

Benefits of extra food to reproduction depend on maternal condition

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2

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15

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17

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20

1 **Benefits of extra food to reproduction depend on** 2 **maternal condition**

3

4 **Abstract**

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

27

28 **Keywords:** body condition, egg size, food limitation, food provisioning, income breeding, moult-
29 breeding overlap, offspring development, oxidative status, sex allocation

30

31 **Introduction**

32

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

43 The relevance of food limitation during reproduction for population dynamics can be
44 assessed by analysing the effects of resource availability on breeding success, or via experimental
45 manipulation (removal or addition) of food resources. The most widespread experimental approach
46 to investigate the extent to which reproduction is limited by food resources, and to highlight the
47 resulting life-history trade-offs, is to provide extra food to breeders, while concomitantly assessing
48 variation in reproductive investment and output of individuals receiving the extra food compared to
49 unsupplemented controls (reviews in Martin 1987, Boutin 1990). Among vertebrates, birds have
50 been the favourite subject of food supplementation experiments during breeding (Martin 1987,
51 Boutin 1990, Ruffino et al. 2014). In spite of broad differences in food provisioning protocols and
52 of the heterogeneity of effects among studies, **which may be partly due to variable background**
53 **ecological conditions (in terms of e.g. food availability) during the experiments** (Ruffino et al.
54 2014), individuals receiving extra food generally achieved reproductive benefits relative to controls,
55 indicating that most bird populations are limited by food availability during the energy-demanding
56 reproductive period (Martin 1987, Boutin 1990, Ruffino et al. 2014). These benefits include

57 advancing egg laying (Meijer and Drent 1999, Aparicio and Bonal 2002), laying heavier eggs
58 and/or larger clutches (Wiebe and Bortolotti 1995, Korpimäki and Wiehn 1998, Karell et al. 2008,
59 Saino et al. 2010), and enjoying improved nestling growth and survival (Dewey and Kennedy 2001,
60 Hipkiss et al. 2002).

61 Besides breeding output, extra food could affect parental condition. Food-supplemented
62 parents may indeed spare energy resources that are otherwise required for self-maintenance and
63 offspring provisioning, or directly use extra food to enhance their own survival prospects. Extra
64 food may improve parental body condition (Garcia et al. 1993, Schoech 1996, Cucco and
65 Malacarne 1997, Dewey and Kennedy 2001) and physiological state, in terms of e.g. immune
66 system functioning or oxidative status (Karell et al. 2008, Alan and McWilliams 2013, Fletcher et
67 al. 2013, Giordano et al. 2015). For instance, extra food may lower oxidative damage by reducing
68 physical activity for self-provisioning (Giordano et al. 2015). Moreover, food provisioning may
69 affect the timing and extent of feather moult, a highly energy-demanding process in the avian life
70 cycle (Murphy 1996), and a reduction of the costs of the overlap between moult and competing
71 activities, such as reproduction and migration (Siikamäki 1998, Danner et al. 2014).

72 In general, it may be expected that the advantages provided by extra food vary according to
73 the resource allocation and consumption decisions that parents adopt during the breeding season
74 (Roff 1992, Stearns 1992). For instance, breeding success of ‘capital breeders’ (whose reproduction
75 relies on energy stored in advance of breeding; Jönsson 1997) may show limited sensitivity to extra
76 food provisioning during the reproductive period, whereas that of ‘income breeders’ (which do not
77 accumulate reserves prior to breeding and fuel reproduction with concurrent energy intake) should
78 be more positively affected (Meijer and Drent 1999). Similarly, the behavioural response to food
79 supplementation by parents may vary between species, populations or individuals, depending on
80 which strategy maximises lifetime reproductive success under specific environmental contexts (e.g.
81 high or low background prey availability) or physiological constraints (Kacelnik and Cuthill 1990,
82 Ydenberg 1994, Markman et al. 2002). On the one hand, providing parents with extra food may

83 reduce the amount of resources delivered to the progeny, reducing reproductive costs and enhancing
84 parental residual reproductive value, while offspring quality and breeding success are unaltered
85 (Dawson and Bortolotti 2002). On the other hand, extra food may not reduce offspring provisioning
86 rates with natural food items, markedly increasing fledging success (Gonzalez et al. 2006).

87 Finally, whenever sexes differ in their susceptibility to harsh rearing environments, parents
88 may adaptively tune the sex ratio of their offspring in relation to extrinsic conditions (West et al.
89 2000, West and Sheldon 2002). Indeed, nutritional constraints may affect avian sex allocation
90 (Wiebe and Bortolotti 1992, Korpimäki et al. 2000, Saino et al. 2010), with mothers biasing the sex
91 ratio of their clutches towards the larger sex, which is more susceptible to harsh rearing
92 environments, when food resources are abundant (Wiebe and Bortolotti 1992, Nager et al. 1999,
93 Korpimäki et al 2000).

94 In this study of the lesser kestrel (*Falco naumanni*), a small (ca. 120 g), sexually dimorphic,
95 cavity-nesting diurnal raptor with biparental care of the progeny (Cramp 1998), we provided extra
96 food to breeders from the onset of egg laying to the early nestling-rearing period, and assessed the
97 effects of food supplementation on different short-term fitness components, such as: 1) parental
98 body condition and oxidative status (in terms of plasma non-enzymatic total antioxidant capacity,
99 TAC, and total oxidant status, TOS; Erel 2004, 2005); 2) moult timing and extent (lesser kestrels
100 may initiate the annual moult of primary feathers during reproduction; Cramp 1998, Zuberogoitia et
101 al. 2018); 3) breeding performance, including egg and clutch characteristics (egg mass, clutch size,
102 hatching success, duration of the incubation period), biparental nest desertion (i.e. the abandonment
103 of eggs and/or nestlings by both parents, leading to reproductive failure for the current breeding
104 season; Székely et al. 1996), offspring growth and mortality; 4) patterns of primary sex allocation
105 and sex-biased offspring mortality. We expected: 1) an overall positive effect of food
106 supplementation on parental condition and oxidative status (increased TAC and/or decreased TOS);
107 2) earlier onset of annual moult and/or faster primary feathers growth among food-supplemented
108 individuals compared to controls; 3) extra food to have an overall positive effect on breeding

109 performance (Ruffino et al. 2014) and to shorten incubation (Sanz 1996), as reduced self-
110 provisioning needs of food-supplemented parents may induce them to spend more time incubating
111 eggs compared to controls. In the sexually-size dimorphic lesser kestrel (males are ca. 15 % lighter
112 than females; Cramp 1998, Donázar et al. 1992), we might also expect 4) food-supplemented
113 females to lay female-biased clutches and/or raise female-biased broods (Korpimäki et al. 2000; but
114 see Aparicio and Cordero 2001).

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

120

121 **Material and methods**

122

123 *Study species, study area and general field procedures*

124 The lesser kestrel is a long-distance Afro-palearctic migrant (Cramp 1998). European populations
125 spend the winter mainly in the Sahel and reach the breeding areas in March-April (Cramp 1998).
126 Egg laying takes place in late April-early May, and a previous food provisioning experiment
127 beginning before egg laying revealed that food-supplemented females advanced first egg laying
128 date by ca. one week compared to control ones (Aparicio and Bonal 2002), suggesting that egg
129 laying may be food-limited. Females lay clutches of 3-5 eggs with a 2-3 days laying interval
130 between consecutive eggs. Eggs are incubated for ca. 30 days by both parents. Altricial nestlings
131 hatch asynchronously, generating strong size hierarchies among nestmates, with last-hatched, low-
132 ranking nestlings often dying when resources are insufficient (Aparicio 1997). Fledging occurs at
133 ca. 40 days post-hatching. Lesser kestrels feed mainly on invertebrates (Orthoptera, Coleoptera),
134 lizards (chiefly *Podarcis siculus*) and small rodents (voles *Microtus* spp.) (Cramp 1998, Rodríguez
135 et al. 2010, Catry et al. 2016, Di Maggio et al. 2018) that are captured in open farmland or grassland
136 areas surrounding breeding colonies (Cecere et al. 2018). Both parents contribute to rearing
137 nestlings (Cramp 1998). During breeding, some adults initiate their complete annual moult by
138 shedding a few primary feathers (usually between 1 and 3 feathers, mostly P4-P6; primaries
139 numbered descendantly) (Cramp 1998; see also Zuberogoitia et al. 2018).

140 The study was carried out during April-July 2016 in the Matera (Southern Italy; 40°67' N,
141 16°60' E) colony (ca. 1000 pairs, La Gioia et al. 2017). In this colony, many pairs breed in specially
142 designed concrete nestboxes (external size: 30 cm height × 30 cm width × 37 cm length; entrance
143 hole diameter 65 mm) with wooden front and rear panels (see Podofillini et al. 2018 for further
144 details of nestboxes). For the present study, we relied on 209 nestboxes that were checked three
145 times a week during the entire breeding season (late April - end July) to determine the onset of egg
146 laying, egg hatching, duration of the incubation period, nestling body mass, morphology, and

147 mortality. Eggs were weighted using a digital scale (accuracy 0.1 g) and individually marked using
148 a non-toxic black marker to record the laying sequence. In those cases when two (or more) eggs
149 were found in a same nestbox during the same monitoring session, we coded each egg using their
150 mean laying order value (e.g. in the case of uncertainty between the fourth and the fifth egg, we
151 coded both eggs as 4.5). Duration of the incubation period was expressed as the difference (in days)
152 between the day of hatching of the first egg and the day of laying of the first egg in a clutch (laying
153 date hereafter).

154 After hatching of the first egg, each nestbox was checked five times to assess nestling
155 growth. Over this period, nestbox monitoring sessions occurred at an average of 0.8 (range 0-3), 3.0
156 (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
157 nestboxes after the fifth session because nestlings may start wandering outside nestboxes when ca.
158 15 days old, making monitoring difficult and increasing the risk of inducing premature fledging
159 (Podofillini et al. 2018). Nestling body mass was recorded during all monitoring sessions, tarsus
160 and forearm length (the latter measured from the front of the folded wrist to the proximal end of the
161 ulna) were recorded at the fourth monitoring session, and the length of primary feather P8 (a
162 measure of nestling feather growth) was recorded at the fifth monitoring session (it could not be
163 accurately recorded at earlier sessions). Nestlings were ranked according to hatch order, or to body
164 mass (assigning the higher rank to the heavier nestling) when two or more newly hatched nestlings
165 were found on the same monitoring session (see Podofillini et al. 2018). The first hatched nestling
166 was assigned the highest rank (i.e. rank 1). During the first four monitoring sessions, we recorded
167 the intensity of infestation by *Carnus hemapterus*, a common blood-sucking dipteran ectoparasite of
168 cavity-nesting birds (Capelle and Whitworth 1973). Ectoparasite infestation was assessed on each
169 nestling for three body districts (interclavicular depression and right and left underwings) on a 0-3
170 scale (0: no ectoparasites, 1: 1–3 flies, 2: 4–6 flies and 3: > 6 flies). Nestling ectoparasite load was
171 expressed as the mean value of ectoparasite infestation across the three districts (see Podofillini et
172 al. 2018). At the fourth monitoring session, a small (ca. 200 μ l) blood sample was collected in

173 capillary tubes by puncturing the brachial vein with sterile needles. Blood was kept at -20°C and
174 later used to molecularly determine sex (according to Griffiths et al. 1998).

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

184 Starting from ca. 10-15 days before the expected time of hatching, adults were captured
185 opportunistically by hand in the nestbox or by nestbox traps while brooding their eggs or feeding
186 newly hatched nestlings. We captured ca. 80 % of the adults breeding in experimental nestboxes
187 (see Statistical analyses). Upon capture, birds were individually marked, and body mass (0.1 g) and
188 keel length (using a dial calliper, accuracy 0.1 mm) were recorded. **As an index of body condition,**
189 **we used the scaled mass index (SMI hereafter), which standardizes body mass at a fixed value**
190 **of a linear body measurement (keel length in our case) based on the scaling relationship**
191 **between mass and length (Peig and Green 2009, 2010). Body mass and keel length were**
192 **moderately positively correlated in both sexes; females: $r = 0.27$, $p = 0.016$, $n = 82$; males: $r =$**
193 **0.33 , $p = 0.004$, $n = 74$). As the scaling exponent significantly differed between the sexes**
194 **(Supplementary material Appendix 1, Table A1), SMI was computed for each sex separately.**
195 We recorded moult status by inspecting flight feathers of the right wing (moult was mostly
196 symmetrical; our unpubl. data). When growing/newly grown primary feathers were found, we
197 measured their length using a ruler (accuracy 1 mm); in case of a shed primary feather with no signs
198 of quill growth, we recorded a value of 0. Moult status was expressed as moult initiation (i.e.

199 whether an individual had begun moulting, including the presence of shed feathers, or not) and total
200 moult investment. Total moult investment was assumed to reflect the total amount of resources
201 invested in the synthesis of new feathers. It was expressed as the sum of the length of all growing
202 feathers, and was assigned a value of 0 if no sign of moult was detected or if feathers were shed but
203 had not yet grown (i.e. no resources allocated yet to new feather synthesis). Finally, for each
204 individual we collected ca. 500 μ l of blood into microhematocrit capillary tubes by puncturing the
205 brachial vein using a sterile needle. To separate plasma from blood cells, two capillary tubes per
206 individual were centrifuged (11500 rpm \times 10 min) within 4 hours of sampling. Plasma was then
207 stored at -20° C for later biochemical assays.

208

209 *Food supplementation*

210 We alternately assigned each nestbox where an egg was found to a food supplementation or a
211 control treatment. Breeding pairs were supplemented with commercial white laboratory mice (*Mus*
212 *musculus*, ca. 20 g each) [Rapax Mangimi, Santo Stino di Livenza (VE), Italy] that were placed
213 within the nestbox (at the rear end). We provided three mice every two days during the egg laying
214 period and after hatching, and one mouse every two days during the incubation period (**visits were**
215 **reduced during incubation to limit disturbance to brooding adults**). In the vast majority of
216 cases, mice disappeared between consecutive monitoring sessions. Although we could not directly
217 assess mice consumption by the target breeding pair, the consumption of extra food was confirmed
218 by regularly observing regurgitated pellets containing white fur within nestboxes where mice were
219 placed. Food supplementation ceased when nestlings were ca. 8 days old (i.e. at the fourth
220 monitoring session) because by the time of the subsequent nest visit (14-18 days old) they may start
221 wandering outside nestboxes (see above), where they are fed by parents, and we could not provide
222 food outside nestboxes (as we could not control whether it was actually consumed by the target
223 individuals or by other birds). Overall, each food-supplemented pair received ca. 40 mice (ca. 800 g
224 of extra food). To standardize disturbance, control nestboxes were inspected in exactly the same

225 way and with the same frequency as those receiving the extra food, simulating mice insertion into
226 the nestbox. The lesser kestrel performs intensive mate-feeding (Cramp 1998, Donázar et al. 1992):
227 before and during egg laying/incubation, the male feeds its partner, and deposits prey within the
228 nest cavity for later consumption by the female if mate is absent (pers. obs.; Cramp 1998). Hence,
229 placing extra food within the nestbox mimicked a natural condition and assured that only the target
230 breeding female received most of the extra food, at least during egg laying and early incubation,
231 avoiding common pitfalls of food provisioning experiments (where target individuals may not
232 actually consume the extra food; Ruffino et al. 2014). During nestling rearing, parents may have
233 used the extra food both to feed themselves or to provision their nestlings.

234

235 *Oxidative status of breeding adults*

236 The oxidative status of individuals reflects the balance between circulating antioxidants and pro-
237 oxidants (e.g. free radicals), deriving from normal physiological activity, pathological states, or the
238 external environment (Halliwell and Gutteridge 2007). Pro-oxidants may cause oxidative damage to
239 biomolecules, cells and tissues, impairing organismal functions (Halliwell and Gutteridge 2007).
240 Oxidative stress arises whenever an organism's antioxidant defences are insufficient to counteract
241 oxidative damage (Halliwell and Gutteridge 2007). High levels of antioxidants and low levels of
242 pro-oxidants are regarded as indicators of good health state and positively predict fitness (e.g.
243 survival; Bize et al. 2008, Saino et al. 2011). Food is a major source of antioxidants such as
244 vitamins and carotenoids, as well as of substances (e.g. proteins) that do not have direct antioxidant
245 activity, but may affect an organism's resistance to oxidative stress (Halliwell and Gutteridge 2007,
246 Costantini 2014). Moreover, high food availability might reduce the oxidative costs of foraging for
247 self and offspring provisioning (Costantini 2014, Giordano et al. 2015). Hence, extra food may
248 positively affect oxidative status through different mechanisms, leading to high levels of
249 antioxidants/low levels of pro-oxidants. As proxies of the oxidative status of breeding adults, we
250 measured TAC through a global test of blood non-enzymatic antioxidant capacity, and TOS,

251 reflecting the overall concentration of circulating pro-oxidants in the blood flow. High TAC
252 indicates high antioxidant capacity, while high TOS indicate high levels of circulating pro-oxidants
253 and an increased risk of oxidative damage.

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

261 TOS was measured according to Erel (2005). Briefly, 20 μl of plasma were added to 237 μl
262 of a ferrous ion-*o*-dianisidine and Xylenol Orange solution. Oxidant molecules oxidise the ferrous
263 ion to the ferric ion, which reacts with Xylenol Orange to give a coloured (blue) complex. Colour
264 intensity was measured by a spectrophotometer at an absorbance of $\lambda = 535 \text{ nm}$ and it is
265 proportional to the total amount of oxidant agents in the plasma. The assay was calibrated by
266 drawing a standard curve with serial dilution of hydrogen peroxide (H_2O_2) and the results were
267 expressed as $\text{nM H}_2\text{O}_2$ equivalent ml^{-1} .

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

273

274 *Statistical analyses*

275 To investigate the effects of food supplementation (0 = control, 1 = food-supplemented) on fitness,
276 we relied on generalized linear, linear mixed or generalized linear mixed models (GLMs, LMMs or

277 GLMMs, respectively), as summarized in Table 1. Below we provide details on reasons for
278 including specific predictors in models and on coding of dichotomous variables.

279 To control for intra-seasonal variation in SMI, oxidative and moult status (birds were
280 captured over 38 days, during both incubation and nestling-rearing phases), in GLMs of these
281 variables we included either breeding stage (0 = incubation, 1 = nestling rearing) or sampling date
282 (Julian date; day 1 = January 1) as predictors, choosing the one which better fitted the data
283 (Supplementary material Appendix 1, Table A2) (selected predictors are shown in Table 1). Due to
284 sex differences in body mass [mean body mass: females = 155 g (11 s.d.), males = 135 g (10 s.d.), n
285 = 82 and 76, respectively; $t_{156} = 12.1$, $p < 0.001$; see also Donázar et al. 1992], and consequently in
286 SMI (see Results), in GLMs where SMI was included as a predictor together with sex (0 = female,
287 1 = male), we centred SMI within each sex category to eliminate the possibility of spurious SMI/sex
288 effects on dependent variables (e.g. Lewin and Mitchell 1999). In GLMs of body condition and
289 oxidative status we included total moult investment among predictors, as moult might affect
290 physiological state (e.g. Hemborg and Lundberg 1998, Rubolini et al. 2002, Costantini 2014).
291 Although adults were food-supplemented for a variable number of days before sampling [mean
292 value = 27 days (s.d. 7)], there was no evidence that such variation affected food supplementation
293 effects on SMI, oxidative and moult status (Supplementary material Appendix 1, Table A3).

294 Owing to the intrinsic association between laying order and clutch size (only large clutches
295 can have large values of laying order), in LMMs of egg mass and hatching success we coded laying
296 order as relative laying order, assigning value 1 to the first egg and 3 to the last one. Intermediate
297 eggs were assigned values between 1 and 3 according to clutch size (e.g. eggs from a 3-egg clutch
298 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
299 LMMs we included the squared term of relative laying order because the change in egg mass along
300 the laying sequence was best described by a quadratic function of relative laying order
301 (Supplementary material Appendix 1, Table A4). Because food supplementation began after laying
302 of the first egg, the mass of the first egg could not be affected by food supplementation. The effect

303 of food supplementation on egg mass was therefore evaluated as the food supplementation \times
304 relative laying order interaction.

305 The GLM of nest desertion (0 = nest not deserted, 1 = nest deserted) was fitted by including
306 both female and male SMI as a predictor (in separate models by sex): although desertion in related
307 species is always initiated by females (see '*Study species, study area and general field*
308 *procedures*'), we cannot rule out the possibility that it was initiated by males and depended on male
309 (rather than female) condition.

310 Primary sex ratio (PSR) was expressed as the ratio between number of sons and brood size,
311 computed for the subset of nests where all eggs hatched. To investigate whether sex allocation
312 varied along the laying sequence according to food supplementation, we fitted a binomial GLMM
313 of nestling sex and tested the food supplementation \times rank interaction. Because we could not assign
314 most of the nestlings to their egg of origin, we assumed that laying order was closely reflected by
315 nestling rank, an assumption supported by the strong correlation between these variables (for
316 nestlings from eggs with known laying order; $r = 0.86$, $n = 49$).

317 In LMMs of nestling body mass (recorded at four monitoring sessions) and morphology
318 (tarsus, forearm and feather length recorded at a single session), we included ectoparasite load
319 among predictors (see Podofillini et al. 2018). Age effects were controlled for by including the
320 linear term of age, as growth is mostly linear during the sampled age range (see Podofillini et al.
321 2018). Nestling mortality was evaluated as a nestling being alive (0) or dead (1) by the fifth
322 monitoring session. Nestlings that disappeared before they were able to move outside nestboxes
323 were assumed to be dead, even if no remains were found (likely removed/eaten by
324 parents/nestmates). In tarsus, forearm and feather length LMMs, and in the mortality GLMM, brood
325 size and ectoparasite load were the maximum values recorded across all monitoring sessions
326 (Podofillini et al. 2018).

327 Due to weak sex differences in body size (Supplementary material Appendix 1, Table A5;
328 see Podofillini et al. 2018), we did not consider sex in the analyses of nestling body mass,

329 morphology, and mortality to ensure the largest possible sample size (some nestlings could not be
330 sexed due to premature death/disappearance).

331 Differential effects of food supplementation on target traits according to other model
332 predictors were tested by including two-way interactions between food supplementation and
333 additional predictors in initial models. In the nestling body mass LMM, we also included the rank \times
334 age interaction (accounting for differential growth of nestlings according to rank; see Podofillini et
335 al. 2018). Final models included all main effects and significant interaction terms, while non-
336 significant ($p > 0.05$) interactions were removed in a single step. Analyses were run in R 3.3.3 (R
337 Core Team 2017). LMMs/GLMMs were fitted using the *lme4* package (Bates et al. 2014). Non-
338 Gaussian models were not overdispersed (see Results). GLMMs overdispersion was computed
339 using the *blme4* package (Korner-Nievergelt et al. 2015). When GLM residuals showed a highly
340 skewed distribution, significance was calculated by randomization (Manly 1991) (*permuco*
341 package; Frossard and Renaud 2018) (see Table 1). For all models, we report R^2 as computed by the
342 *rsq* (GLMs) and *r2glmm* (GLMMs) packages (Dabao 2017, Jaeger et al. 2017). To facilitate
343 comparisons of food supplementation effects between different models, and to compare effects
344 between different predictors, we report the absolute value of Pearson's r (obtained from the partial
345 correlation/semi-partial R^2 values returned by the *rsq* and *r2glmm* packages).

346 We considered data from 100 nestboxes (50 food-supplemented, 50 controls), in which we
347 found 423 eggs and captured 160 adults [80 food-supplemented (36 males, 44 females), 80 controls
348 (42 males, 38 females)]. To ensure the largest possible sample size in egg and clutch characteristics
349 models, if SMI was not significant we reported results while excluding this variable. Twenty-two
350 clutches/broods (out of 100) were deserted (13/50 controls, 9/50 food-supplemented). Among these,
351 16 were deserted at the clutch stage. We recorded data for 288 nestlings from 42 food-supplemented
352 and 43 control broods. Sample size may vary between analyses because of missing data.

353

354

355 **Results**

356

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

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

363 Food supplementation increased resource allocation to primary feather moult. Although the
364 proportion of individuals initiating moult did not significantly differ between treatments [controls =
365 0.27 (19/70); food-supplemented = 0.38 (28/74), Table 2], the increase of total moult investment
366 with sampling date was significantly larger for food-supplemented individuals [estimate = 4.17
367 (0.50 s.e.) mm/day] than controls [1.71 (0.43 s.e.) mm/day] (food supplementation \times sampling date
368 interaction, Table 2, Fig. 2). Besides, females initiated moult much more frequently (0.52) than
369 males (0.13) (Table 2), and the probability of initiating moult markedly increased with sampling
370 date (Table 2). However, the total moult investment, after accounting for the strong sampling date
371 effect, did not significantly differ between the sexes (Table 2).

372

373 *Effects of food supplementation on egg mass and hatching success*

374 Food supplementation significantly mitigated the (non-linear) decline in egg mass along the laying
375 sequence observed in control clutches (food supplementation \times relative laying order interaction,
376 Table 3), food-supplemented females producing larger last-laid eggs compared to controls (Fig. 3)
377 (see Supplementary material Appendix 1, Table A6 for details of egg mass models selection). The
378 predicted egg mass among last eggs laid by food-supplemented females was 14.58 g, while it was
379 13.93 g among control females (Fig. 3). Egg mass peaked at relative laying order 0.96 among

380 control (implying a continuous decline within the actual relative laying order values) and 1.54
381 among food-supplemented females, respectively (Fig. 3).

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

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

397

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

399 Extra food did not significantly affect clutch size [food-supplemented females = 4.3 (0.7 s.d.),
400 controls = 4.2 (0.7 s.d.), n = 50 in both groups] and duration of the incubation period [food-
401 supplemented clutches = 32.6 d (2.4 s.d.), controls = 32.5 (2.3 s.d.), n = 41 and 43, respectively],
402 the latter becoming significantly shorter in late-laid clutches compared to early-laid ones (Table 3).

403 Body condition significantly mediated the effects of food supplementation on the likelihood
404 of nest desertion (food supplementation \times female SMI interaction, Table 4): control females in good
405 body condition were less likely to abandon their nests than those with poor body condition [estimate

406 = -0.147 (0.065 s.e.)], while this was not the case among food-supplemented females [estimate =
407 0.009 (0.044 s.e.)] (Fig. 5). Hence, in the food-supplemented group, females with low SMI were as
408 likely to desert their nest as those with high SMI (Fig. 5). This analysis could not be performed by
409 including male (instead of female) SMI because we could obtain male SMI data for 5 deserted nests
410 only, all of which were controls. However, when restricting the analyses to control clutches/broods,
411 female SMI significantly negatively predicted the probability of nest desertion, while male SMI did
412 not (Supplementary material Appendix 1, Table A9).

413

414 *Effects of food supplementation on sex allocation*

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

419 When considering the entire set of sexed nestlings, the proportion of males was 0.48 ($n =$
420 123 males and 130 females), again not significantly deviating from 0.5 (intercept-only binomial
421 GLMM with clutch identity as a random effect, $Z = 0.46$, $p = 0.64$). Food supplementation did not
422 significantly affect sex allocation along the laying sequence [food supplementation \times nestling rank
423 interaction, estimate = -0.31 (0.24 s.e.), $Z = -1.29$, $p = 0.20$]. The final model disclosed a strong sex
424 bias along the laying sequence (effect of rank, Table 4), with a female bias among high-ranking
425 nestlings (hatched from first-laid eggs) and a male bias among low-ranking nestlings (hatched from
426 last-laid eggs). A similar tendency emerged also when analysing those nestlings whose egg of
427 origin was known (Supplementary material Appendix 1, Table A10). In this subset, there was no
428 significant difference in mass between male and female eggs, and no significant difference in mass
429 allocation to male and female eggs according to food supplementation (Supplementary material
430 Appendix 1, Table A11).

431

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

433 Food supplementation significantly improved nestlings' body mass growth, and significantly
434 mitigated body mass loss induced by haematophagous ectoparasites (Table 5, Fig. 6): the mass
435 increase of food-supplemented nestlings was ca. 10 % greater than controls, a significant difference
436 (food supplementation \times age interaction) [food supplemented: 7.17 (0.13 s.e.) g/d; controls: 6.47
437 (0.12 s.e.) g/d; Table 5], and body mass significantly decreased with parasite load among control
438 nestlings [estimate: -2.62 (0.89 s.e.)], whereas this was not the case among food-supplemented ones
439 [0.16 (0.85 s.e.)] (food supplementation \times ectoparasite load interaction, Table 5, Fig. 6). Besides,
440 high ranking nestlings were significantly larger and grew faster than low ranking ones (Table 5),
441 nestlings from late clutches were significantly lighter than those from early clutches, and those from
442 larger clutches were lighter than those from smaller clutches (Table 5).

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

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

452 Overall, 31 % (44/143) control nestlings and 23 % (33/145) food-supplemented ones died by
453 16 days of age, a non-significant difference (Table 5). Mortality was considerably higher among
454 low ranking nestlings (strong positive effect of rank on mortality) and among those growing in
455 larger clutches (Table 5). Results were qualitatively similar if deserted broods were excluded
456 (Supplementary material Appendix 1, Table A12).

457

458 **Discussion**

459

460 In this study of a mesopredatory avian species, we simulated favourable environmental conditions
461 during reproduction by providing extra food to breeders, and assessed the short-term consequences
462 of food supplementation for adult conditions, resource allocation to an energy-demanding process
463 (wing feather moult) competing with breeding, breeding output, and early offspring growth. Below
464 we discuss the main findings.

465

466 *Moult-breeding overlap and extra food provisioning*

467 Although moult is mostly temporally separated from competing activities such as reproduction and
468 migration (Jenni and Winkler 1994, Barta et al. 2008), in several species, including the migratory
469 lesser kestrel, tight annual scheduling of the yearly cycle has promoted the evolution of moult-
470 breeding overlap (Hemborg and Lundberg 1998, Hemborg 1999, Zuberogoitia et al. 2018).

471 Similarly to other raptors, lesser kestrels start their annual wing feather moult when incubating,
472 females being more likely to do so than males (review in Zuberogoitia et al. 2018). Males, as in
473 most falcons, are smaller, more agile, perform extensive mate-feeding and carry most of the prey to
474 their progeny (Donázar et al. 1992, Krüger 2005): they are thus likely to pay a greater cost than
475 females for the moult-breeding overlap (Espie et al. 1996). Extra food resulted however in greater
476 moult investment in both sexes, after statistically controlling for seasonal effects on timing of
477 moult. The positive effect of food supplementation on wing feather renewal supports the idea that
478 moult-breeding overlap is costly (Hemborg and Lundberg 1998, Saino et al. 2014) and that
479 favourable environmental conditions promote a greater allocation of resources to feather renewal
480 (Espie et al. 1996, Siikamäki 1998, Danner et al. 2014). A greater resource allocation to moulting
481 feathers may either be a direct consequence of food supplementation, with birds investing extra
482 resources in new feathers' synthesis, or a consequence of lower mobility of fed individuals
483 compared to controls, which may have reduced maintenance costs and promoted feather renewal.

484

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

486 Females invested part of resources gained from the extra food in producing heavier last-laid eggs.
487 This result is in line with evidence that egg size is a plastic trait that rapidly responds to the
488 ecological conditions to which the mother is exposed to (Wiebe and Bortolotti 1995, Karell et al.
489 2008, Saino et al. 2010). Extra food led to a ca. 4 % increase in the mass of last-laid eggs compared
490 to control eggs (see also Christians 2002). Although egg size is a critical trait for offspring fitness
491 soon after hatching (Williams 1994), such a relatively minor increase in egg size did not produce
492 any significant survival/growth advantage of last hatched (low ranking) food-supplemented
493 nestlings compared to controls. The lack of detectable egg mass effects on offspring fitness could be
494 due to the moderately favourable ecological conditions in the study year (in terms of food supplies
495 and weather; authors' pers. obs.), as the effects of extra food provisioning on fitness may vary
496 according to contingent ecological conditions (e.g. Hipkiss et al. 2002, Karell et al. 2008, Ruffino et
497 al. 2014).

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

506 A similar finding emerged for the likelihood of nest desertion, which was higher for poor
507 condition control females compared to poor condition food-supplemented ones. Nest desertion is
508 widespread in birds, especially among long-lived species (Székely et al. 1996). It occurs whenever
509 the perceived costs of current reproduction for parents outweigh the expected fitness payoffs of

510 future reproduction (Kelly and Kennedy 1993, Székely et al. 1996), which may be the case under
511 harsh ecological conditions (Anderson et al. 1982, Hörnfeldt et al. 1990, Wiggins et al. 1994,
512 Oppliger et al. 1994) or among low-quality parents with poor body condition (Kelly and Kennedy
513 1993, Yorio and Boersma 1994, Wiggins et al. 1994). It may also follow from mortality of one
514 parent (Roche et al. 2010, Santema and Kempenaers 2018), which may dramatically increase the
515 costs of current reproduction for the remaining parent in biparental species (Székely et al. 1996).
516 Our results suggest that extra food alleviated the costs of reproduction for females of low
517 phenotypic quality, reducing their probability of completely failing reproduction, in accordance
518 with the hypothesis that nest desertion is the outcome of an adaptive life-history decision
519 conditional on maternal state (Székely et al. 1996).

520 Among nestlings, extra food resulted in significantly higher mass gain and increased feather
521 growth. Such an effect was most likely due to parents using the extra food to feed their nestlings, as
522 by 10-15 days post hatching nestlings are not able to swallow or split to pieces a relatively large
523 food item (mice) by themselves (Cramp 1998). It also suggests that parents did not markedly reduce
524 nestling provisioning with natural prey items. Furthermore, extra food provisioning affected
525 nestling growth dynamics in combination with ectoparasite infestation. First, it significantly
526 alleviated the negative effects of an haematophagous ectoparasite on mass gain, whereby body mass
527 significantly decreased with ectoparasite load among control nestlings but not among food-
528 supplemented ones. Second, it increased resource allocation to flight apparatus development in
529 highly parasitized nestlings compared to controls. These two results were not due to differences in
530 ectoparasite load between food-supplemented and control nestlings (Supplementary material
531 Appendix 1, Table A13). Haematophagous ectoparasites are well known to exert detrimental effects
532 on early growth dynamics, either by directly withdrawing resources (blood) or by activating the
533 immune system (Møller 1993, Merino and Potti 1995, Saino et al. 1998, Lochmiller and
534 Deerenberg 2000, Nilsson 2003, Tschirren et al. 2003). Under food limitation, parasites may impose
535 a trade-off between allocation of resources to somatic growth and immunity, diverting limiting

536 resources from somatic growth to immune defences (Saino et al. 1998, Lochmiller and Deerenberg
537 2000, Soler et al. 2003, Brommer 2004, Tschirren and Richner 2006). Extra food may relax such
538 constraints, resulting in weaker direct/indirect negative ectoparasite effects (Merino and Potti 1998,
539 Brommer et al. 2011). Furthermore, growing nestlings may respond to ectoparasites by
540 differentially allocating resources to growth of specific traits in order to increase their short-term
541 fitness prospects (Mainwaring and Hartley 2012). For instance, ectoparasite infestation may
542 promote investment in growth of feathers at the expense of mass or other skeletal traits, because an
543 earlier maturation of the flight apparatus may facilitate escape from the highly parasitized nest
544 environment to avoid detrimental ectoparasite effects (Saino et al. 1998). The observation that
545 ectoparasites significantly promoted resource allocation to growth of the flight apparatus (forearm
546 length) when provisioned with extra food is coherent with the latter suggestion.

547

548 *Other findings unrelated to extra food provisioning*

549 Non-enzymatic antioxidant defences increased during the breeding season, which may be due to
550 variation in external conditions, diet, or physiological state (Costantini et al. 2010). For instance, the
551 strong increase of ambient temperature during the breeding season (ca. 10°C increase between April
552 and July; data from <http://www.ssabasilicata.it/>) may improve flight efficiency in the lesser kestrel
553 (Hernández-Pliego et al. 2017) and reduce the oxidative costs of locomotion (e.g. Costantini et al.
554 2008), promoting mobilization/redistribution of non-enzymatic antioxidants. Seasonal changes in
555 hormone profile (Meijer and Schawbl 1989, Pereira et al. 2010) may also play a role (Costantini et
556 al. 2011, Costantini 2014), whereas this is unlikely for seasonal dietary changes (see Rodríguez et
557 al. 2010), because extra food did not significantly affect oxidative status. In addition, the strong
558 positive covariation of antioxidant defences with body condition indicates that levels of non-
559 enzymatic antioxidants may represent a reliable indicator of general physiological state and
560 individual quality (e.g. Costantini and Bonadonna 2010).

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

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

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

576

577 *Concluding remarks*

578 Our comprehensive analysis of the benefits of extra food provisioning to reproduction under natural
579 conditions suggests that parent lesser kestrels invested the extra food mainly in improving current
580 reproduction, similarly to most of the bird species studied so far (Ruffino et al. 2014), rather than
581 using it to accumulate resources (in terms of e.g. body fat or muscle fibres) for improving their
582 residual reproductive value. Indeed, parents mainly used the extra resources for laying larger eggs
583 and raising heavier/larger offspring, while the extra food did not improve their own body condition
584 or oxidative status. The increase of egg size following extra food provisioning suggests that egg
585 formation by females relies partly on resources acquired during the laying period, besides pre-
586 laying food provisioning by the male partner through courtship feeding (Donázar et al. 1992), in

587 line with an ‘income breeding’ strategy of energy storage for reproduction (Jönsson 1997, Meijer
588 and Drent 1999). **Our findings indicate that food availability during the breeding season can**
589 **limit population growth of this species.** Importantly, maternal condition appears to be a major
590 trait modulating the benefits of extra food provisioning to reproduction, whereby such benefits
591 accrued mostly to low-quality females with poor body condition. Moreover, extra food reduced the
592 costs of the moult-breeding overlap, and affected early growth trade-offs by fostering development
593 of the flight apparatus traits in response to ectoparasite infestation. To sum up, our results illustrate
594 the pervasive consequences of food limitation in natural environments for resource allocation to
595 competing energy-demanding activities (e.g. moult and reproduction), breeding output and
596 offspring development, at the same time highlighting that the negative consequences of food
597 limitation on reproductive output may be disproportionately larger for individuals of low
598 phenotypic quality.

599

600 **Data policy/repositories** – Data used in statistical analyses will be archived on Dryad upon
601 acceptance of the manuscript.

602 **Legend to figures**

603

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

609

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

618

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

627

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

633

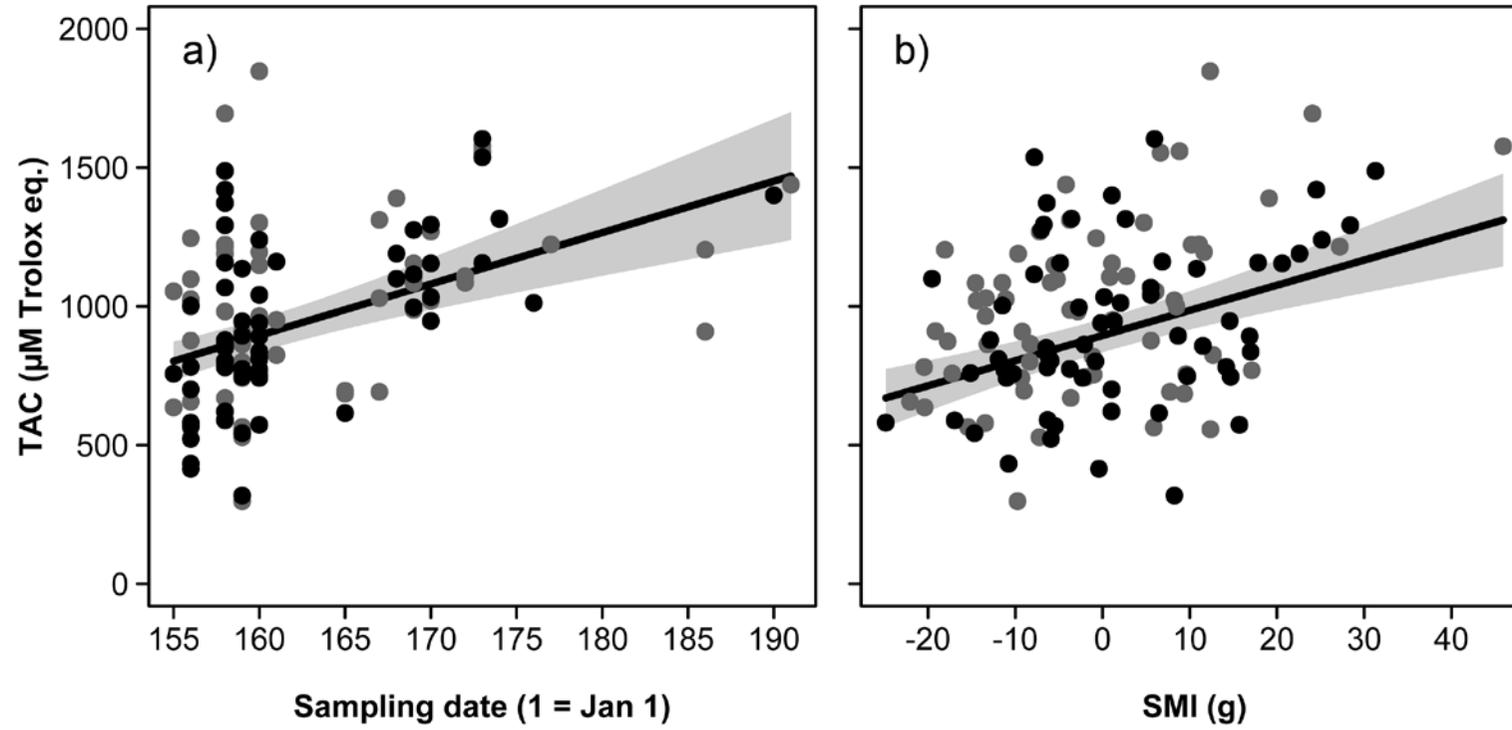
634 **Figure 5. The probability of nest desertion significantly declined with female body condition**
635 **(scaled mass index, SMI) among control females (a), but not among food-supplemented ones**
636 **(b). The fitted lines (with 95 % confidence bands) from the corresponding binomial model**
637 **reported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

639

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

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Figure 1

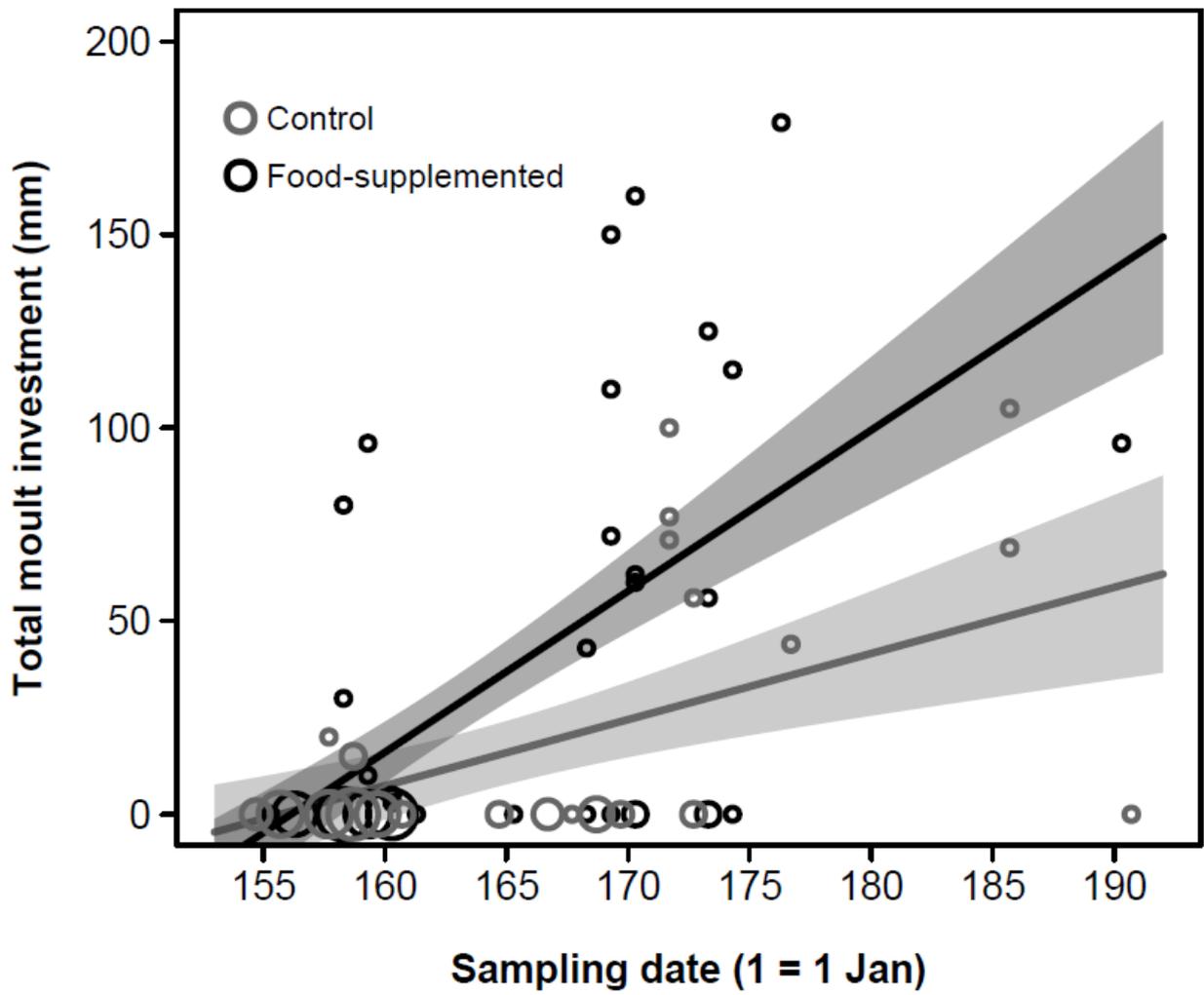


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Figure 2

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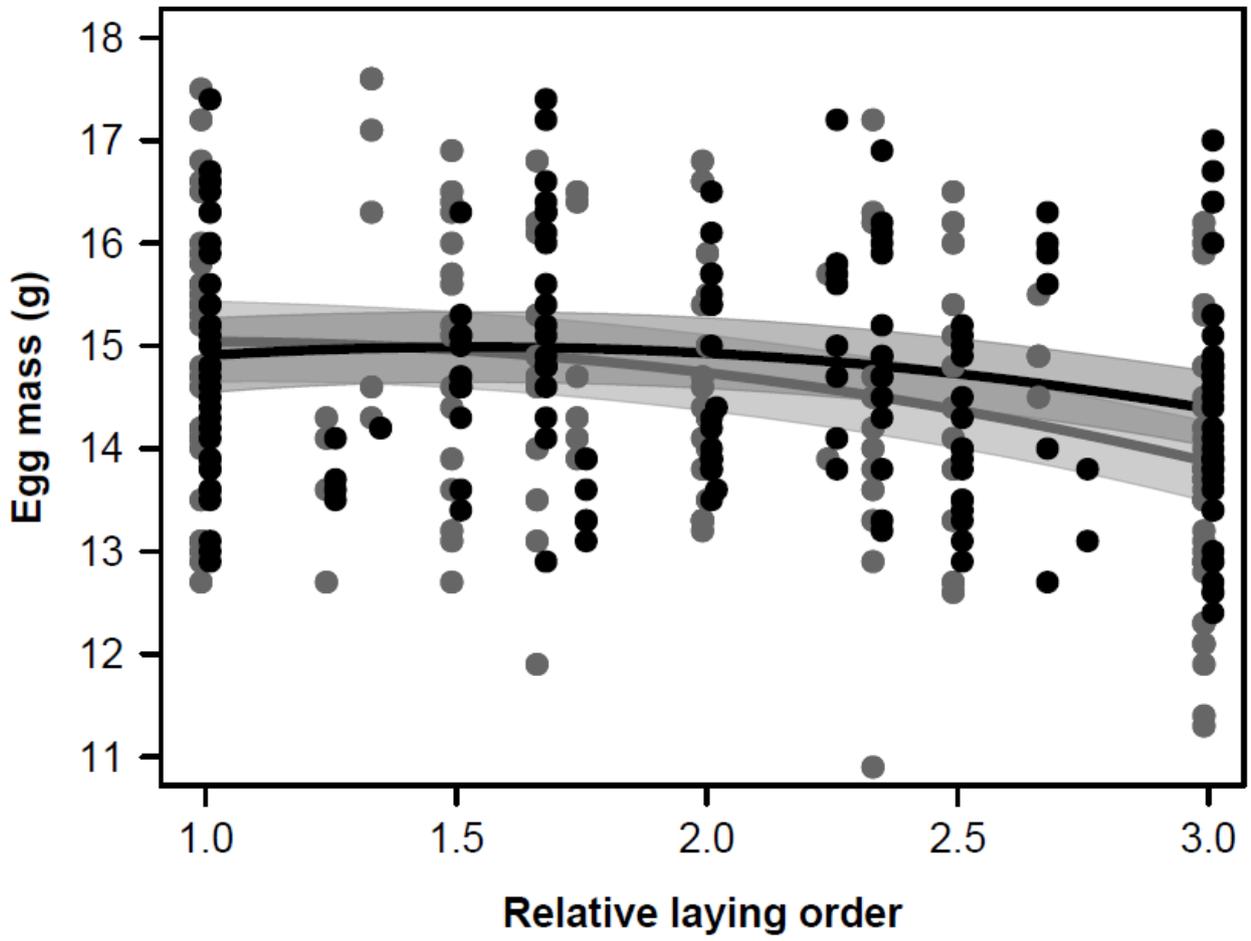


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Figure 3



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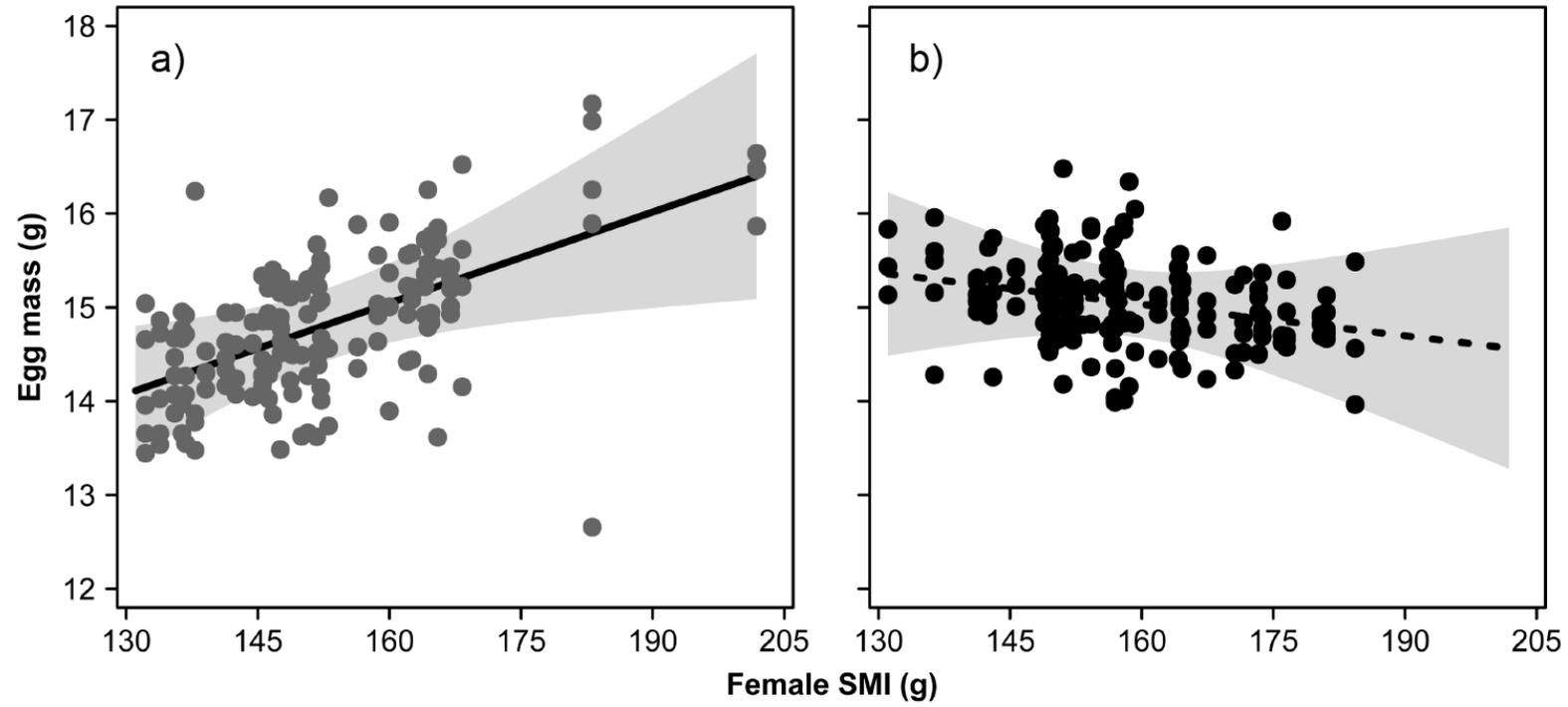
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Figure 4



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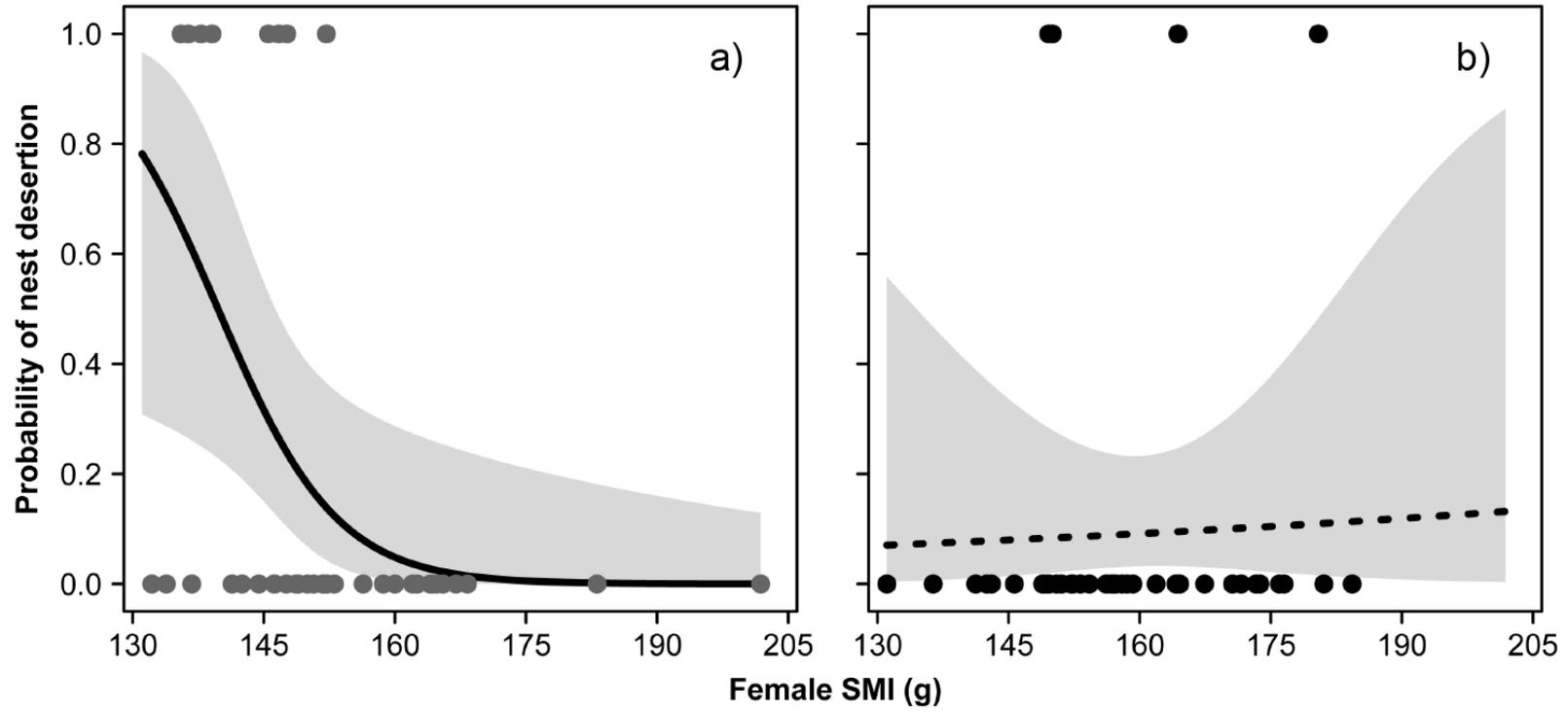
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Figure 5



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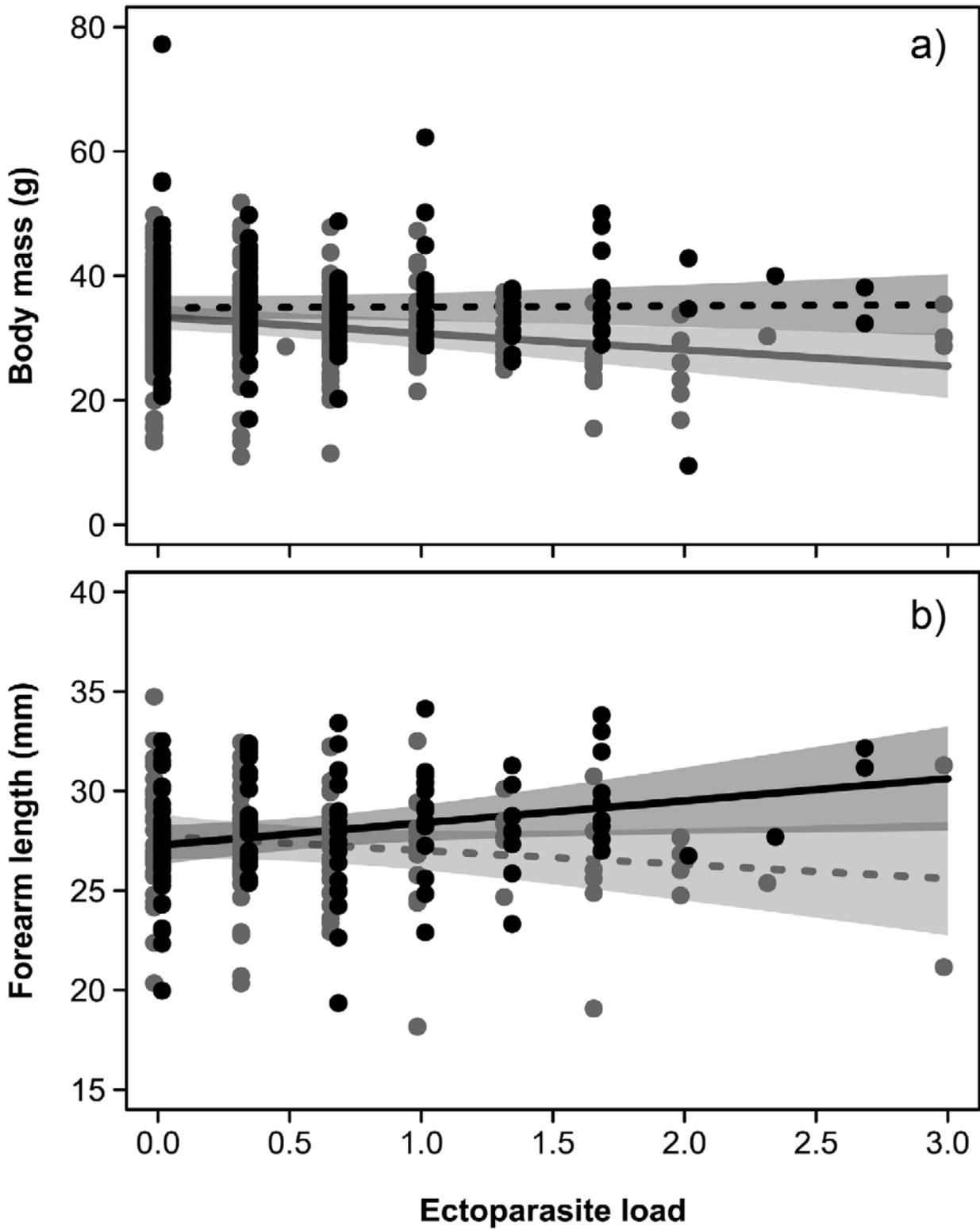
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Figure 6

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681

682

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

693

Table 1

Dependent variable	Additional predictors (confounding variables)	Random intercept effects	Error distribution	Details of fitted model	Notes
<i>Effects of food supplementation on body condition, oxidative and moult status</i>					
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
<i>Effects of food supplementation on egg mass and hatching success</i>					
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
<i>Effects of food supplementation on clutch size, duration of the incubation period, and nest desertion</i>					
Clutch size	Laying date, female SMI	-	Gaussian	Table 4	
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	
<i>Effects of food supplementation on sex allocation</i>					
Primary sex ratio (PSR)	Laying date, clutch size, female SMI	Clutch identity	Binomial	Table 4	
Nestling sex	Rank, laying date	Clutch identity	Binomial	Table 4	
<i>Effects of food supplementation on nestling body mass, morphology, and mortality</i>					
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	

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

Predictors	Estimate (s.e.)	t/Z	p	Effect size r
<i>SMI (n = 144) (R² = 0.43)</i>				
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
<i>TAC (n = 126) (R² = 0.38)</i>				
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
<i>TOS (n = 71) (R² = 0.04)</i>				
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
<i>Probability of initiating moult (n = 144)^b (R² = 0.30)</i>				
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
<i>Total moult investment (n = 144)^c (R² = 0.43)</i>				
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 (see Statistical analyses)

b: binomial GLM

c: p-values from randomization test (see Statistical analyses)

d: estimate for mean-centered covariate

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

706

Predictors	Estimate (s.e.)	F/Z	d.f.	p	Effect size r
<i>Egg mass (n = 349 eggs, n = 82 clutches) (R² = 0.30)</i>					
Food supplementation ^a	0.19 (0.25)	0.59	76	0.45	0.08
Relative laying order ^a	0.72 (0.31)	5.21	265	0.023	0.06
(Relative laying order ²) ^a	-0.28 (0.08)	13.29	265	< 0.001	0.10
Laying date	-0.01 (0.02)	0.31	77	0.58	0.05
Clutch size	-0.50 (0.18)	7.48	77	0.008	0.25
Female SMI ^a	0.01 (0.01)	0.76	76	0.39	0.09
Food supplementation × relative laying order	0.33 (0.09)	13.12	264	< 0.001	0.09
Food supplementation × female SMI	-0.04 (0.02)	5.14	75	0.026	0.23
<i>Egg hatching success (n = 351 eggs, n = 83 clutches)^b (R² = 0.03)</i>					
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; see Statistical analyses)

707

708

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

Predictors	Estimate (s.e.)	t/Z	p	Effect size r
<i>Clutch size (n = 100 clutches) (R² = 0.01)</i>				
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 ^a	-0.01 (0.01)	0.62	0.54	0.07
<i>Duration of the incubation period (n = 84 clutches)^b (R² = 0.15)</i>				
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
<i>Probability of nest desertion (n = 82 clutches) (R² = 0.19)</i>				
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
<i>PSR (n = 31 broods)^e (R² = 0.06)</i>				
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
<i>Probability of a nestling being male (n = 253 nestlings, n = 80 broods)^g (R² = 0.05)</i>				
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: estimate from a different model with smaller sample size (n = 82 clutches; see Statistical analyses)

b: p-values are from a randomization test (see Statistical analyses)

c: estimate from a different model with smaller sample size (n = 72 clutches; see Statistical analyses)

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; see Statistical analyses)

g: dispersion parameter = 1.15

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

Predictors	Estimate (s.e.)	F/Z	d.f.	p	Effect size r
<i>Body mass (n = 288 nestlings, n = 85 broods) (R² = 0.87)</i>					
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)	5.20	1, 901	0.023	0.09
Age × rank	-1.00 (0.08)	171.50	1, 806	< 0.001	0.37
<i>Tarsus length (n = 249 nestlings, n = 79 broods) (R² = 0.66)</i>					
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
<i>Forearm length (n = 250 nestlings, n = 79 broods) (R² = 0.70)</i>					
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
<i>Feather length (n = 186 nestlings, n = 69 broods) (R² = 0.61)</i>					
Food supplementation	2.10 (1.04)	4.05	1, 59	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
<i>Mortality (n = 285 nestlings, n = 85 broods)^b (R² = 0.17)</i>					
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

718 **References**

719

720 Alan, R. R. and McWilliams, S. R. 2013. Oxidative stress, circulating antioxidants, and dietary
721 preferences in songbirds. – *Comp. Biochem. Physiol.* 164: 185-193.

722

723 Anderson, D. W. et al. 1982. Brown pelicans: influence of food supply on reproduction. – *Oikos* 39:
724 23-31.

725

726 Aparicio, J. M. 1997. Cost and benefits of surplus offspring in the lesser kestrel (*Falco naumanni*).
727 – *Behav. Ecol. Sociobiol.* 41: 129–137.

728

729 Aparicio, J. M. and Bonal, R. 2002. Effects of food supplementation and habitat selection on timing
730 of lesser kestrel breeding. – *Ecology* 83: 873-877.

731

732 Aparicio, J. M. and Cordero, P. J. 2001. The effects of the minimum threshold condition for
733 breeding on offspring sex-ratio adjustment in the lesser kestrel. – *Evolution* 55: 1188-1197.

734

735 Ardia, D. R. et al. 2006. Warm temperatures lead to early onset of incubation, shorter incubation
736 periods and greater hatching asynchrony in tree swallows *Tachycineta bicolor* at the extremes of
737 their range. – *J. Avian Biol.* 37: 137-142.

738

739 Bates, D. et al. 2014. Fitting linear mixed-effects models using lme4. – *J. Stat. Softw.* 67: 1–48.

740

741 Barta, Z. et al. 2008. Optimal moult strategies in migratory birds. – *Phil. Trans. R. Soc. B* 363: 211–
742 229.

743

744 Bize, P. et al. 2008. Fecundity and survival in relation to resistance to oxidative stress in a free-
745 living bird. – *Ecology* 89: 2584–2593.

746

747 Boutin, S. 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems,
748 and the future. – *Can. J. Zool.* 68: 203-220.

749

750 Brommer, J. E. 2004. Immunocompetence and its costs during development: an experimental study
751 in blue tit nestlings. – *Proc. R. Soc. B* 271: S110-S113.

752

753 Brommer, J. E. et al. 2011. Body size and immune defense of nestling Blue Tits (*Cyanistes*
754 *caeruleus*) in response to manipulation of ectoparasites and food supply. – *Auk* 128: 556-563.

755

756 Capelle, K. J. and Whitworth, T. L. 1973. The distribution and avian hosts of *Carnus hemapterus*
757 (Diptera: Milichiidae) in North America. – *J. Med. Entomol.* 10: 525–526.

758

759 Catry, I. et al. 2016. Sexual and parent-offspring dietary segregation in a colonial raptor as revealed
760 by stable isotopes. – *J. Zool.* 299: 58-67.

761

762 Cecere, J. G. et al. 2018. Spatial segregation of foraging areas between neighbouring colonies in a
763 diurnal raptor. – *Sci. Rep.* 8: 11762.
764

765 Christians, J. K. 2002. Avian egg size: variation within species and inflexibility within individuals.
766 – *Biol. Rev.* 77: 1-26.
767

768 Costantini, D. et al. 2008. Long flights and age affect oxidative status of homing pigeons (*Columba*
769 *livia*). – *J. Exp. Biol.* 211: 377-381.
770

771 Costantini, D. and Bonadonna, F. 2010. Patterns of variation of serum oxidative stress markers in
772 two seabird species. – *Polar Res.* 29: 30-35.
773

774 Costantini, D. et al. 2010. Relationships among oxidative status, breeding conditions and life-
775 history traits in free-living Great Tits *Parus major* and Common Starlings *Sturnus vulgaris*. – *Ibis*
776 152: 793-802.
777

778 Costantini, D. et al. 2011. A meta-analysis of glucocorticoids as modulators of oxidative stress in
779 vertebrates. – *J. Comp. Physiol. B* 181: 447-456.
780

781 Costantini, D. 2014. Oxidative stress and hormesis in evolutionary ecology and physiology. A
782 marriage between mechanistic and evolutionary approaches. – Springer.
783

784 Cramp, S. 1998. The complete birds of the western Palearctic on CDROM. – Oxford University
785 Press.
786

787 Cucco, M. and Malacarne, G. 1997. The effect of supplemental food on time budget and body
788 condition in the black redstart *Phoenicurus ochruros*. – *Ardea* 85: 211-221.
789

790 Dabao, Z. 2017. A coefficient of determination for Generalized Linear Models. – *Am. Stat.* 71: 310-
791 316.
792

793 Danner, M. R. et al. 2014. Winter food limits timing of pre-alternate moult in a short-distance
794 migratory bird. – *Funct. Ecol.* 29: 259-267.
795

796 Dawson, R. and Bortolotti, G. 2002. Experimental evidence for food limitation and sex-specific
797 strategies of American kestrel (*Falco sparvierus*) provisioning offspring. – *Behav. Ecol. Sociobiol.*
798 52: 43-52.
799

800 Dewey, S. R. and Kennedy, P. L. 2001. Effects of supplemental food on parental-care strategies and
801 juvenile survival of Northern Goshawks. – *Auk* 118: 352-365.
802

803 Di Maggio, R., Campobello, D. and Sarà, M. 2018. Lesser kestrel diet and agricultural
804 intensification in the Mediterranean: An unexpected win-win solution? *J. Nat. Conserv.* 45: 122-
805 130.
806

807 Dietz, M. W. et al. 1992. Energy requirements for molt in the kestrel *Falco tinnunculus*. *Physiol.*
808 *Zool.* 65: 1217-1235.

809

810 Donázar, J. A. et al. 1992. Functional analysis of mate-feeding in the Lesser Kestrel *Falco*
811 *naumanni*. – *Ornis Scand.* 23: 190-194.

812

813 Erel, O. 2004. A novel automated direct measurement method for total antioxidant capacity using a
814 new generation, more stable ABTS radical cation. – *Clin. Biochem.* 37: 277-285.

815

816 Erel, O. 2005. A new automated colorimetric method for measuring total oxidant status. – *Clin.*
817 *Biochem.* 8: 1103–1111.

818

819 Espie, R.H. et al. 1996. Ecological correlates of molt in Merlins (*Falco columbarius*). – *Auk* 113:
820 363-369.

821

822 Fletcher, Q. E. et al. 2013. Oxidative damage increases with reproductive energy expenditure and is
823 reduced by food-supplementation. – *Evolution* 67: 1527-1536.

824

825 Frossard, J. and Renaud, O. 2018. Permutation tests for regression, ANOVA and comparison of
826 signals: the permuco package. – <https://cran.r-project.org/web/packages/permuco/index.html>

827

828 Garcia, P. F. J. et al. 1993. Energy allocation to reproduction and maintenance in Mountain
829 Bluebirds (*Sialia currucoides*): a food supplementation experiment. – *Can. J. Zool.* 71: 2352-2357.

830

831 Giordano, M. et al. 2015. Female oxidative status, egg antioxidant protection and eggshell
832 pigmentation: a supplemental feeding experiment in great tits. – *Behav. Ecol. Sociobiol.* 69: 777-
833 785.

834

835 Gonzalez, L. M. et al. 2006. Supplementary feeding as an effective tool for improving breeding
836 success in the Spanish imperial eagle (*Aquila adalberti*). – *Biol. Conserv.* 129: 477-486.

837

838 Griffiths, R. et al. 1998. A DNA test to sex most birds. – *Molec. Ecol.* 7: 1071–1075.

839

840 Halliwell, B. and Gutteridge, J. M. C. 2007. *Free Radicals in Biology and Medicine*. – Oxford
841 University Press.

842

843 Hemborg, C. 1999. Sexual differences in moult–breeding overlap and female reproductive costs in
844 pied flycatchers, *Ficedula hypoleuca*. – *J. Anim. Ecol.* 68: 429-436.

845

846 Hemborg, C. and Lundberg, A. 1998. Costs of overlapping reproduction and moult in passerine
847 birds: an experiment with the pied flycatcher. – *Behav. Ecol. Sociobiol.* 43: 19-23.

848

849 Hernández-Pliego, J. et al. 2017. Combined use of tri-axial accelerometers and GPS reveals the
850 flexible foraging strategy of a bird in relation to weather conditions. – *PloS ONE* 12: e0177892.

851

852 Hipfner, J. et al. 2001. Seasonal declines in incubation periods of Brunnich's guillemots *Uria*
853 *lomvia*: testing proximate causes. – Ibis 143: 92-98.

854

855 Hipkiss, T et al. 2002. Year-dependent sex-biased mortality in supplementary-fed Tengmalm's owl
856 nestlings. – J. Anim. Ecol. 71: 693-699.

857

858 Hörnfeldt, B. et al. 1990. Effects of cyclic food supply on breeding performance in Tengmalm's owl
859 (*Aegolius funereus*). – Can. J. Zool. 68: 522-530.

860

861 Jaeger, B. C. et al. 2017. An R^2 statistic for fixed effects in the generalized linear mixed model. – J.
862 Appl. Stat. 44: 1086-1105.

863

864 Jenni, L. and Winkler, R. 1994. Molt and ageing of European passerines. – Academic Press.

865

866 Jönsson, K. I. 1997. Capital and income breeding as alternative tactics of resource use in
867 reproduction. – Oikos 78: 57-66.

868

869 Kacelnik, A. and Cuthill, I. C. 1990. Central place foraging in starlings (*Sturnus vulgaris*). II. Food
870 allocation to chicks. – J. Anim. Ecol. 59: 655–674.

871

872 Karell, P. et al. 2008. Maternal effects on offspring Igs and egg size in relation to natural and
873 experimentally improved food supply. – Funct. Ecol. 22: 682-690.

874

875 Kelly, E. J. and Kennedy, P. L. 1993. A dynamic state variable model of mate desertion in Cooper's
876 hawks. – Ecology 74: 351-366.

877

878 Korner-Nievergelt, F. et al. 2015. Bayesian data analysis in ecology using linear models with R,
879 BUGS, and Stan. – Academic Press.

880

881 Korpimäki, E. and Wiehn, J. 1998. Clutch size of kestrels: seasonal decline and experimental
882 evidence for food limitation under fluctuating food conditions. – Oikos 83: 259–272.

883

884 Korpimäki, E. et al. 2000. Environmental-and parental condition-related variation in sex ratio of
885 kestrel broods. – J. Avian Biol. 31: 128-134.

886

887 Krüger, O. 2005. The evolution of reversed sexual size dimorphism in hawks, falcons and owls: a
888 comparative study. – Evol. Ecol. 19: 467-486.

889

890 Lack, D. 1954. The natural regulation of animal numbers. - Oxford Univ. Press.

891

892 Lack, D. 1966. Population studies of bird. – Clarendon Press.

893

894 La Gioia, G. et al. 2017. Piano d'Azione Nazionale per il grillaio (*Falco naumanni*). – MATTM-
895 ISPRA.

896

897 Lewin, A. C. and Mitchell, M. N. 1999. Using group mean centering for computing adjusted means
898 by site in a randomized experimental design: the case of California's Work Pays Demonstration
899 Project. – *Evaluation Rev.* 23: 146-161.
900

901 Lochmiller, R. L. and Deerenberg, C. 2000. Trade-offs in evolutionary immunology: just what is
902 the cost of immunity? – *Oikos* 88: 87-98.
903

904 Magrath, R. D. 1990. Hatching asynchrony in altricial birds. *Biol. Rev.* 65: 587-622.
905

906 Mainwaring, M. C. and Hartley, I. R. 2012. Causes and consequences of differential growth in
907 birds: a behavioral perspective. – *Adv. Stud. Behav.* 44: 225-277.
908

909 Manly, B. F. J. 1991. *Randomization, Bootstrap and Monte Carlo Methods in Biology.* – CRC
910 Press.
911

912 Markman, S. et al. 2002. The manipulation of food resources reveals sex-specific trade-offs
913 between parental self-feeding and offspring care. – *Proc. R. Soc. B* 269: 1931-1938.
914

915 Martin, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. – *Annu. Rev. Ecol.*
916 *Syst.* 18: 453-487.
917

918 Meijer, T. and Schwabl, H. 1989. Hormonal patterns in breeding and nonbreeding kestrels, *Falco*
919 *tinnunculus*: field and laboratory studies. – *Gen. Comp. Endocrinol.* 74: 148-160.
920

921 Meijer, T. and Drent, R. 1999. Re-examination of the capital and income dichotomy in breeding
922 birds. – *Ibis* 141: 399-414.
923

924 Merino, S. and Potti, J. 1995. Mites and blowflies decrease growth and survival in nestling pied
925 flycatchers. – *Oikos* 73: 95-103.
926

927 Merino, S. and Potti, J. 1998. Growth, nutrition, and blow fly parasitism in nestling Pied
928 Flycatchers. – *Can. J. Zool.* 76: 936-941.
929

930 Møller, A. P. 1993. Ectoparasites increase the cost of reproduction in their hosts. – *J. Anim. Ecol.*
931 62: 309-322.
932

933 Murphy, M. E. 1996. Energetics and nutrition in molt. – In: Carey, C. (ed.), *Avian Energetics and*
934 *Nutritional Ecology.* Chapman and Hall, pp. 158-198.
935

936 Nager, R. G. et al. 1999. Experimental demonstration that offspring sex ratio varies with maternal
937 condition. – *Proc. Natl Acad. Sci. USA* 96: 570-573.
938

939 Newton, I. and Marquiss, M. 1984. Seasonal trend in the breeding performance of Sparrowhawks. –
940 *J. Anim. Ecol.* 53: 809-829.
941

942 Nilsson, J.-Å. 2003. Ectoparasitism in marsh tits: costs and functional explanations. *Behav. Ecol.*
943 14: 175–181.

944

945 Oppliger, A. et al. 1994. Effect of an ectoparasite on lay date, nest-site choice, desertion, and
946 hatching success in the great tit (*Parus major*). – *Behav. Ecol.* 5: 130-134.

947

948 Peig, J. and Green, A. J. 2009. New perspectives for estimating body condition from mass/length
949 data: the scaled mass index as an alternative method. – *Oikos* 118: 1883-1891.

950

951 Peig, J. and Green, A. J. 2010. The paradigm of body condition: a critical reappraisal of current
952 methods based on mass and length. – *Funct. Ecol.* 24: 1323–1332.

953

954 Pereira, R. J. G. et al. 2010. Annual profile of fecal androgen and glucocorticoid levels in free-
955 living male American kestrels from southern mid-latitude areas. – *Gen. Comp. Endocrinol.* 166: 94-
956 103.

957

958 Podofillini, S. et al. 2018. Home, dirty home: effect of old nest material on nest-site selection and
959 breeding performance in a cavity-nesting raptor. – *Curr. Zool.* (doi: 10.1093/cz/zoy012).

960

961 R Core Team, 2017. R: A Language and Environment for Statistical Computing. – R Foundation
962 for Statistical Computing.

963

964 Roche, E. A. et al. 2010. Apparent nest abandonment as evidence of breeding-season mortality in
965 Great Lakes Piping Plovers (*Charadrius melodus*). – *Auk* 127: 402-410.

966

967 Roff, D. A. 1992. The evolution of life histories: theory and analysis. – Chapman and Hall.

968

969 Rodríguez, C. et al. 2010. Temporal changes in lesser kestrel (*Falco naumanni*) diet during the
970 breeding season in southern Spain. – *J. Rapt. Res.* 44: 120-128.

971

972 Rubolini, D. et al. 2002. Replacement of body feathers is associated with low pre-migratory energy
973 stores in a long-distance migratory bird, the barn swallow (*Hirundo rustica*). – *J. Zool.* 258: 441-
974 447.

975

976 Ruffino, L. et al. 2014. Reproductive responses of birds to experimental food supplementation: a
977 meta-analysis. – *Front. Zool.* 11: 80-93.

978

979 Runde, O. J. and Barrett, R.T. 1981. Variations in egg size and incubation period of the Kittiwake
980 *Rissa tridactyla* in Norway. – *Ornis Scand.* 12: 80-86.

981

982 Saino, N. et al. 1998. Effects of a dipteran ectoparasite on immune response and growth trade-offs
983 in barn swallow (*Hirundo rustica*) nestlings. – *Oikos* 81: 217–228.

984

985 Saino, N. et al. 2010. Sex allocation in yellow-legged gulls (*Larus michahellis*) depends on
986 nutritional constraints on production of large last eggs. – *Proc. R. Soc. B* 277: 1203-1208.

987
988 Saino, N. et al. 2011. Antioxidant defenses predict long-term survival in a passerine bird. – PLoS
989 ONE 6: e19593.
990
991 Saino, N. et al. 2014. A trade-off between reproduction and feather growth in the barn swallow
992 (*Hirundo rustica*). – PloS ONE 9: e96428.
993
994 Santema, P. and Kempenaers, B. 2018. Complete brood failure in an altricial bird is almost always
995 associated with the sudden and permanent disappearance of a parent. – J. Anim. Ecol. (doi:
996 10.1111/1365-2656.12848).
997
998 Sanz, J. J. 1996. Effect of food availability on incubation period in the pied flycatcher (*Ficedula*
999 *hypoleuca*). – Auk 113: 249-253.
1000
1001 Schoech, S. J. 1996. The effect of supplemental food on body condition and the timing of
1002 reproduction in a cooperative breeder, the Florida scrub-jay. – Condor 98: 234-244.
1003
1004 Serra, L. et al. 2012. Seasonal decline of offspring quality in the European starling *Sturnus vulgaris*:
1005 an immune challenge experiment. – Behav. Ecol. Sociobiol. 66: 697-709.
1006
1007 Siikamäki, P. 1998. Limitation of reproductive success by food availability and breeding time in
1008 pied flycatchers. – Ecology 79: 1789-1796.
1009
1010 Soler, J. J. et al. 2003. Trade-off between immunocompetence and growth in magpies: an
1011 experimental study. – Proc. R. Soc. B 270: 241-248.
1012
1013 Stearns, S. C. 1992. The evolution of life histories. – Oxford Univ. Press.
1014
1015 Székely, T. et al. 1996. An evolutionary approach to offspring desertion in birds. – In: Nolan, V.
1016 and Ketterson, E. D. (Eds.), Current Ornithology, Vol. 13. Springer, pp. 271-330.
1017
1018 Tella, J. L. et al. 1996. Seasonal and interannual variations in the sex-ratio of lesser kestrel *Falco*
1019 *naumanni* broods. – Ibis 138: 342–345.
1020
1021 Tschirren, B. et al. 2003. Sexual dimorphism in susceptibility to parasites and cell-mediated
1022 immunity in great tit nestlings. – J. Anim. Ecol. 72: 839-845.
1023
1024 Tschirren, B. and Richner, H. 2006. Parasites shape the optimal investment in immunity. – Proc. R.
1025 Soc. B 273: 1773-1777.
1026
1027 van Noordwijk, A. J. and de Jong, G. 1986. Acquisition and allocation of resources: their influence
1028 on variation in life-history tactics. – Am. Nat. 128: 137-142.
1029
1030 Wagner, R. H. and Danchin, E. 2010. A taxonomy of biological information. – Oikos 119: 203-209.
1031

1032 Weiser, E. L. et al. 2018. Life-history tradeoffs revealed by seasonal declines in reproductive traits
1033 of Arctic-breeding shorebirds. – J. Avian Biol. 49: e01531.
1034

1035 West, S. A. and Sheldon, B. C. 2002. Constraints in the evolution of facultative sex ratio
1036 adjustment. – Science 295: 1685–1688.
1037

1038 West, S. A. et al. 2000. The benefits of allocating sex. – Science 290: 288–290.
1039

1040 Wiebe, K. L. and Bortolotti, G. R. 1992. Facultative sex ratio manipulation in American Kestrels. –
1041 Behav. Ecol. Sociobiol. 30: 379-386.
1042

1043 Wiebe, K. L. and Bortolotti, G. R. 1995. Egg size and clutch size in the reproductive investment of
1044 American kestrels. – J. Zool. 237: 285–301.
1045

1046 Williams, T. D. 1994. Intraspecific variation in egg size and egg composition: effects on offspring
1047 fitness. – Biol. Rev. 68: 35-59.
1048

1049 Wiggins, D. A. et al. 1994. Correlates of clutch desertion by female collared flycatchers *Ficedula*
1050 *albicollis*. – J. Avian Biol. 25: 93-97.
1051

1052 Ydenberg, R. C. 1994. The behavioral ecology of provisioning in birds. – Ecoscience 1: 1–14.
1053

1054 Yorio, P. and Boersma, P. D. 1994. Causes of nest desertion during incubation in the Magellanic
1055 Penguin (*Spheniscus magellanicus*). – Condor 96: 1076-1083.
1056

1057 Zuberogoitia, I. et al. 2018. Molt in birds of prey: a review of current knowledge and future
1058 challenges for research. – Ardeola 65: 183-207.
1059