected nestling growth dynamics in combination with ectoparasite infestation. First, it significantly alleviated the negative effects of an haematophagous ectoparasite on mass gain, whereby body mass significantly decreased with ectoparasite load among control nestlings but not among food-supplemented ones. Second, it increased resource allocation to flight apparatus development in highly parasitized nestlings compared to controls. These two results were not due to differences in ectoparasite load between food-supplemented and control nestlings (Supplementary material Appendix 1 Table A13). Haematophagous ectoparasites are well known to exert detrimental effects on early growth dynamics, either by directly withdrawing resources (blood) or by activating the immune system (Møller 1993, Merino and Potti 1995, Saino et al. 1998, Lochmiller and Deerenberg 2000, Nilsson 2003, Tschirren et al. 2003). Under food limitation, parasites may impose a tradeoff between allocation of resources to somatic growth and immunity, diverting limiting resources from somatic growth to immune defences (Saino et al. 1998, Lochmiller and Deerenberg 2000, Soler et al. 2003, Brommer 2004, Tschirren and Richner 2006). Extra food may relax such constraints, resulting in weaker direct/indirect negative ectoparasite effects (Merino and Potti 1998, Brommer et al. 2011). Furthermore, growing nestlings may respond to ectoparasites by differentially allocating resources to growth of specific traits in order to increase their short-term fitness prospects (Mainwaring and Hartley 2012). For instance, ectoparasite infestation may promote investment in growth of feathers at the expense of mass or other skeletal traits, because an earlier maturation of the flight apparatus may facilitate escape from the highly parasitized nest environment to avoid detrimental ectoparasite effects (Saino et al. 1998). The observation that ectoparasites significantly promoted resource allocation to growth of the flight apparatus (forearm length) when provisioned with extra food is coherent with the latter suggestion.

Other findings unrelated to extra food provisioning

Non-enzymatic antioxidant defences increased during the breeding season, which may be due to variation in external conditions, diet or physiological state (Costantini et al. 2010). For instance, the strong increase of ambient temperature during the breeding season (ca 10°C increase between April and July; data from <www.ssabasilicata.it/>) may improve flight efficiency in the lesser kestrel (Hernández-Pliego et al. 2017) and reduce the oxidative costs of locomotion (Costantini et al. 2008), promoting mobilization/redistribution of non-enzymatic antioxidants. Seasonal changes in hormone profile

(Meijer and Schwabl 1989, Pereira et al. 2010) may also play a role (Costantini et al. 2011, Costantini 2014), whereas this is unlikely for seasonal dietary changes (Rodríguez et al. 2010), because extra food did not significantly affect oxidative status. In addition, the strong positive covariation of antioxidant defences with body condition indicates that levels of non-enzymatic antioxidants may represent a reliable indicator of general physiological state and individual quality (Costantini and Bonadonna 2010).

Irrespective of food provisioning, the duration of the incubation period strongly decreased with laying date, a common pattern in birds (Runde and Barrett 1981, Hipfner et al. 2001, Weiser et al. 2018). In our case, it might be due to seasonal increase in ambient temperature (Ardia et al. 2006), or differences in incubation behaviour between early- and late-breeders (late-breeders partly compensating for delayed timing by more intense incubation; Hipfner et al. 2001).

Offspring sex ratio was female-biased among early- and male-biased among late-laid eggs. This may suggest that females (the larger sex in terms of adult mass) are more susceptible to harsh rearing environments, and that mothers may adaptively bias sex along the laying sequence in order to provide daughters with a competitive advantage over their sons (due to earlier hatching of early laid eggs; Magrath 1990). In spite of this, no sex difference in nestling mortality was detected, and nestling sex ratio was unbiased, in line with previous studies (Tella et al. 1996, Aparicio and Cordero 2001).

Finally, nestling pre-fledging mortality significantly decreased in birds raising larger broods, suggesting that parents of high quality (in terms of e.g. nestling provisioning or resource acquisition ability) may be able to raise more offspring (van Noordwijk and de Jong 1986).

Concluding remarks

Our comprehensive analysis of the benefits of extra food provisioning to reproduction under natural conditions suggests that parent lesser kestrels invested the extra food mainly in improving current reproduction, similarly to most of the bird species studied so far (Ruffino et al. 2014), rather than using it to accumulate resources (in terms of e.g. body fat or muscle fibres) for improving their residual reproductive value. Indeed, parents mainly used the extra resources for laying larger eggs and raising heavier/larger offspring, while the extra food did not improve their own body condition or oxidative status. The increase of egg size following extra food provisioning indicates that egg formation by females relies partly on resources acquired during egg laying, besides pre-laying food provisioning by the male partner through courtship feeding (Donazar et al. 1992), in line with an ‘income breeding’ strategy of energy storage for reproduction (Jönsson 1997, Meijer and Drent 1999). Our findings suggest that food availability during the breeding season can limit population growth of this species. Importantly, maternal condition appears to be a major trait modulating the benefits of extra food provisioning to reproduction, whereby such benefits accrued mostly

to low-quality females with poor body condition. Moreover, extra food reduced the costs of the moult–breeding overlap, and affected early growth tradeoffs by fostering development of flight apparatus traits in response to ectoparasite infestation. To sum up, our results illustrate the pervasive consequences of food limitation in natural environments for resource allocation to competing energy-demanding activities (e.g. moult and reproduction), breeding output and offspring development, at the same time highlighting that the negative consequences of food limitation on reproductive output may be disproportionately larger for individuals of low phenotypic quality.

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References

- Alan, R. R. and McWilliams, S. R. 2013. Oxidative stress, circulating antioxidants and dietary preferences in songbirds. – *Comp. Biochem. Physiol.* 164: 185–193.
- Anderson, D. W. et al. 1982. Brown pelicans: influence of food supply on reproduction. – *Oikos* 39: 23–31.
- Aparicio, J. M. 1997. Cost and benefits of surplus offspring in the lesser kestrel (*Falco naumanni*). – *Behav. Ecol. Sociobiol.* 41: 129–137.
- Aparicio, J. M. and Bonal, R. 2002. Effects of food supplementation and habitat selection on timing of lesser kestrel breeding. – *Ecology* 83: 873–877.
- Aparicio, J. M. and Cordero, P. J. 2001. The effects of the minimum threshold condition for breeding on offspring sex-ratio adjustment in the lesser kestrel. – *Evolution* 55: 1188–1197.
- Ardia, D. R. et al. 2006. Warm temperatures lead to early onset of incubation, shorter incubation periods and greater hatching asynchrony in tree swallows *Tachycineta bicolor* at the extremes of their range. – *J. Avian Biol.* 37: 137–142.
- Bates, D. et al. 2014. Fitting linear mixed-effects models using lme4. – *J. Stat. Softw.* 67: 1–48.
- Barta, Z. et al. 2008. Optimal moult strategies in migratory birds. – *Phil. Trans. R. Soc. B* 363: 211–229.
- Bize, P. et al. 2008. Fecundity and survival in relation to resistance to oxidative stress in a free-living bird. – *Ecology* 89: 2584–2593.
- Boutin, S. 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems and the future. – *Can. J. Zool.* 68: 203–220.
- Brommer, J. E. 2004. Immunocompetence and its costs during development: an experimental study in blue tit nestlings. – *Proc. R. Soc. B* 271: S110–S113.
- Brommer, J. E. et al. 2011. Body size and immune defense of nestling blue tits (*Cyanistes caeruleus*) in response to manipulation of ectoparasites and food supply. – *Auk* 128: 556–563.
- Capelle, K. J. and Whitworth, T. L. 1973. The distribution and avian hosts of *Carnus hemapterus* (Diptera: Milichiidae) in North America. – *J. Med. Entomol.* 10: 525–526.
- Catry, I. et al. 2016. Sexual and parent–offspring dietary segregation in a colonial raptor as revealed by stable isotopes. – *J. Zool.* 299: 58–67.
- Cecere, J. G. et al. 2018. Spatial segregation of foraging areas between neighbouring colonies in a diurnal raptor. – *Sci. Rep.* 8: 11762.
- Christians, J. K. 2002. Avian egg size: variation within species and inflexibility within individuals. – *Biol. Rev.* 77: 1–26.
- Costantini, D. 2014. Oxidative stress and hormesis in evolutionary ecology and physiology. A marriage between mechanistic and evolutionary approaches. – Springer.
- Costantini, D. and Bonadonna, F. 2010. Patterns of variation of serum oxidative stress markers in two seabird species. – *Polar Res.* 29: 30–35.
- Costantini, D. et al. 2008. Long flights and age affect oxidative status of homing pigeons (*Columba livia*). – *J. Exp. Biol.* 211: 377–381.
- Costantini, D. et al. 2010. Relationships among oxidative status, breeding conditions and life-history traits in free-living great tits *Parus major* and common starlings *Sturnus vulgaris*. – *Ibis* 152: 793–802.
- Costantini, D. et al. 2011. A meta-analysis of glucocorticoids as modulators of oxidative stress in vertebrates. – *J. Comp. Physiol. B* 181: 447–456.
- Cramp, S. 1998. The complete birds of the western Palearctic on CDROM. – Oxford Univ. Press.
- Cucco, M. and Malacarne, G. 1997. The effect of supplemental food on time budget and body condition in the black redstart *Phoenicurus ochrurus*. – *Ardea* 85: 211–221.
- Dabao, Z. 2017. A coefficient of determination for generalized linear models. – *Am. Stat.* 71: 310–316.
- Danner, M. R. et al. 2014. Winter food limits timing of pre-alternate moult in a short-distance migratory bird. – *Funct. Ecol.* 29: 259–267.
- Dawson, R. and Bortolotti, G. 2002. Experimental evidence for food limitation and sex-specific strategies of American kestrel (*Falco sparverius*) provisioning offspring. – *Behav. Ecol. Sociobiol.* 52: 43–52.
- 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.
- Di Maggio, R., Campobello, D. and Sarà, M. 2018. Lesser kestrel diet and agricultural intensification in the Mediterranean: an unexpected win–win solution? – *J. Nat. Conserv.* 45: 122–130.
- Donazar, J. A. et al. 1992. Functional analysis of mate-feeding in the lesser kestrel *Falco naumanni*. – *Ornis Scand.* 23: 190–194.
- Erel, O. 2004. A novel automated direct measurement method for total antioxidant capacity using a new generation, more stable ABTS radical cation. – *Clin. Biochem.* 37: 277–285.

- Erel, O. 2005. A new automated colorimetric method for measuring total oxidant status. – Clin. Biochem. 8: 1103–1111.
- Espie, R. H. et al. 1996. Ecological correlates of molt in merlins (*Falco columbarius*). – Auk 113: 363–369.
- Fletcher, Q. E. et al. 2013. Oxidative damage increases with reproductive energy expenditure and is reduced by food-supplementation. – Evolution 67: 1527–1536.
- Frossard, J. and Renaud, O. 2018. Permutation tests for regression, ANOVA and comparison of signals: the permuco package. – <<https://cran.r-project.org/web/packages/permuco/index.html>>
- Garcia, P. F. J. et al. 1993. Energy allocation to reproduction and maintenance in mountain bluebirds (*Sialia currucoides*): a food supplementation experiment. – Can. J. Zool. 71: 2352–2357.
- Giordano, M. et al. 2015. Female oxidative status, egg antioxidant protection and eggshell pigmentation: a supplemental feeding experiment in great tits. – Behav. Ecol. Sociobiol. 69: 777–785.
- Gonzalez, L. M. et al. 2006. Supplementary feeding as an effective tool for improving breeding success in the Spanish imperial eagle (*Aquila adalberti*). – Biol. Conserv. 129: 477–486.
- Griffiths, R. et al. 1998. A DNA test to sex most birds. – Mol. Ecol. 7: 1071–1075.
- Halliwell, B. and Gutteridge, J. M. C. 2007. Free radicals in biology and medicine. – Oxford Univ. Press.
- Hemborg, C. 1999. Sexual differences in moult–breeding overlap and female reproductive costs in pied flycatchers, *Ficedula hypoleuca*. – J. Anim. Ecol. 68: 429–436.
- Hemborg, C. and Lundberg, A. 1998. Costs of overlapping reproduction and moult in passerine birds: an experiment with the pied flycatcher. – Behav. Ecol. Sociobiol. 43: 19–23.
- Hernández-Pliego, J. et al. 2017. Combined use of tri-axial accelerometers and GPS reveals the flexible foraging strategy of a bird in relation to weather conditions. – PLoS One 12: e0177892.
- Hipfner, J. et al. 2001. Seasonal declines in incubation periods of Brunnich's guillemots *Uria lomvia*: testing proximate causes. – Ibis 143: 92–98.
- Hipkiss, T. et al. 2002. Year-dependent sex-biased mortality in supplementary-fed Tengmalm's owl nestlings. – J. Anim. Ecol. 71: 693–699.
- Hörnfeldt, B. et al. 1990. Effects of cyclic food supply on breeding performance in Tengmalm's owl (*Aegolius funereus*). – Can. J. Zool. 68: 522–530.
- Jaeger, B. C. et al. 2017. An R^2 statistic for fixed effects in the generalized linear mixed model. – J. Appl. Stat. 44: 1086–1105.
- Jenni, L. and Winkler, R. 1994. Molt and ageing of European passerines. – Academic Press.
- Jönsson, K. I. 1997. Capital and income breeding as alternative tactics of resource use in reproduction. – Oikos 78: 57–66.
- Kacelnik, A. and Cuthill, I. C. 1990. Central place foraging in starlings (*Sturnus vulgaris*). II. Food allocation to chicks. – J. Anim. Ecol. 59: 655–674.
- Karell, P. et al. 2008. Maternal effects on offspring Igs and egg size in relation to natural and experimentally improved food supply. – Funct. Ecol. 22: 682–690.
- Kelly, E. J. and Kennedy, P. L. 1993. A dynamic state variable model of mate desertion in Cooper's hawks. – Ecology 74: 351–366.
- Korner-Nievergelt, F. et al. 2015. Bayesian data analysis in ecology using linear models with R, BUGS and Stan. – Academic Press.
- Korpimäki, E. and Wiehn, J. 1998. Clutch size of kestrels: seasonal decline and experimental evidence for food limitation under fluctuating food conditions. – Oikos 83: 259–272.
- Korpimäki, E. et al. 2000. Environmental- and parental condition-related variation in sex ratio of kestrel broods. – J. Avian Biol. 31: 128–134.
- Krüger, O. 2005. The evolution of reversed sexual size dimorphism in hawks, falcons and owls: a comparative study. – Evol. Ecol. 19: 467–486.
- Lack, D. 1954. The natural regulation of animal numbers. – Oxford Univ. Press.
- Lack, D. 1966. Population studies of bird. – Clarendon Press.
- La Gioia, G. et al. 2017. Piano d'Azione Nazionale per il grillaio (*Falco naumanni*). – MATTM-ISPRA.
- Lewin, A. C. and Mitchell, M. N. 1999. Using group mean centering for computing adjusted means by site in a randomized experimental design: the case of California's Work Pays Demonstration Project. – Eval. Rev. 23: 146–161.
- Lochmiller, R. L. and Deerenberg, C. 2000. Tradeoffs in evolutionary immunology: just what is the cost of immunity? – Oikos 88: 87–98.
- Magrath, R. D. 1990. Hatching asynchrony in altricial birds. – Biol. Rev. 65: 587–622.
- Mainwaring, M. C. and Hartley, I. R. 2012. Causes and consequences of differential growth in birds: a behavioral perspective. – Adv. Study Behav. 44: 225–277.
- Manly, B. F. J. 1991. Randomization, bootstrap and Monte Carlo methods in biology. – CRC Press.
- Markman, S. et al. 2002. The manipulation of food resources reveals sex-specific tradeoffs between parental self-feeding and offspring care. – Proc. R. Soc. B 269: 1931–1938.
- Martin, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. – Annu. Rev. Ecol. Syst. 18: 453–487.
- Meijer, T. and Drent, R. 1999. Re-examination of the capital and income dichotomy in breeding birds. – Ibis 141: 399–414.
- Meijer, T. and Schwabl, H. 1989. Hormonal patterns in breeding and nonbreeding kestrels, *Falco tinnunculus*: field and laboratory studies. – Gen. Comp. Endocrinol. 74: 148–160.
- Merino, S. and Potti, J. 1995. Mites and blowflies decrease growth and survival in nestling pied flycatchers. – Oikos 73: 95–103.
- Merino, S. and Potti, J. 1998. Growth, nutrition and blow fly parasitism in nestling pied flycatchers. – Can. J. Zool. 76: 936–941.
- Møller, A. P. 1993. Ectoparasites increase the cost of reproduction in their hosts. – J. Anim. Ecol. 62: 309–322.
- Morganti, M. et al. 2016. An exploration of isotopic variability in feathers and claws of lesser kestrel *Falco naumanni* chicks from southern Sicily. – Avocetta 40: 23–32.
- Murphy, M. E. 1996. Energetics and nutrition in molt. – In: Carey, C. (ed.), Avian energetics and nutritional ecology. – Chapman and Hall, pp. 158–198.
- Nager, R. G. et al. 1999. Experimental demonstration that offspring sex ratio varies with maternal condition. – Proc. Natl Acad. Sci. USA 96: 570–573.
- Newton, I. and Marquiss, M. 1984. Seasonal trend in the breeding performance of sparrowhawks. – J. Anim. Ecol. 53: 809–829.
- Nilsson, J.-Å. 2003. Ectoparasitism in marsh tits: costs and functional explanations. – Behav. Ecol. 14: 175–181.
- Oppliger, A. et al. 1994. Effect of an ectoparasite on lay date, nest-site choice, desertion and hatching success in the great tit (*Parus major*). – Behav. Ecol. 5: 130–134.
- Peig, J. and Green, A. J. 2009. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. – Oikos 118: 1883–1891.

- Peig, J. and Green, A. J. 2010. The paradigm of body condition: a critical reappraisal of current methods based on mass and length. – *Funct. Ecol.* 24: 1323–1332.
- Pereira, R. J. G. et al. 2010. Annual profile of fecal androgen and glucocorticoid levels in free-living male American kestrels from southern mid-latitude areas. – *Gen. Comp. Endocrinol.* 166: 94–103.
- Podofillini, S. et al. 2018. Home, dirty home: effect of old nest material on nest-site selection and breeding performance in a cavity-nesting raptor. – *Curr. Zool.* 64: 693–702.
- Podofillini, S. et al. 2019. Data from: benefits of extra food to reproduction depend on maternal condition. – Dryad Digital Repository, <<http://dx.doi.org/10.5061/dryad.5db0168>>.
- Roche, E. A. et al. 2010. Apparent nest abandonment as evidence of breeding-season mortality in Great Lakes piping plovers (*Charadrius melodus*). – *Auk* 127: 402–410.
- Roff, D. A. 1992. The evolution of life histories: theory and analysis. – Chapman and Hall.
- Rodríguez, C. et al. 2010. Temporal changes in lesser kestrel (*Falco naumanni*) diet during the breeding season in southern Spain. – *J. Rapt. Res.* 44: 120–128.
- Rubolini, D. et al. 2002. Replacement of body feathers is associated with low pre-migratory energy stores in a long-distance migratory bird, the barn swallow (*Hirundo rustica*). – *J. Zool.* 258: 441–447.
- Ruffino, L. et al. 2014. Reproductive responses of birds to experimental food supplementation: a meta-analysis. – *Front. Zool.* 11: 80–93.
- Runde, O. J. and Barrett, R. T. 1981. Variations in egg size and incubation period of the kittiwake *Rissa tridactyla* in Norway. – *Ornis Scand.* 12: 80–86.
- Saino, N. et al. 1998. Effects of a dipteran ectoparasite on immune response and growth tradeoffs in barn swallow (*Hirundo rustica*) nestlings. – *Oikos* 81: 217–228.
- Saino, N. et al. 2010. Sex allocation in yellow-legged gulls (*Larus michahellis*) depends on nutritional constraints on production of large last eggs. – *Proc. R. Soc. B* 277: 1203–1208.
- Saino, N. et al. 2011. Antioxidant defenses predict long-term survival in a passerine bird. – *PLoS One* 6: e19593.
- Saino, N. et al. 2014. A tradeoff between reproduction and feather growth in the barn swallow (*Hirundo rustica*). – *PLoS One* 9: e96428.
- Santema, P. and Kempenaers, B. 2018. Complete brood failure in an altricial bird is almost always associated with the sudden and permanent disappearance of a parent. – *J. Anim. Ecol.* 87: 1239–1250.
- Sanz, J. J. 1996. Effect of food availability on incubation period in the pied flycatcher (*Ficedula hypoleuca*). – *Auk* 113: 249–253.
- Schoech, S. J. 1996. The effect of supplemental food on body condition and the timing of reproduction in a cooperative breeder, the Florida scrub-jay. – *Condor* 98: 234–244.
- Siikamäki, P. 1998. Limitation of reproductive success by food availability and breeding time in pied flycatchers. – *Ecology* 79: 1789–1796.
- Soler, J. J. et al. 2003. Tradeoff between immunocompetence and growth in magpies: an experimental study. – *Proc. R. Soc. B* 270: 241–248.
- Stearns, S. C. 1992. The evolution of life histories. – Oxford Univ. Press.
- Székely, T. et al. 1996. An evolutionary approach to offspring desertion in birds. – In: Nolan, V. and Ketterson, E. D. (eds), *Current ornithology*, vol. 13. Springer, pp. 271–330.
- Tella, J. L. et al. 1996. Seasonal and interannual variations in the sex-ratio of lesser kestrel *Falco naumanni* broods. – *Ibis* 138: 342–345.
- Tschirren, B. and Richner, H. 2006. Parasites shape the optimal investment in immunity. – *Proc. R. Soc. B* 273: 1773–1777.
- Tschirren, B. et al. 2003. Sexual dimorphism in susceptibility to parasites and cell-mediated immunity in great tit nestlings. – *J. Anim. Ecol.* 72: 839–845.
- van Noordwijk, A. J. and de Jong, G. 1986. Acquisition and allocation of resources: their influence on variation in life-history tactics. – *Am. Nat.* 128: 137–142.
- Wagner, R. H. and Danchin, E. 2010. A taxonomy of biological information. – *Oikos* 119: 203–209.
- Weiser, E. L. et al. 2018. Life-history tradeoffs revealed by seasonal declines in reproductive traits of arctic-breeding shorebirds. – *J. Avian Biol.* 49: e01531.
- West, S. A. and Sheldon, B. C. 2002. Constraints in the evolution of facultative sex ratio adjustment. – *Science* 295: 1685–1688.
- West, S. A. et al. 2000. The benefits of allocating sex. – *Science* 290: 288–290.
- Wiebe, K. L. and Bortolotti, G. R. 1992. Facultative sex ratio manipulation in American kestrels. – *Behav. Ecol. Sociobiol.* 30: 379–386.
- Wiebe, K. L. and Bortolotti, G. R. 1995. Egg size and clutch size in the reproductive investment of American kestrels. – *J. Zool.* 237: 285–301.
- Williams, T. D. 1994. Intraspecific variation in egg size and egg composition: effects on offspring fitness. – *Biol. Rev.* 68: 35–59.
- Wiggins, D. A. et al. 1994. Correlates of clutch desertion by female collared flycatchers *Ficedula albicollis*. – *J. Avian Biol.* 25: 93–97.
- Ydenberg, R. C. 1994. The behavioral ecology of provisioning in birds. – *Ecoscience* 1: 1–14.
- Yorio, P. and Boersma, P. D. 1994. Causes of nest desertion during incubation in the Magellanic penguin (*Spheniscus magellanicus*). – *Condor* 96: 1076–1083.
- Zuberogoitia, I. et al. 2018. Moults in birds of prey: a review of current knowledge and future challenges for research. – *Ardeola* 65: 183–207.

Supplementary material (available online as Appendix oik-06067 at <www.oikosjournal.org/appendix/oik-06067>). Appendix 1.