

Pre-hatching maternal effects and the tasty chick hypothesis

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ABSTRACT

Question: Are maternal effects (i.e. maternal transfer of immune components to their offspring via the placenta or the egg) specifically directed to the offspring on which ectoparasites predictably aggregate?

Organisms: The barn owl (*Tyto alba*) because late-hatched offspring are the main target of the ectoparasitic fly *Carnus hemapterus*.

Hypothesis: Pre-hatching maternal effects enhance parasite resistance of late- compared with early-hatched nestlings.

Search method: To disentangle the effect of natal from rearing ranks on parasite intensity, we exchanged hatchlings between nests to allocate early- and late-hatched hatchlings randomly in the within-brood age hierarchy.

Result: After controlling for rearing ranks, cross-fostered late-hatched nestlings were less parasitized but lighter than cross-fostered early-hatched nestlings.

Conclusion: Pre-hatching maternal effects increase parasite resistance of late-hatched offspring at a growth cost.

Keywords: growth, hatching asynchrony, host–parasite interactions, maternal effects, tasty chick hypothesis.

INTRODUCTION

Parasites are ubiquitous and reduce fitness of their hosts by depressing growth rate and impairing survival (Clayton and Moore, 1997). To diminish the negative impact of parasites on offspring, parents select uninfected breeding sites (Brown and Brown, 1991), incorporate anti-pathogenic plants in their nest (Petit *et al.*, 2002), increase food provisioning (Christe *et al.*, 1996), or transfer immune compounds through placenta, milk or eggs. In organisms producing more than one offspring per breeding attempt, parents often stagger the timing of offspring birth, which generates a gradual decline in competitiveness over food supply from first- to last-born offspring. As junior offspring have less access to food resources (Drummond, 2006), the maturation of their immune system can be penalized (Roulin *et al.*, 2003) making them

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potentially attractive to nest-based ectoparasites. Gradual augmentation in ectoparasitic infestation from the first- to last-born sibling hosts may exacerbate the competitive advantage of senior offspring and in turn enhance parental fitness. Based on these observations, Christie *et al.* (1998) proposed the so-called 'tasty chick hypothesis', which postulates that from the parental point of view hatching asynchrony has evolved as an anti-parasite mechanism.

Although the observation that late-hatched chicks bear more parasites than their early-hatched siblings is consistent with the tasty chick hypothesis, other interpretations are equally plausible. Even if parasites preferentially attack the last-hatched nestling hosts, giving an advantage to their older 'parasite-free' siblings, parents may not necessarily benefit from this uneven distribution of ectoparasites. Hatching asynchrony may indeed favour the build up of larger populations of parasites compared with the case where siblings hatch simultaneously (i.e. hatching synchrony). This situation may prevail if in synchronous broods parasites do not have enough time to complete their cycle, in which case parasites feed preferentially upon middle-aged chicks whose immune system is not yet fully matured or whose body is not yet too feathered. In that case, the period of time over which there is at least one middle-aged nestling host is longer in asynchronous than synchronous broods. The production of late-hatched tasty chicks may therefore not be sufficient to decrease the cost of ectoparasitism paid by early-hatched siblings, because the extra number of ectoparasites due to hatching asynchrony may affect all nestlings and not only the tasty ones. In other words, the number of parasites found on early-hatched nestlings may be similar in synchronous and asynchronous broods, a proposition that deserves experimental testing. Furthermore, hatching asynchrony may have evolved for other reasons than to reduce the cost of parasitism (see review in Stenning, 1996), and the larger than equal proportion of ectoparasites attacking late-hatched nestlings may be a by-product of hatching asynchrony rather than an adaptive feature. Therefore, the high burden of ectoparasites found on late-hatched nestlings may be one of the negative consequences of hatching asynchrony. This interpretation is plausible because in several species mothers feed preferentially their late-hatched offspring, suggesting that mothers compensate for the bad start of their weaker offspring (Slagsvold, 1997; Lessells, 2002; Ploger and Medeiros, 2004; Rosivall *et al.*, 2005). To help their late-hatched offspring resist parasite attacks, mothers may not only feed them at a high rate but also increase the level of immuno-stimulatory components packed in the late-laid eggs. Evidence for pre-hatching maternal effects associated with laying order comes from measurements of antibody (e.g. Hargitai *et al.*, 2006; Blount *et al.*, 2002), androgen (e.g. Cariello *et al.*, 2006; Gasparini *et al.*, 2007), carotenoids (Blount *et al.*, 2002), and albumen egg contents (Ferrari *et al.*, 2006), as well as egg size (e.g. Slagsvold *et al.*, 1984). However, it is not yet clear whether laying order-dependent maternal effects result in an improved resistance to parasites of late-hatched offspring compared with their early-hatched siblings.

Whether maternal effects adaptively enhance parasite resistance of late- or early-hatched offspring requires the test of four assumptions: (i) assessing resistance to parasites of early- and late-hatched offspring; (ii) investigating whether maternal components that enhance parasite resistance are differentially packed in the different eggs; (iii) injecting these compounds in eggs to show that they cause variation in parasite resistance between early- and late-hatched offspring; and (iv) demonstrating that the observed pattern of laying order-dependent deposition of maternal compounds allows parents to produce the largest number of high-quality offspring. In the present paper, we report an experiment in the barn owl (*Tyto alba*) aimed at testing the first assumption, namely that early- and late-hatched

nestlings are differentially resistant to the nest-based ectoparasitic fly *Carnus hemapterus*. This fly preferentially attacks birds that are not too feathered, and hence parasite population size increases until the last-hatched nestling hosts become feathered. As a consequence, the late-hatched individuals bear the greatest burden of ectoparasites of their brood. This non-random within-brood pattern of parasite infestation raises the question of whether it serves the parental interest as predicted by the tasty chick hypothesis. Thus, mothers may enhance resistance to *C. hemapterus* of the early-hatched offspring as predicted by the tasty chick hypothesis or of the late-hatched nestlings on which most ectoparasites aggregate (Roulin *et al.*, 2003). To test which offspring pre-hatching maternal effects improve parasite resistance, we exchanged hatchlings between nests to allocate them randomly with respect to the within-brood age hierarchy in the nest of rearing. We were therefore able to compare number of ectoparasites found on cross-fostered junior and senior nest-mates in relation to laying rank of the egg out of which they hatched in their nest of origin. In other words, we were able to compare number of parasites on late- and early-hatched nestlings raised at the top or bottom of the age hierarchy in the nest of rearing. The hypothesis of laying-order dependent maternal effects predicts that independently of the rank in the within-brood age hierarchy in the nest of rearing, early-hatched individuals bear a consistently different number of ectoparasites than late-hatched individuals.

METHODS

Study system

In Switzerland, barn owls breed from March to November. Eggs are laid every 2–3 days, and since the female starts to incubate her clutch just after the first egg has been laid, a linear age hierarchy is established among the offspring (Roulin, 2002). There is therefore no runt offspring, since it is not the case that all siblings hatch simultaneously except the runt individual, which hatches a couple of days later. In large broods [mean brood size = 4.0; range = 1–9 (Altwegg *et al.*, 2007)], the first-hatched nestling can be up to 25 days older than its last-hatched sibling (personal observation). Growth is impaired in late-hatched nestlings mainly when rearing conditions are poor, which can lead to death usually within the first 20 days after hatching (Taylor, 1994; Roulin, 1998; Roulin *et al.*, 1999). In our population between 1990 and 2006, brood reduction due to the death of late-hatched nestlings occurred in 245 of 708 (65.4%) broods with at least one fledgling. As a consequence, the nestling that bears the largest burden of ectoparasites is the smallest surviving individual (Roulin *et al.*, 2003). If mothers can influence parasite resistance by adding biochemical components to their eggs, the magnitude of such maternal effects may vary linearly with respect to laying-order, with the amount of components added in eggs declining or increasing with egg-laying sequence. During the first 2–3 weeks after hatching, the mother broods the offspring and distributes food (i.e. small mammals) among them. Extra-pair paternity is rare (Roulin *et al.*, 2004).

The 2-mm long fly *Carnus hemapterus* is the most frequent ectoparasite, with nestlings harbouring between 0 and 383 flies [mean \pm standard deviation: 39 ± 40 ; prevalence 97% (Roulin *et al.*, 2007)]. This diptera feeds upon the blood (Kirkpatrick and Colvin, 1989) of nestlings in many bird species, and is not found on adults (Büttiker, 1975). *Carnus hemapterus* emerge a couple of days before the first host egg hatches, and in the first days of life when the population of ectoparasites is still low, elder owlets are infested to a greater extent than their younger nest-mates. Progressively, the population of ectoparasites increases and the elder

nestlings are the least infested, flies being able to switch hosts on foot. The peak in ectoparasitic population size occurs when the first-hatched nestling is about 3–4 weeks of age, and thus over the rearing period late-hatched nestlings are on average more infested than their early-hatched siblings (Roulin, 1998; Roulin *et al.*, 2003). Aggregation of *C. hemapterus* on late-hatched nestlings is apparently due to the avoidance by parasites of nestlings that are too feathered (Kirkpatrick and Colvin, 1989; Dawson and Bortolotti, 1997; Roulin, 1998; Liker *et al.*, 2001; Roulin *et al.*, 2003). Therefore, the population of ectoparasites increases until all but one nestling is not too feathered to be the target (Roulin, 1998; Valera *et al.*, 2003). This could explain why the total number of parasites found in a nest is larger in bigger broods, since there is one medium-sized nestling for a longer period of time (Roulin, 1998). When population size has reached its peak, the number of flies declines rapidly and at fledging ectoparasites have virtually disappeared (Roulin, 1998).

Experimental procedure

The study was performed in western Switzerland in 1996 (48 nestlings raised in 39 foster nests and for which we had data on ectoparasitism), 1998 (13 nestlings raised in 11 foster nests), 2001 (4 nestlings raised in 4 foster nests), 2002 (29 nestlings raised in 25 foster nests), and 2004 (14 nestlings raised in 11 foster nests). Nests were matched in pairs and approximately half of their hatchlings were exchanged. Each experimental nest was therefore composed of nestlings from two origins – foster nestlings and nestlings born and raised in the same nest. At the time of cross-fostering, we removed any parasite on hatchlings to be cross-fostered. In the present study, we considered only nestlings that were cross-fostered within their first 2 days of life, and we excluded three broods tended by females breeding in more than one year. In this way, only one brood per female appears in the analyses. Before being ringed, we marked nestlings with non-toxic colour paint. Chicks were ranked according to hatching order in the nest of origin (so-called natal rank), starting with rank 1 for the first-hatched chick. Nestlings with a rank below the median hatching rank of their natal brood were denoted ‘early-hatched’, while the remaining siblings were called ‘late-hatched’. In 14 broods of five chicks, the third-hatched individual was considered to be ‘late-hatched’. At each nest visit, we ranked cross-fostered and non-cross-fostered nestlings by age, starting with 1 for the oldest nestling. Individuals with a rank below the median age rank in the nest of rearing were called ‘senior’, while the remaining nest-mates were denoted ‘junior’. In 18 broods of five nestlings, the third youngest individual was allocated to the ‘junior’ category. We considered natal (i.e. early- vs. late-hatched) and rearing rank categories (senior vs. junior) rather than the actual rank of each individual (i.e. 1, 2, 3, 4, and so on) to avoid any covariation with brood size (e.g. rank 7 can be found only in large broods while junior and senior ranks are found in both small and large broods).

Nestlings were sexed using molecular analyses (for method, see Roulin *et al.*, 1999), but because we did not collect enough blood from some nestlings we could not identify their sex. Considering only cross-fostered nestlings for which we had data on number of ectoparasites, 22 early-hatched individuals were raised as seniors (8 females, 13 males, and 1 unknown) and 22 others as juniors (13 females, 7 males, and 2 unknown). Also, 18 late-hatched individuals were raised as seniors (11 females, 6 males, and 1 unknown) and 46 others as juniors (27 females, 16 males, and 3 unknown). Early- and late-hatched cross-fostered nestlings were placed at the same mean rank (defined as 1, 2, 3, and so on) in

the senior (Student's t -test: $t_{38} = 0.01$, $P = 0.99$) and junior ($t_{66} = 1.39$, $P = 0.17$) rearing categories. Senior and junior cross-fostered nestlings were born at the same mean natal rank both when early- ($t_{42} = 1.39$, $P = 0.17$) and late-hatched ($t_{45} = 0.55$, $P = 0.58$). On different nest visits with 15- to 40-day-old nestlings (24.2 ± 0.3 days), one of the authors (A.R.) reliably counted *C. hemapterus* on the body surface of each nestling (Roulin, 1998). We did not visit nests to count parasites in older individuals because fledglings are virtually free of parasites. The number of parasites varied between 0 and 349 (59 ± 3). Because nests with few parasites are likely to provide unreliable results, we considered only nests where at least five *C. hemapterus* were found (i.e. 90 nests with 108 cross-fostered nestlings on which parasites were counted 332 times in total). At each visit and for each cross-fostered nestling, we calculated a standardized parasite load as 'number of *C. hemapterus* found on this nestling/mean number of *C. hemapterus* found on all cross-fostered and non-cross-fostered nest-mates'. Values below and above 1 indicate that nestlings are less and more infected than the average of the brood, respectively. This measure indicates the extent to which ectoparasites are aggregated on each individual. At each visit, we measured body mass to the nearest gram and wing length to the nearest millimetre. Size of the eggs out of which each nestling hatched was unknown

Statistical procedure

Statistical analyses were performed with the SAS system (version 9.1; SAS Institute Inc., Cary, NC, USA). To investigate the interaction between natal (i.e. early- vs. late-hatched) and rearing rank categories (i.e. senior vs. junior) on standardized parasite load (square-root transformed to obtain a normal distribution) as well as nestling body mass and wing length, we performed mixed-model analyses of covariance (ANCOVA) for repeated measures [proc mixed (Littell *et al.*, 2006)], with these three nestling components entered in separate analyses as dependent variables. Natal and rearing ranks were categorical variables, wing length was a covariate to control for body size, and we computed their interactions. For the analysis of standardized parasite load, we introduced nestling body mass and sex, but since these factors were neither significant alone nor in interaction, we removed them from the final model presented in Table 1. Preliminary analyses were conducted with a full model; non-significant terms, starting with non-significant interactions, were then backward removed from our final model. To avoid pseudo-replication, we added into the models the identity of rearing nests as random factors (note that the nests of origin and of rearing are confounded, since cross-fostered siblings were raised in the same nest). Chick identity was a subject repeat nested within the rearing nest, year, natal, and rearing rank categories. We chose the within-nestling covariance structure according to the AIC criterion (Littell *et al.*, 2006); in all cases, autoregressive order 1 provided the most reliable results, and was thus selected. The degrees of freedom for fixed effects were estimated according to the Satterthwaite approximation, which takes better account of the within-nestling covariance structure (Littell *et al.*, 2006). For the analysis of body mass and wing length, we added the term nestling age² in the model, since quadratic regression fitted the growth curves better than linear regression. Mean values \pm standard errors are reported. All tests were two-tailed and P -values less than 0.05 were considered significant.

Table 1. Mixed-model ANCOVAs with nestling standardized parasite load (square-root transformed), body mass, and wing length as dependent variables in separate models

Source	Standardized parasite load			Nestling body mass			Nestling wing length		
	<i>F</i>	d.f.	<i>P</i>	<i>F</i>	d.f.	<i>P</i>	<i>F</i>	d.f.	<i>P</i>
Nestling age	0.11	1,229	0.74	180.97	1,235	<0.0001	540.98	1,221	<0.0001
Nestling age ²	—	—	—	85.62	1,235	<0.0001	36.00	1,221	<0.0001
Natal rank category	3.83	1,108	0.05	0.32	1,99.3	0.57	0.12	1,89.5	0.72
Rearing rank category	25.48	1,112	<0.0001	2.09	1,245	0.15	3.13	1,252	0.08
Natal × rearing rank category	4.45	1,108	0.04	6.14	1,104	0.01	3.87	1,90.3	0.05
Nestling age × rearing rank category	—	—	—	4.86	1,235	0.03	5.98	1,221	0.02
Nestling age ² × rearing rank category	—	—	—	6.44	1,235	0.01	6.01	1,221	0.02

Note: Nestling age was a covariate, and natal (early- vs. late-hatched) and rearing nestling rank categories (junior vs. senior) were co-factors. We included year, nest of rearing, and nestling identity (nested within nest, natal and rearing rank categories) as three random factors. We report *F*-values, degrees of freedom, and *P*-values for the fixed effects.

RESULTS

Natal rank category (i.e. early- vs. late-hatched) had different effects on the standardized parasite load of nestlings reared as juniors and seniors, as shown by the significant interaction between natal and rearing rank categories (Table 1). As predicted, if mothers protect their weaker offspring against parasite attacks, late-hatched nestlings had a reduced standardized parasite load compared with early-hatched nestlings. However, contrary to our expectation, this effect was observed when the parasite load was relatively low – that is, when these nestlings were reared as seniors (i.e. similar mixed-model ANCOVA as in Table 1: $F_{1,33.4} = 8.11$, $P = 0.008$, Fig. 1) – but not when reared as juniors, when the parasite load was relatively high ($F_{1,61.7} = 0.02$, $P = 0.89$, Fig. 1). To better understand this result, we performed another analysis where, for each individual, we replaced its ‘rearing rank category’ by body size (i.e. wing length). In this analysis, the difference in ectoparasitism between late- and early-hatched nestlings increased with wing length (similar model as in Table 1 except that we replaced rearing rank categories by nestling wing length: $F_{1,236} = 4.31$, $P = 0.04$), suggesting that the effect of natal rank on ectoparasitism among senior nestlings is explained by developmental stage. Late-hatched nestlings showed a significant decrease in standardized parasite load with wing length (similar mixed-model ANCOVA as in Table 1: $F_{1,132} = 4.14$, $P = 0.04$; Fig. 2), which was not the case in early-hatched nestlings ($F_{1,109} = 0.10$, $P = 0.76$; Fig. 2).

As for standardized parasite load, there was a significant interaction between natal and rearing rank categories on nestling body mass and wing length (Table 1). Early-hatched nestlings were heavier and tended to have longer wings than late-hatched nestlings when they were reared as juniors (similar mixed-model ANCOVA as in Table 1: body mass,

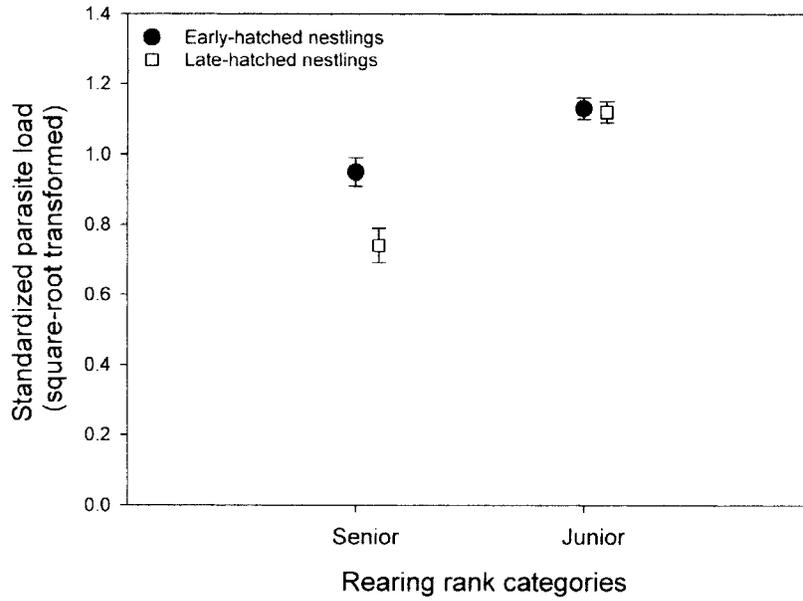


Fig. 1. Standardized (\pm standard error) parasite load (square-root transformed) of early- and late-hatched nestlings in relation to their rearing rank categories (senior vs. junior). Higher parasite loads correspond to more heavily parasitized individuals.

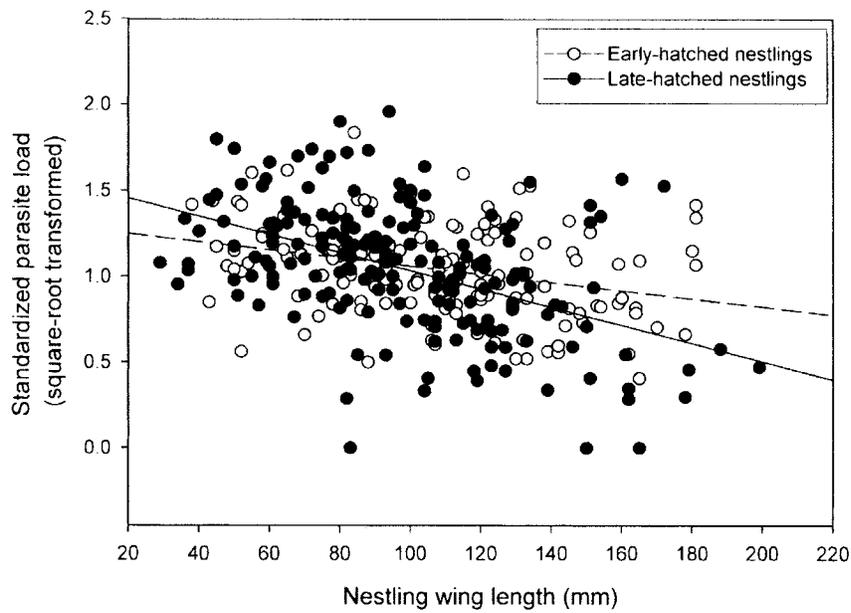


Fig. 2. Standardized parasite load (square-root transformed) of early- and late-hatched nestlings in relation to wing length (mm). Linear regression lines are shown. Higher parasite loads correspond to more heavily parasitized individuals.

$F_{1,57.4} = 5.96$, $P = 0.02$, Fig. 3a; wing length, $F_{1,43.5} = 3.38$, $P = 0.07$) but not as seniors (body mass, $F_{1,32.1} = 0.60$, $P = 0.44$, Fig. 3b; wing length, $F_{1,34} = 0.36$, $P = 0.55$).

DISCUSSION

Under the tasty chick hypothesis (Christe *et al.*, 1998), hatching asynchrony allows parents to reduce the cost of parasitism by enhancing parasite resistance of offspring with the highest reproductive value (i.e. the early-hatched individuals). Increasing the degree of hatching asynchrony to produce weaker late-hatched offspring that will attract most nest-based ectoparasites is one solution to achieve this goal, and maternal effects could be another solution. Applying the tasty chick hypothesis to maternal effects, mothers may add components to the early-laid eggs (Blount *et al.*, 2002; but see Cariello *et al.*, 2006; Ferrari *et al.*, 2006; Hargitai *et al.*, 2006; Gasparini *et al.*, 2007) to enhance resistance to parasites of the offspring showing the highest reproductive value. Cross-fostering experiments allowed us to decouple the effect of natal from rearing ranks on nestling phenotypic traits, and thus we were able to compare ectoparasite loads of early- and late-hatched nestlings raised at the top (i.e. seniors) and bottom (i.e. juniors) of the within-brood age hierarchy. Our results contradict the tasty chick hypothesis because after controlling for rearing ranks (i.e. junior vs. senior), late-hatched nestlings were less rather than more parasitized than early-hatched nestlings, a difference that was most pronounced in larger individuals. This suggests that a high degree of development is required for late-hatched nestlings to fully express this anti-parasitic maternal effect. Assuming that our findings are the result of pre-hatching maternal effects (we did not measure egg contents) and that these effects are adaptive, from the parental point of view the apparent preference of *C. hemapterus* to draw resources mainly from late-hatched nestlings (i.e. in non-manipulated nests where nestlings have not been cross-fostered) is not adaptive but results from processes that parents cannot control and which do not serve their interest. As explained in the Introduction, *C. hemapterus* preferentially attack chicks that are not yet too feathered, and hence population size increases until the last-hatched chick has reached the optimal size for the parasites. To counteract these negative effects, mothers may have evolved the capacity to enhance parasite resistance of their late-hatched offspring in the form of immune compounds added to eggs or biochemical compounds that speed up feather growth. In sum, in the barn owl hatching asynchrony may not have evolved as an anti-parasite strategy. This interpretation remains speculative because, as stated in the Introduction, a firm demonstration that these maternal effects are adaptive requires further observational and experimental studies. Nevertheless, we have highlighted an interesting pattern that should stimulate further research on the adaptive value of the role of laying-order maternal effects in parasite resistance.

The cross-fostering experiment suggests that pre-hatching maternal effects favoured parasite resistance in late-hatched nestlings and body mass growth in early-hatched nestlings. Assuming that these potential maternal effects are adaptive, three mechanisms can account for such maternal effects. First, mothers added components to eggs that improved the growth rate of early-hatched nestlings and other components that enhanced parasite resistance of late-hatched nestlings. This hypothesis is unlikely because the size advantage of senior chicks is sufficient to ensure priority of access to food resources (Roulin, 2004) without some pre-hatching assistance from their mother. Second, mothers added components to the early-laid eggs that improved the growth rate of senior offspring at the cost of parasite

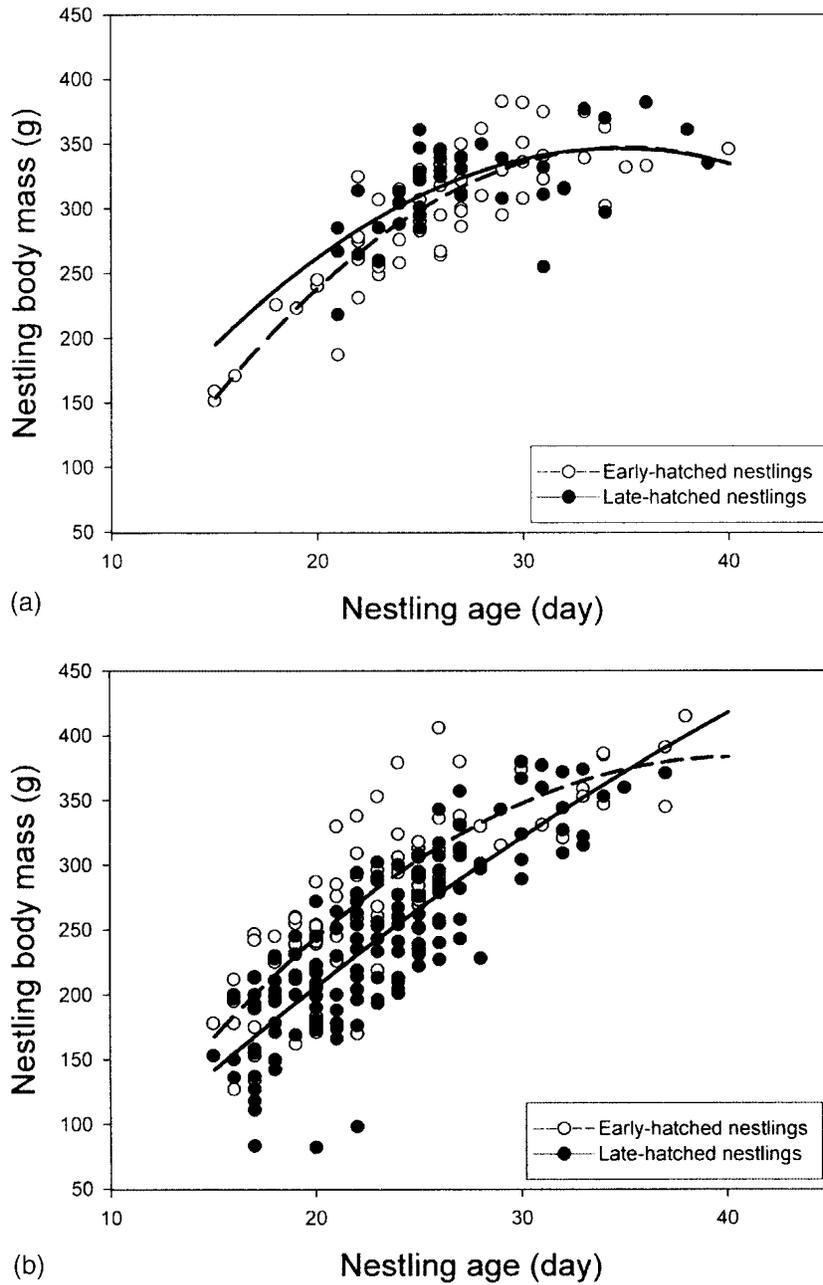


Fig. 3. Body mass (g) growth of early- and late-hatched nestlings reared as senior (a) or junior (b). Quadratic curves are given.

resistance. For similar reasons as before, this interpretation is unlikely. Third, mothers added components to the late-laid eggs to improve parasite resistance at the cost of growth rate. This last mechanism is consistent with the observation that the increase in resistance to

C. hemapterus with wing length was detected only among late-hatched nestlings. Future studies should focus on the identity and amounts of these maternal components.

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