BRILL

Behaviour 163 (2026) 125–146

Behaviour
brill.com/beh

Begging efficiency rather than food received causes brood size effect on growth in zebra finches

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Received 18 August 2025; initial decision 23 December 2025; revised 18 February 2026; accepted 18 February 2026; published online 6 March 2026

Abstract

Altricial species rely on parental provisioning for early-life sustenance, and a larger brood or litter size leads to higher levels of competition between siblings for parental resources. Early-life stress can have severe and lifelong effects on Darwinian fitness. Indeed, it is well established that being reared in a larger brood impairs growth and fitness prospects of birds, but the mechanistic underpinnings of this effect are still largely unknown. Specifically, it is not well known to what extent the reduced growth and fitness prospects of nestlings reared in large broods is due to increased resource allocation to competition versus a per capita reduction in parental provisioning rate, or a combination of the two. We cross-fostered zebra finch (*Taeniopygia castanotis*) chicks into small and large broods, and recorded their growth as well as the behaviour of parents and offspring throughout the nestling period. As in previous experiments, growth rate was higher in small broods. In large broods, chicks begged more and parents fed more frequently, fully compensating for brood size differences to yield comparable per capita feeding rates. We therefore conclude that the lower growth rate for nestlings raised in large broods is likely attributable, at least in part, to increased energy expenditure on begging and limits to parental allocation efficiency, rather than solely a reduction in their feeding frequency. These patterns are consistent with significant energetic costs associated with begging and raise the interesting possibility that brood size would not have negatively affected growth in large broods if chicks had not increased their begging effort due to increased levels of competition in the nest.

Published with license by Koninklijke Brill BV | DOI: 10.1163/1568539X-bja10358
| ISSN: 0005-7959 (print) 1568-539X (online)

Keywords
begging, cross-fostering, growth rate, parent–offspring interaction, parental provisioning.

1. Introduction

Early-life stress can have profound and long-lasting effects on the Darwinian fitness of individuals. Animals exposed to adversity during the developmental stages of their lives can exhibit reduced reproductive success (van de Pol et al., 2006) and lifespan (Tung et al., 2016; Briga et al., 2017), altered rates of senescence (Nussey et al., 2007) and differential social behaviour (Goldenberg & Wittemyer, 2018; Patterson et al., 2022; Gerritsma, 2025). In birds, early-life stress has been found to affect foraging behaviour and mass regulation (Andrews et al., 2015), attractiveness to mates (Holveck & Riebel, 2010; Mainwaring et al., 2012), telomere shortening rates (Boonekamp et al., 2014; Nettle et al., 2015) as well as inflammation (Nettle et al., 2017). Early-life challenges can have direct effects on Darwinian fitness by affecting growth (de Kogel, 1997; Nilsson & Svensson, 2001), recruitment (Schwagmeyer & Mock, 2008), nestling survival (Mock et al., 2009), foraging behaviour (Andrews et al., 2015) and reproductive success (Spagopoulou et al., 2020).

In altricial avian species, for whom early-life sustenance is reliant on parental provisioning, intricate family dynamics emerge among individual chicks, their siblings, and their parents (e.g., Davies, 1976; Wright & Leonard, 2002). An increased brood size presents numerous challenges for parents and offspring. For parents, having to care for more offspring increases care demands, forcing parents to either reallocate resources that would otherwise be used for their own somatic maintenance (compensation hypothesis) or increase their own energy intake (increased-intake hypothesis) (Nilsson, 2002). In zebra finches, when faced with food restriction post-natally, parents appear to prioritize their current reproductive bout over self-maintenance (Gerritsma et al., 2022; Coutts et al., 2024). For nestlings, being raised in larger broods results in higher rates of sibling competition for parental resources (Godfray & Parker, 1992; Godfray, 1995; Grodzinski & Johnstone, 2012) and the prioritization of investment in the development of structures that enhance their competitive ability, such as their gapes (Gil et al., 2008). Ultimately, being raised in a larger brood can not only lead to reduced growth rates and nestling mortality but also have long-term effects on fitness prospects in adulthood (Dijkstra et al., 1990; Hõrak, 2003; Nicolaus et al., 2009; Boonekamp et al., 2014, 2020; Briga et al., 2017).

Begging is the main behaviour displayed by the chicks in the nest to attract the parents' attention and compete for parental resources with siblings (Godfray & Johnstone, 2000). Begging consists of intense and conspicuous vocalizations as well as head and body movements (e.g., wing flapping, gaping; Zann, 1996; Kilner & Johnstone, 1997). Theoretical work on begging behaviour often relies on the assumption that begging entails a cost, either physiological as increased energy expenditure or by increasing predation risk. Yet, a review of the empirical literature can challenge this view. Experimental studies have suggested that nestling begging calls can increase the risk of predation (Haskell, 1994, 1999; Leech & Leonard, 1997; Haff & Magrath, 2011) and affect nestling immunocompetence (Moreno-Rueda, 2010). However, some recent studies find effects of begging on immunocompetence but not on growth (Redondo et al., 2016) and even no effects at all on nestling health (Parejo-Pulido et al., 2025). The energetic costs of begging appear modest (Leech & Leonard, 1996; Mccarty, 1996), but even a modest energetic cost may constitute a substantial part of the energy that is available for growth (Verhulst & Wiersma, 1997) as confirmed by experiments that manipulated begging effort independent from the amount of food received (Rodriguez-Girones et al., 2001; Soler et al., 2014; Nettle et al., 2017).

Given that begging is a possibly dangerous and energetically costly behaviour, theory has been developed to understand how this behaviour has evolved. Central in theoretical considerations is that there is an inherent evolutionary conflict between parents and chicks: due to divergent genetic interests, the optimal level of parental care from the perspective of the offspring is usually higher than the optimal level from the perspective of the parents, hence there is a "parent-offspring conflict" (Trivers, 1974). In this context, begging may serve as an honest signal of need, defined as the marginal fitness benefit of additional food, enabling parents to make informed decisions on the allocation of resources to the brood and between nestlings (Godfray, 1991; Royle et al., 2002). Offspring need, and possibly thereby the optimal begging effort, depends on brood size, because brood size manipulation typically modulates nestling growth (de Kogel, 1997; Burness et al., 2000). At the same time, competition for food is likely to increase with increasing brood size unless parents increase provisioning rate sufficiently to fully match the demands of an increased brood size. Both the increased level of competition and incomplete parental compensation for a larger brood are likely to increase 'nestling need', and hence begging effort (Harper, 1986). The above suggests that begging activity can be a response to not only physiological need but also to perceived competition and positive reinforcement from successful feeds (Grodzinski et al., 2007).

Brood size manipulation has often been applied as tool to manipulate early-life conditions, because it is a fair assumption that the responses to alterations in brood size within the natural range are not treatment artefacts. At the same time, due to responses of both parents and offspring to the manipulated brood size, many aspects of physiology, behaviour and even the (bio-)physical environment change in concert when brood size is manipulated, hampering investigation of the mechanisms underlying long-term effects. An understanding of the mechanisms causing the long-term effects of early-life conditions therefore requires a better insight in the dynamics within families in early life. In this context, we here concentrate on the provisioning behaviour of the parents, and the begging behaviour of the chicks in zebra finches (*Taeniopygia castanotis*), where it is well established that being raised in larger broods has multiple phenotypic effects that reduce fitness prospects, possibly through reduced growth (de Kogel, 1997; Griffith & Buchanan, 2010; Briga et al., 2017). These effects include reduced immunocompetence (Naguib et al., 2004), higher standard metabolic rate (Verhulst et al., 2006, but see Briga & Verhulst, 2021), and altered mating preferences (Holveck & Riebel, 2010). Furthermore, a higher mass on day 15 (meaning when 15 full days have elapsed since hatching) has been associated with better short-term survival (Gerritsma et al., 2022). Our aim was to determine whether diminished growth results from increased resource allocation to competition, a per capita reduction in parental provisioning rate, or a combination of the two. We therefore cross-fostered zebra finch chicks into broods of either two or six young, providing parents with food ad libitum and filmed the manipulated broods to record the behaviour of parents and offspring. We envisaged three different mechanistic scenarios that could emerge, depending on responses of parents and offspring to the brood size manipulation: (i) if provisioning behaviour and begging effort remain unchanged, the resulting reduction in *per capita* provisioning would depress growth, (ii) if parents maintain the same *per capita* provisioning rate, while the offspring increase their begging effort, growth in large broods would be reduced due to increased resource allocation to begging, and (iii) intermediate responses of both parents and offspring would lead to reduced growth due to a combination of reduced *per capita* provisioning and increased resource allocation to begging.

2. Methods

2.1. Cross fostering

Zebra finch pairs were randomly matched and placed in breeding cages (L × H × D = 80 × 40 × 40 cm) on a 14L:10D schedule at approx. 25°C temperature and approx. 60% humidity. In the cages, there were nestboxes (Griffith et al., 2008), nesting material (hay) as well as food and water ad libitum. Up until the hatching of the first egg in the nest, egg food was also supplied to the parents. Nestboxes were checked daily for the presence of eggs or chicks. Chicks were cross-fostered until the maximum age of five days to broods of either two ($n = 21$ broods) or six ($n = 14$ broods) chicks, which matches the brood size range observed in the wild (Zann, 1996). On the day of cross-fostering, all chicks were weighed and marked by clipping one or more of the head tufts for individual recognition (Adam, Scharff & Honarmand, 2014). Captive zebra finch eggs hatch asynchronously, and age differences within broods remained similar after manipulation. The mean age at cross-fostering was 3.2 ± 1.5 (SD) days (range = 0–5.5 days). No siblings were placed in the same nests and no parents were taking care of their own offspring. Chicks were ringed at the age of 12 days, and weighed again at 15 and 35 days. Zebra finch chicks typically fledge around 16–18 days and reach nutritional independence at 35 days (Zann, 1996). At 35 days, chicks were moved from the breeding cage into larger indoor aviaries (153 × 76 × 110 cm), with two pairs of foster parents for sexual imprinting. We here define nestling age as whole days since hatching, with hatching date marked as 0.

Extra-pair fertilizations are rare in natural zebra finch populations (Zann, 1996; Griffith et al., 2010), and we assume therefore that as a rule the species has evolved to perceive other brood members as siblings. This is relevant insofar that potential effects of variation in relatedness within the families on interactions between brood members and parents can be ignored in the context of this study.

2.2. Camera observations

Based on previous, personal observations, cameras were placed above the nest an hour before the start of the recording, to allow the birds to adjust to them. Each observation consisted of an hour of filming per nest and each nest was recorded multiple times at multiple ages of the chicks until they fledged. The video recordings were then uploaded and analyzed in BORIS, an interactive software program for behavioural observations (Friard & Gamba, 2016). The duration of the following behaviours in the span of 1 h was recorded:

(1) Resting, the individual rests and does nothing else or the adult is just sitting in the nest;

(2) Begging, the chick makes mouth and body movements to attract parental attention;

(3) Feeding, the chick takes food from the parent or the parent gives food to the chick (foraging time not included for the parents).

(4) Cleaning, the individual (either chick or parent) cleans its feathers;

(5) Moving, the individual (either chick or parent) moves within the nest or the parent makes changes in the nest (e.g., nest-building);

(6) Other, the individual does not display any of the behaviours mentioned above, is outside of the nest or is not visible.

We recorded 463 individual observations of chicks and 263 of adults (18 individuals) in rearing small broods and 614 observations of chicks and 120 of adults (6 individuals) in rearing large broods. Two chicks were observed in each video, randomly selected. Note that we could track individuals for the duration of the video but could not identify the chicks individually. The distribution of ages at which the chick observations were made can be found in Figure A1 in the Appendix.

2.3. Statistical analyses

All analyses were performed in R v.4.1.2 (R Core Team, 2023). All models were fitted using package lme4 v. 1.1.35.1 (Bates et al., 2015) and we tested the statistical significance of variables and their interactions using the package car v. 3.1.2 (Fox & Weisberg, 2019), and visually inspected the residuals to verify adherence to the model assumptions. When analyzing variation in proportion of time, proportions were arcsine square root transformed ($\theta = \arcsin\sqrt{p}$, where p is the proportion) prior to analysis to meet the homoscedasticity assumption. Video recordings were made in different breeding rounds and analysed by different observers ($n = 3$), and to account for possible differences between breeding rounds and the co-varying identity of the observers (that may differ in the details of scoring behaviour) we included observed ID as random effect in the analyses. Video recordings were made at different ages, and we grouped observations in age categories (0–4, 5–9, 10–15 and 16+ days) to avoid losing too many degrees of freedom when chick age effects on provisioning.

2.3.1. *Chick mass*

We used linear mixed models to determine the effect of brood size on chick mass. To account for variations in the age at cross-fostering, we included the age at which mass was recorded as a covariate. Since not all chicks were cross-fostered and therefore weighed at the same age, the average age at cross-fostering per brood served as the reference point for the first timepoint, and day 15 served as the second timepoint for each observation. In zebra finches, measuring chick growth rate from cross fostering until day 15 is informative because it captures the main period of rapid nestling growth, right after cross-fostering and before fledging when chicks are still fully dependent on parental provisioning. As random effects we included identity of each chick and brood. We used the F-statistic metric derived from a Type III Analysis of Variance Table with Satterthwaite's method to test the significance of the interactions between brood size and age category. Note that mass data was not available for all chicks included in the experiment.

2.3.2. *Chick behaviour*

We used linear mixed models with the arcsine transformed proportion of time spent on each behaviour per observation as the response variable using brood size and age category at recording as explanatory variables while brood and observer identities and were included as random intercepts.

2.3.3. *Parent behaviour*

We used linear mixed models of proportion of time spent transferring food to the chicks (parental provisioning) per parent as the response variable using brood size as the explanatory variable and included brood identity as random effect. Since parental behaviour was not always recorded, parent provision rate to the broods were calculated from chick provision rate data by extrapolating the observed provisioning rate from the observed chicks to the entire brood. Specifically, because two chicks were observed in each video, we averaged the proportion of time the two chicks were observed being fed per observation. In order to account for chick mortality within the brood, we then multiplied by the number of chicks still alive at the time of observation (usually two or six as mortality was very low). Lastly, we divided the result by two to obtain the proportion of time spent feeding per parent (sex of the feeding parent could not always be recorded).

3. Results

3.1. Chick mass

Chick mass at first weighing did not significantly differ between brood sizes ($p = 0.4$). Brood size affected chick growth as evidenced by a significant interaction between age and brood size, confirming diminished growth rate in chicks in large broods (Table 1). Being raised in large broods resulted in gaining 0.04 ± 0.03 g (mean ± SE) less per day (Fig. 1a). Age at cross-fostering did not significantly increase the explained variance ($p = 0.8$) and was therefore excluded from the final model. At age 15 days, chicks raised in large broods weighed on average 0.6 ± 0.35 g less than chicks reared in small broods (Fig. 1b).

3.2. Begging behaviour

Chicks in large broods begged on average 6.58% (SE = 1.07) more than chicks from small broods. This increase was not at the expense of resting time, which was not affected by brood size, but rather of other behaviours (Fig. 2). The proportion of time at which chicks displayed each behaviour per age category is summarized in Figure A2 in the Appendix. Chicks in large broods consistently begged more throughout the nestling period, independent of age ($F_{1,168} = 0.44$, $p > 0.05$). Begging intensity for all chicks peaked between days 5 and 15 (Table 2, Fig. 3).

3.3. Parent provisioning

Parents caring for large broods spent 6.56% (SE = 2.52) more time transferring food to their chicks than parents caring for small broods (Fig. 4, Table 3). The amount of time parents spent feeding their brood did not significantly

Table 1.
Linear mixed effects model results of the effects of brood size and age on chick mass.

	Chick mass (g)			
	Estimate ± SE	t-value	df	Pr(>|t|)
Fixed effects				
Intercept	0.31 ± 0.30	1.1	85.62	0.29
Large brood	0.18 ± 0.44	0.42	67.4	0.68
Age (days)	0.75 ± 0.02	35.55	89.35	< 0.001
Large brood × age	0.07 ± 0.03	−2.27	89.85	0.03
Random effects				
Bird id	0.14			
Brood id	0.64			
Residual	1.41			

$N = 182$ observations, from 20 small broods and 13 large broods. Brood size is coded as a factor with small broods being the reference and the main effect estimate represents the average difference in chick mass for chicks raised in large broods when compared to small broods when comparing for age at measurement.

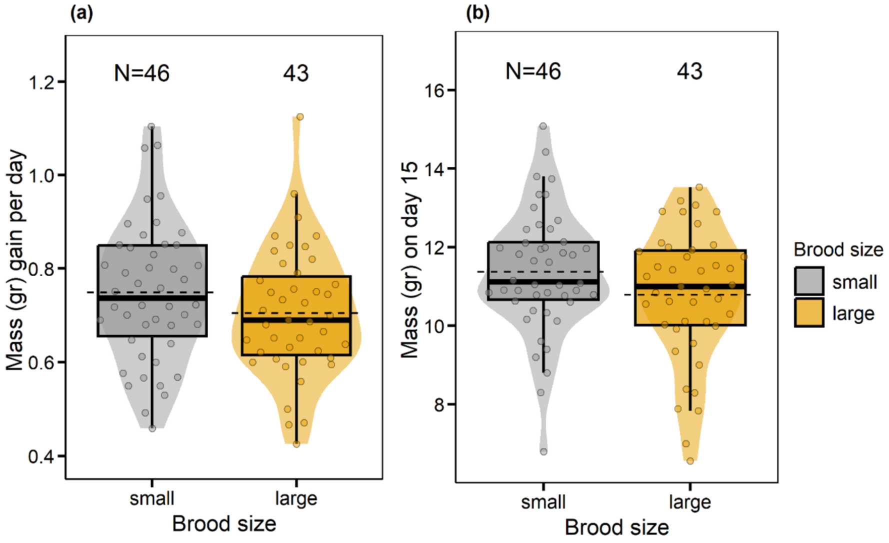

Figure 1. Mass gain per day of chicks raised in small and large broods (a). Mass of chicks raised in small and large broods on day 15 (b). Violin plot widths represent the data density, boxplots show the median and quartiles while dashed lines show the average daily mass gain and average mass on day 15 for chicks raised in small and large broods.

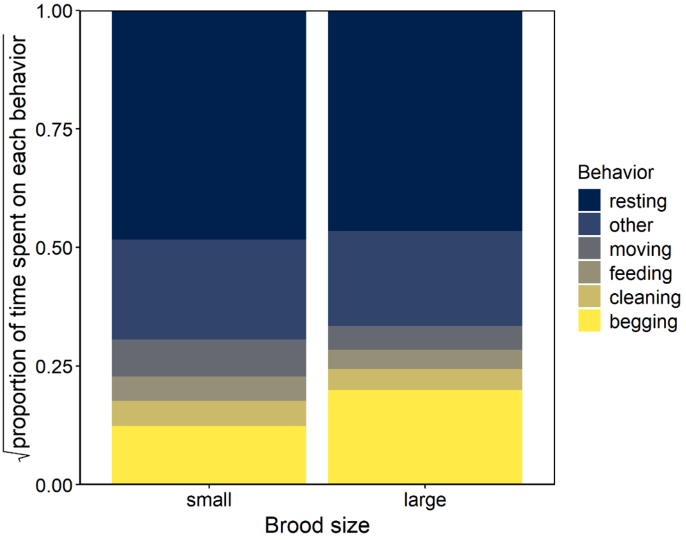

Figure 2. Proportion of time chicks in small and large broods spent on each behaviour over all ages pooled. Proportions of each behaviour per observation were normalized and then square root transformed. See Figure A2 in the Appendix for the results for the different age categories.

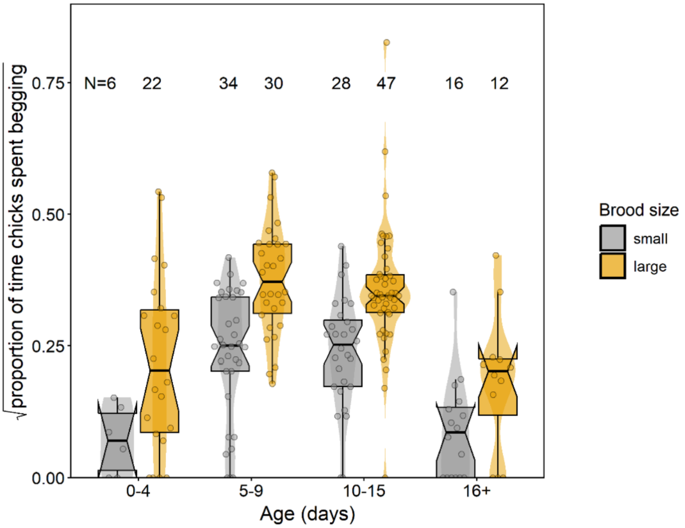

Figure 3. Proportion of time chicks in small and large broods spent begging over the nestling period ($N = 195$ observations). For graphical purposes proportions were square root transformed. Violin plot widths represent the data density, boxplots show the median and quartiles.

Table 2.
Linear mixed effects model results brood size and age effects on the proportion of time (arcsin square root transformed) that nestlings spent begging.

	Proportion of time chicks spent begging			
	Estimate ± SE	t-value	df	Pr(>|t|)
Fixed effects				
Intercept	0.009 ± 0.004	2.26	5.14	0.07
Large brood	0.014 ± 0.002	5.22	20.37	<0.001
Age 5–9 days	0.017 ± 0.003	6.34	187.4	<0.001
Age 10–15 days	0.014 ± 0.003	5.2	175.8	<0.001
Age 16+ days	0.003 ± 0.003	1.1	189.3	0.27
Random effects				
Brood id	2.13e-05			
Observer	2.62e-05			
Residual	1.07e-04			

$N = 195$ observations, from 21 small broods and 13 large broods. Brood size is coded as a factor and small broods and age 1-4 days are the reference. Omnibus tests are shown as a footnote. Estimates are on the arcsine-square-root-transformed scale. Note that observer identity is fully confounded with breeding round (the year of breeding, N = 3) and effects of breeding round and observer identity can therefore not be separated.

*Omnibus tests: brood size $F_{1,20.4} = 27.28$, $p < 0.001$; age category $F_{3,187.8} = 18.37$, $p < 0.001$, brood size × age category $F_{3,167.94} = 0.44$, $p < 0.05$.

differ between the early days of the chicks' lives and the later age categories (Fig. 4, Table 3).

3.4. Per capita chick feeding

Chicks reared in small broods spent on average 0.41% (SE = 0.27) more time being fed than chicks in large broods, which was not significant, and when accounting for other factors the estimated difference between brood sizes was in the opposite direction and also not statistically significant (Fig. 5, Table 4). The interaction between brood size and age category did not explain a significant part of the variance when added to the model ($F_{1,176} = 0.08$, $p > 0.05$). The proportion of time being fed peaked between five and fifteen days for chicks of both brood sizes (Fig. 5b).

4. Discussion

It is well established that being raised in a larger brood or litter adversely affects growth. To shed light on the mechanistic underpinnings of this effect

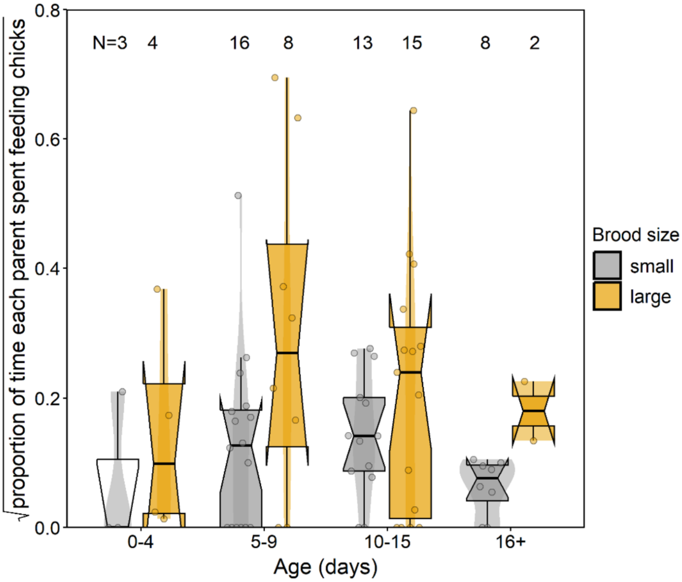

Figure 4. Proportion of time each parent spent transferring food to the chicks in small and large broods over the nestling period ($N = 69$ observations). For graphical purposes proportions were square root transformed. Violin plot widths represent the data density, boxplots show the median and quartiles.

we manipulated brood size and recorded parent and offspring behaviour throughout the nestling period. We found that zebra finch nestlings raised in large broods were faced with a diminished growth rate, despite indistinguishable per capita feeding rates of chicks raised in small and large broods. Nestlings in large broods spent more time begging, as reported in earlier studies across various bird species (Leonard et al., 2000; Wright et al., 2002; Neuenschwander et al., 2003). We hypothesize therefore that the diminished growth results for nestlings in large broods was at least in part due to the increased resource allocation to competition through begging and other motor activities related to competition, which is consistent with empirical studies demonstrating begging to have energetic, metabolic and other physiological costs (Bachman & Chappell, 1998; Roulin, 1998; Abraham & Evans, 1999). Our findings suggest a complex trade-off between competitive behaviour for immediate survival and physical development in the nestling period, in agreement with previous claims of a significant energetic cost associated with begging, but at the expense of long-term fitness prospects.

Table 3.

Linear mixed effects model results of brood size effects on the proportion of time (arcsine square root transformed) each parent spent feeding their chicks.

	Proportion of time each parent spent feeding chicks			
	Estimate ± SE	t-value	df	Pr(>|t|)
Fixed effects				
Intercept	0.006 ± 0.009	0.71	3.32	0.52
Large brood	0.013 ± 0.004	3.58	27.26	<0.001
Age 5–9 days	0.006 ± 0.005	1.26	50.29	0.21
Age 10–15 days	0.003 ± 0.005	0.64	51.49	0.53
Age 16+ days	−0.006 ± 0.005	−1.09	44.68	0.28
Random effects				
Brood id	5.65e-05			
Observer	1.62e-05			
Residual	9.04e-05			

$N = 69$ observations, from 21 small broods and 13 large broods. Brood size is coded as a factor and small broods and age 1–4 days are the reference. Estimates are on the arcsine-square-root-transformed scale.

*Omnibus tests: brood size $F_{1,12.82} = 12.82$, $p = 0.001$; age category $F_{3,45.68} = 2.75$, $p = 0.05$, brood size × age category $F_{3,44.3} = 0.4$, $p > 0.05$.

Parental feeding decisions respond to diverse nest conditions and parents often rely on those cues to help navigate the parent-offspring conflict and adjust feeding strategies. For example, brood size, nestling age and begging frequency have been found to affect parental feeding frequency in red-whiskered bulbuls (Zhang et al., 2025). When parents have to care for more chicks, they can adaptively adjust their provisioning rate to match the needs of a larger brood. Zebra finch parents have been found to compensate for increased brood demands even under food restriction which resulted in comparable growth for chicks in small and large broods (Coutts et al., 2024). Moreover, previous research has demonstrated that larger broods are generally associated with increased parental provisioning rates also in other bird species(Lessells, 1993; Stoehr et al., 2001; Bowers et al., 2014). Similarly, we here observed increased parental feeding for parents caring for chicks in large broods. This increased provisioning is likely, at least in part, a response to the increase in begging, given that begging playback experiments successfully elevated parental provisioning (e.g., Ottosson et al., 1997; Burford et al., 1998; Price, 1998; Tarwater et al., 2009). Our findings suggest that begging intensity- as a reflection of sibling competition- may not merely scale

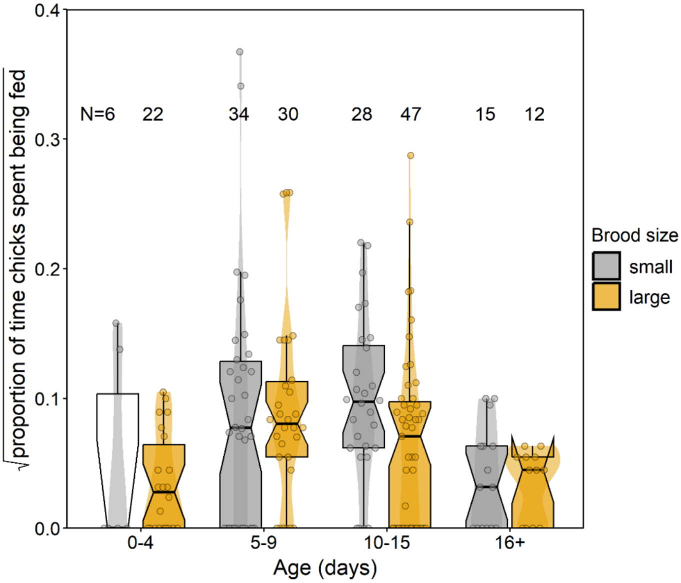

Figure 5. Proportion of time chicks in small and large broods spent being fed over the nestling period ($N = 194$ observations). For graphical purposes proportions were square root transformed. Violin plot widths represent the data density, boxplots show the median and quartiles.

linearly with nestling hunger, but is also driven by the nestlings' perception of competition, suggesting how competitive cues shape parental responses beyond simple need-based signalling.

In most studies, the effect of brood size manipulation on parental provisioning only partly compensated for the change in brood size, and, as a consequence, per capita provisioning rate is typically lower in enlarged broods (e.g. Dijkstra et al., 1990). Our study is unusual in this respect, in that the brood size effect on provisioning rate was such that there was a comparable per capita feeding rate in large broods. Begging is the foraging technique of altricial nestlings, and, as any foraging technique, the yield will depend on food availability in the environment. In our study, food availability was ad libitum from the perspective of the parents, which is likely to have shaped our results, in that the energy yield of begging was probably higher than it would have been in a more natural environment where parents usually have to make a greater effort to gather food. Nonetheless, feeding frequency might not fully reflect the actual amount of food received as in zebra finches the number of regurgitations per bout has been found to vary (Gilby et al.,

Table 4.
Linear mixed effects model results of brood size and age effects on proportion of time (arcsine square root transformed) individual chicks spent being fed.

	Proportion of time chicks spent being fed			
	Estimate ± SE	t-value	df	Pr(>|t|)
Fixed effects				
Intercept	0.0053 ± 0.004	1.33	2.35	0.3
Large brood	0.0004 ± 0.0014	0.31	24.43	0.76
Age 5–9 days	0.0027 ± 0.0012	2.25	184	0.03
Age 10–15 days	0.0015 ± 0.0013	1.23	186.6	0.22
Age 16+ days	−0.0031 ± 0.0014	−2.23	177.8	0.03
Random effects				
Brood id	1e-05			
Observer	4.19e-05			
Residual	1.94e-05			

$N = 194$ observations, from 21 small broods and 13 large broods. Brood size is coded as a factor and small broods and age 1–4 days are the reference. Estimates are on the arcsine-square-root-transformed scale.

*Omnibus tests: brood size $F_{1,24.43} = 0.1$, $p > 0.05$; age category $F_{3,180.99} = 8.75$, $p < 0.001$, brood size × age category $F_{3,176.41} = 0.08$, $p > 0.05$.

2011), potentially modulating per capita food intake independently of feeding frequency.

With respect to the question how the brood size effect on nestling growth arises, we infer from the present findings that brood size increased per capita provisioning rate and that the brood size effect on growth must therefore be due to other factors than the amount of food received. Instead, we consider the increased energy allocation to begging and other aspects of sibling competition the most likely cause of the brood size effect on nestling growth. Our findings are consistent with a significant energetic cost associated with begging, similar to experiments in which nestlings were forced to beg at a higher rate for the same amount of food, which also depressed growth (Rodriguez-Girones et al., 2001; Soler et al., 2014; Nettle et al., 2017). In addition to begging costs, chicks in large broods might also face increased energetic demands associated with increased motor activity, such as changing their position within the nest to secure more favourable feeding positions (Neuenschwander et al., 2003). Moreover, in large broods where parents have to care for more chicks and might have a greater difficulty tracking individual needs, low parental feeding coordination (Royle, Hartley & Parker, 2006) or sex-related parental favouritism (Mainwaring et al., 2011) can result in uneven chick feeding which might contribute to the lower average chick mass observed (Grodzinski & Lotem, 2007). The above scenarios are not mutually exclusive and likely act in combination to drive the growth patterns observed.

A new dimension revealed by the present study is that family dynamics can impair nestling growth (and therefore decrease Darwinian fitness) even under parental provisioning compensation and in the absence of an experimentally set limit on how much food the nestlings consume. Interestingly, our findings suggest that the brood size effect on growth is -at least in part- self-inflicted and competition-based: if the nestlings had not increased begging and other competition-related motor activity, equivalent per capita feeding rates might have yielded comparable growth across brood sizes. Paying the begging costs, though potentially reducing inclusive fitness of all family members, may be the evolutionary stable solution, where honest signaling and reinforcement dynamics interact with limits to parental responsiveness, sustaining elevated begging intensity even when energetic and parental food allocation costs are incurred.

Acknowledgements

We thank the animal caretakers of the University of Groningen as well as numerous students including Gillian Bakx and Wietske van Buiten for assistance with data collection. MB thanks the funding from the Turku Collegium for Science, Medicine and Technology. We also thank two anonymous reviewers for their suggestions, which significantly improved our manuscript.

Conflict of interest

The authors declare no conflict of interest.

Data availability statement

The data and scripts can be found at https://github.com/tangilim/ZF_Begging_Behaviour.

Ethics approval

All methods and experiments for the zebra finches detailed in this manuscript were performed under approval of the Central Committee for Animal Experiments (Centrale Commissie Dierproeven) of the Netherlands, under license AVD1050020174344.

Funding

MT was supported by an Adaptive Life Scholarship awarded by the University of Groningen.

References

Abraham, C.L. & Evans, R.M. (1999). Metabolic costs of heat solicitation calls in relation to thermal need in embryos of American white pelicans. — Anim. Behav. 57: 967-975.

Adam, I., Scharff, C. & Honarmand, M. (2014). Who is Who? Non-invasive methods to individually sex and mark altricial chicks. — J. Vis. Exp.: 1-8.

Andrews, C., Viviani, J., Egan, E., Bedford, T., Brilot, B., Nettle, D. & Bateson, M. (2015). Early life adversity increases foraging and information gathering in European starlings, Sturnus vulgaris. — Anim. Behav. 109: 123-132.

Bachman, G.C. & Chappell, M.A. (1998). The energetic cost of begging behaviour in nestling house wrens. — Anim. Behav. 55: 1607-1618.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using {lme4}. — J. Stat. Softw. 67: 1-48.

Boonekamp, J.J., Bauch, C. & Verhulst, S. (2020). Experimentally increased brood size accelerates actuarial senescence and increases subsequent reproductive effort in a wild bird population. — J. Anim. Ecol. 89: 1395-1407.

Boonekamp, J.J., Mulder, G.A., Salomons, H.M., Dijkstra, C. & Verhulst, S. (2014). Nestling telomere shortening, but not telomere length, reflects developmental stress and predicts survival in wild birds. — Proc. R. Soc. B Biol. Sci. 281: 1-7.

Bowers, E.K., Nietz, D., Charles, F. & Sakaluk, S.K. (2014). Parental provisioning in house wrens: effects of varying brood size and consequences for offspring. — Behav. Ecol. 25: 1485-1493.

Briga, M., Koetsier, E., Boonekamp, J.J., Jimeno, B. & Verhulst, S. (2017). Food availability affects adult survival trajectories depending on early developmental conditions. — Proc. R. Soc. B Biol. Sci. 284: 20162287.

Briga, M. & Verhulst, S. (2021). Mosaic metabolic ageing: Basal and standard metabolic rates age in opposite directions and independent of environmental quality, sex and life span in a passerine. — Funct. Ecol. 35: 1055-1068.

Burford, J.E., Friedrich, T.J. & Yasukawa, K. (1998). Response to playback of nestling begging in the red-winged blackbird, Agelaius phoeniceus. — Anim. Behav. 56: 555-561.

Burness, G.P., McClelland, G.B., Wardrop, S.L. & Hochachka, P.W. (2000). Effect of brood size manipulation on offspring physiology: An experiment with passerine birds. — J. Exp. Biol. 203: 3513-3520.

Coutts, V.M., Pham, K., Gilbert, G. & Wada, H. (2024). Breeding zebra finches prioritize reproductive bout over self-maintenance under food restriction. — Biol. Open 13: 1-10.

Davies, N.B. (1976). Parental Care and the Transition To Independent Feeding in the Young Spotted Flycatcher (Muscicapa Striata). — Behavior: 280-294.

de Kogel, C.H. (1997). Long-Term Effects of Brood Size Manipulation on Morphological Development and Sex-Specific Mortality of Offspring. — J. Anim. Ecol. 66: 167.

Dijkstra, C., Bult, A., Bijlsma, S., Daan, S., Meijer, T. & Ziilster, M. (1990). Brood Size Manipulations in the Kestrel (Falco tinnunculus): Effects on Offspring and Parent Survival. — J. Anim. Ecol. 59: 269-285.

Fox, J. & Weisberg, S. (2019). An *R* Companion to Applied Regression. — Sage, Thousand Oaks, CA.

Friard, O. & Gamba, M. (2016). BORIS: a free, versatile open-source event-logging software for video / audio coding and live observations. — Methods Ecol. Evol. 7: 1325-1330.

Gerritsma, Y.H. (2025). From adversity to personality. The effect of early-life adversity on zebra finch behaviour.

Gerritsma, Y.H., Driessen, M.M.G., Tangili, M., De Boer, S.F. & Verhulst, S. (2022). Experimentally manipulated food availability affects offspring quality but not quantity in zebra finch meso — populations. — Oecologia 199: 769-783.

Gil, D., Bulmer, E., Celis, P. & López-Rull, I. (2008). Adaptive developmental plasticity in growing nestlings: Sibling competition induces differential gape growth. — Proc. R. Soc. B Biol. Sci. 275: 549-554.

Gilby, A.J., Mainwaring, M.C., Ann, L. & Grif, S.C. (2011). Parental care in wild and captive zebra fi nches: measuring food delivery to quantify parental effort. — Anim. Behav.: 81.

Godfray, H.C.J. (1991). Signaling of need by offspring to their parents. — Nature 352: 328-330.

Godfray, H.C.J. (1995). Signaling of need between parents and young: parent-offspring conflict and sibling rivalry. — Am. Nat. 146: 1-24.

Godfray, H.C.J. & Johnstone, R. (2000). Begging and bleating: the evolution of parent – offspring signalling Begging and bleating: the evolution of parent — offspring signalling. — Philos. Trans. R. Soc. B Biol. Sci. 355: 1581-1591.

Godfray, H.C.J. & Parker, G. (1992). Sibling competition, parent-offspring conflict and clutch size. — Anim. Behav. 43: 473-490.

Goldenberg, S.Z. & Wittemyer, G. (2018). Orphaning and natal group dispersal are associated with social costs in female elephants. — Anim. Behav. 143: 1-8.

Griffith, S.C. & Buchanan, K.L. (2010). Maternal effects in the Zebra Finch: A model mother reviewed. — Emu 110: 251-267.

Griffith, S.C., Holleley, C.E., Mariette, M.M., Pryke, S.R. & Svedin, N. (2010). Low level of extrapair parentage in wild zebra finches. — Anim. Behav. 79: 261-264.

Griffith, S.C., Pryke, S.R. & Mariette, M. (2008). Use of nest-boxes by the Zebra Finch (Taeniopygia guttata): implications for reproductive success and research. — Emu 108: 311-319.

Grodzinski, U., Erev, I. & Lotem, A. (2007). Can hungry nestlings be trained to reduce their begging ?. — Behav. Ecol.: 116-125.

Grodzinski, U. & Johnstone, R.A. (2012). Parents and offspring in an evolutionary game: the effect of supply on demand when costs of care vary. — Proc. R. Soc. B Biol. Sci. 279: 109-115.

Grodzinski, U. & Lotem, A. (2007). The adaptive value of parental responsiveness to nestling begging. — Proc. R. Soc. B Biol. Sci. 274: 2449-2456.

Haff, T.M. & Magrath, R.D. (2011). Calling at a cost: elevated nestling calling attracts predators to active nests. — Biol. Lett. 7: 493-495.

Harper, A.B. (1986). The evolution of begging: sibling competition and parent- offspring conflict. — Am. Nat. 128: 99-114.

Haskell, D.G. (1994). Experimental evidence that nestling begging behaviour incurs a cost due to nest predation. — Proc. R. Soc. B Biol. Sci. 257: 161-164.

Haskell, D.G. (1999). The effect of predation on begging-call evolution in nestling wood warblers. — Anim. Behav. 57: 893-901.

Holveck, M.J. & Riebel, K. (2010). Low-quality females prefer low-quality males when choosing a mate. — Proc. R. Soc. B Biol. Sci. 277: 153-160.

Hõrak, P. (2003). When to pay the cost of reproduction? A brood size manipulation experiment in great tits (Parus major). — Behav. Ecol. Sociobiol. 54: 105-112.

Kilner, R.M. & Johnstone, R.A. (1997). Begging the question: are offspring solicitation behaviors signals of need?. — Trends Ecol. Evol. 12: 11-15.

Leech, S.M. & Leonard, M.L. (1996). Is there an energetic cost to begging in nestling tree swallows (Tachycineta bicolor)?. — Proc. R. Soc. B Biol. Sci. 263: 983-987.

Leech, S.M. & Leonard, M.L. (1997). Begging and the risk of predation in nestling birds. — Behav. Ecol. 8: 644-646.

Leonard, M.L., Horn, A.G., Gozna, A. & Ramen, S. (2000). Brood size and begging intensity in nestling birds. — Behav. Ecol. 11: 196-201.

Lessells, C.M. (1993). The cost of reproduction: do experimental manipulations measure the edge of the options set. — Etologia 3: 95-111.

Mainwaring, M.C., Blount, J.D. & Hartley, I.A.N.R. (2012). Hatching asynchrony can have long-term consequences for offspring fitness in zebra finches under captive conditions. — Biol. J. Linn. Soc. 106: 430-438.

Mainwaring, M.C., Lucy, D. & Hartley, I.R. (2011). Parentally biased favouritism in relation to offspring sex in zebra finches. — Behav. Ecol. Sociobiol. 65: 2261-2268.

Mccarty, J.P. (1996). The energetic cost of begging in nestling passerines. — Auk 113: 178-188.

Mock, D.W., Schwagmeyer, P.L. & Dugas, M.B. (2009). Parental provisioning and nestling mortality in house sparrows. — Anim. Behav. 78: 677-684.

Moreno-Rueda, G. (2010). An immunological cost of begging in house sparrow nestlings. — Proc. R. Soc. B Biol. Sci. 277: 2083-2088.

Naguib, M., Riebel, K., Marzal, A. & Gil, D. (2004). Nestling immunocompetence and testosterone covary with brood size in a songbird. — Proc. R. Soc. B Biol. Sci. 271: 833-838.

Nettle, D., Andrews, C., Reichert, S., Bed, T., Kolenda, C., Parker, C., Martin-Ruiz, C., Monaghan, P. & Bateson, M. (2017). Early-life adversity accelerates cellular ageing and affects adult inflammation: Experimental evidence from the European starling. — Sci. Rep. 7: 1-10.

Nettle, D., Monaghan, P., Gillespie, R., Brilot, B., Bedford, T., Bateson, M. & Nettle, D. (2015). An experimental demonstration that early-life competitive disadvantage accelerates telomere loss. — Proc. R. Soc. B Biol. Sci. 282: 1-8.

Neuenschwander, S., Brinkhof, M.W.G. & Ko, M. (2003). Brood size, sibling competition, and the cost of begging in great tits (Parus major) 14: 457–462.

Nicolaus, M., Michler, S.P.M., Ubels, R., Van Der Velde, M., Komdeur, J., Both, C. & Tinbergen, J.M. (2009). Sex-specific effects of altered competition on nestling growth and survival: An experimental manipulation of brood size and sex ratio. — J. Anim. Ecol. 78: 414-426.

Nilsson, J.Å. (2002). Metabolic consequences of hard work. — Proc. R. Soc. B Biol. Sci. 269: 1735-1739.

Nilsson, J.Å. & Svensson, M. (2001). Sibling competition affects individual growth strategies in marsh tit, Parus palustris, nestlings. — Anim. Behav. 61: 357-365.

Nussey, D.H., Kruuk, L.E.B., Morris, A. & Clutton-Brock, T.H. (2007). Environmental conditions in early life influence ageing rates in a wild population of red deer. — Curr. Biol. 17: 1000-1001.

Ottosson, U., Bäckman, J. & Smith, H.G. (1997). Begging affects parental effort in the pied flycatcher, Ficedula hypoleuca. — Behav. Ecol. Sociobiol. 41: 381-384.

Parejo-Pulido, D., Redondo, T., Casquero, S. & Pérez-Rodríguez, L. (2025). Escalated begging does not compromise nestling health. — Behav. Ecol. 36: 1-11.

Patterson, S.K., Strum, S.C., Silk, J.B. & Patterson, S.K. (2022). Early life adversity has long-term effects on sociality and interaction style in female baboons. — Proc. R. Soc. B Biol. Sci. 289: 1-9.

Price, K. (1998). Benefits of begging for yellow-headed blackbird nestlings. — Anim. Behav. 56: 571-577.

R Core Team (2023). R: A language and environment for statistical computing. — Vienna, Austria.

Redondo, T., Ochoa, D., Moreno-Rueda, G. & Potti, J. (2016). Behavioral Pied flycatcher nestlings incur immunological but not growth begging costs. — Behav. Ecol. 00: 1-10.

Rodriguez-Girones, M.A., Zuniga, J.M. & Redondo, T. (2001). Effects of begging on growth rates of nestling chicks. — Behav. Ecol. 12: 269-274.

Roulin, A. (1998). Forum On the cost of begging vocalization: implications of vigilance. — Beha 12: 506-515.

Royle, N.J., Hartley, I.R. & Parker, G.A. (2002). Begging for control: when are offspring solicitation behaviours honest ?. — Trends Ecol. Evol. 17: 434-440.

Royle, N.J., Hartley, I.R. & Parker, G.A. (2006). Consequences of biparental care for begging and growth in zebra finches, Taeniopygia guttata. — Anim. Behav. 72: 123-130.

Schwagmeyer, P. & Mock, D. (2008). Parental provisioning and offspring fitness: size matters. — Anim. Behav. 75: 291-298.

Soler, M., Ruiz-Raya, F., Carra, L.G., Medina-Molina, E., Ibáñez-Alamo, J.D. & Martín-Gálvez, D. (2014). A long-term experimental study demonstrates the costs of begging that were not found over the short term. — PLoS One 9: 1-11.

Spagopoulou, F., Teplitsky, C., Lind, M.I., Chantepie, S., Gustafsson, L. & Maklakov, A.A. (2020). Silver-spoon upbringing improves early-life fitness but promotes reproductive ageing in a wild bird. — Ecol. Lett. 23: 994-1002.

Stoehr, A.M., McGraw, K.J., Nolan, P.M. & Hill, G.E. (2001). Parental Care in Relation To Brood Size in the House Finch. — J. F. Ornithol. 72: 412-418.

Tarwater, C.E., Kelley, J.P. & Brawn, J.D. (2009). Parental response to elevated begging in a high predation, tropical environment. — Anim. Behav. 78: 1239-1245.

Trivers, R.L. (1974). Parent-Offspring Conflict. — Am. Zool. 264: 249-264.

Tung, J., Archie, E.A., Altmann, J. & Alberts, S.C. (2016). Cumulative early life adversity predicts longevity in wild baboons. — Nat. Commun. 7: 1-7.

van de Pol, M., Bruinzeel, L.W., Heg, D., van der Jeugd, H. & Verhulst, S. (2006). A silver spoon for a golden future: long-term effects of natal origin on fitness prospects of oystercatchers (Haematopus ostralegus). — J. Anim. Ecol. 75: 616-626.

Verhulst, S., Holveck, M.J. & Riebel, K. (2006). Long-term effects of manipulated natal brood size on metabolic rate in zebra finches. — Biol. Lett. 2: 478-480.

Verhulst, S. & Wiersma, P. (1997). Is begging cheap?. — Auk 114: 134.

Wright, J., Hinde, C., Fazey, I. & Both, C. (2002). Begging signals more than just short-term need: Cryptic effects of brood size in the pied flycatcher (Ficedula hypoleuca). — Behav. Ecol. Sociobiol. 52: 74-83.

Wright, J. & Leonard, M.L. (2002). The Evolution of Begging. — Kluwer Academic Publishers, New York, Boston, Dordrecht, London, Moscow Print.

Zann, R.A. (1996). The zebra finch. A synthesis of field and laboratory studies. — Oxford University Press, Oxford.

Zhang, Z., Li, Q., Cai, Y. & Yang, C. (2025). Revealing the key signals in nestling begging behavior perceived by parent birds during parent — offspring conflict. — Integr. Zool. 20: 700-711.

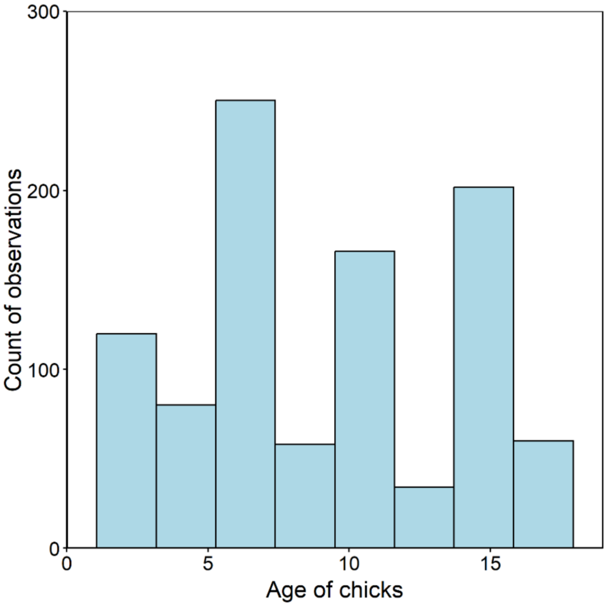

Figure A1. Age of the chicks when observations on chick behaviour were recorded ($N = 1077$ observations).

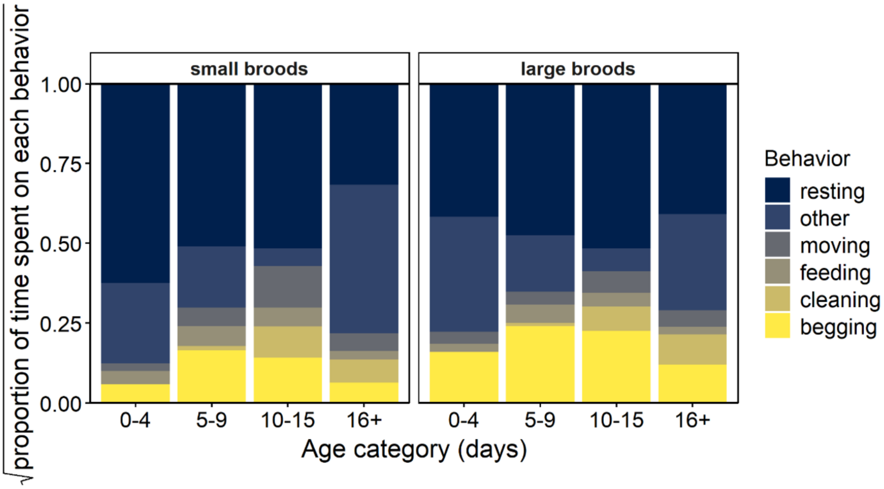

Figure A2. Proportion of time spent on each behaviour by chicks in small and large broods divided in the age categories of the chicks. For graphical purposes proportions of each behaviour per observation were normalized and then square root transformed.