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Sibling competition affects body condition and allostatic load in the colonial nesting lesser kestrel *Falco naumanni*

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Abstract. Sibling competition leading to physiological stress and elevated allostatic load is driven by asymmetrical development and limited resources. To investigate these predictions, we studied broods of the lesser kestrel *Falco naumanni*, from a nest-box population in Armenio, Central Greece. For each nestling reared in nest-boxes, we noted the age (in days) since hatching, measured the wing chord length and body mass. We also clipped the central right rectrix for ptilochronology for subsequent analysis in the laboratory. We measured 206 nestlings from 61 broods (range 2-5 nestlings). In the case of nestlings < 18 days old (n = 198, 96.1% of all) we also measured the length of feathers. As a measure of body condition, we used the residuals of the linear regression for the relationship between wing chord length and body mass, while the growth bar width of feathers was used as a second, independent index of body size and allostatic load. A GLMM and information-theory criterion showed that both measures of body condition decreased incrementally from the first sibling to the most subordinate in the brood. Body condition of subordinate siblings was influenced by the number of siblings in the nest; i.e. the larger the brood size the greater the discrepancy in body condition between siblings. At the same time, we did not find any influence of sex on either measure of fitness. Thus, our results indirectly support the hypothesis that sibling competition may cause physiological developmental stress which is reflected in decreased body condition and increased allostatic load for younger nestlings.

Key words: Greece, growth rate, ptilochronology

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Introduction

Sibling competition is a strong selective force in the evolution of avian growth rates (Werschkul & Jackson 1979). In species with parental care, competition between siblings is a consequence of hatching asynchrony which arises from the differential onset of incubation between the laying of the first and subsequent eggs (Stoleson & Beissinger 1995, Amundsen & Slagsvold 1998). Thus, hatching asynchrony leads to differences in body size among siblings (Yosef et al. 2013). These differences are intensified by asymmetric sibling competition during time spent in the nest, where siblings with different competitive abilities (based mainly on body size) compete for limited resources, such as food, heat loss (mainly before developing thermoregulation), and limited space in the nest (Bortolotti 1986, Smiseth et al. 2007, Braziotis et al. 2017). To date, many hypotheses have been proposed to explain this phenomenon (Lack 1954, Hussell 1972, Hahn 1981, Arnold et al. 1987, Veiga 1992, Szöllősi et al. 2007). The most important in this context is that parents are predicted to distribute resources evenly within the brood to limit competition among chicks; otherwise asymmetric division of food between siblings can lead to severe physiological stress expressed as allostatic load (Ricklefs 1982, Bortolotti 1986).

Allostatic load is the process of maintaining homeostasis through behavioural or physiological responses to environmental challenges and its cumulative energetic cost is regulated by sibling competition (López-Jiménez et al. 2016). Subordinate individuals subject to high-levels of aggression by dominants have higher allostatic loads than dominants, particularly when dominants restrict their access to food (Goymann & Wingfield 2004). High allostatic loads can be reflected in lower body condition. Yosef et al. (2013) and López-Jiménez et al. (2016) showed that in upland buzzards (*Buteo hemilasius*) and black kites (*Milvus migrans*) younger siblings had significantly higher levels of corticosterone, suggestive of increased levels of stress because of sibling competition. Similarly, Eraud et al. (2008) found that in collared doves (*Streptopelia decaocto*) although corticosterone levels were higher in younger siblings, only cell-mediated immunoresponsiveness remained weaker. Similar patterns have also been reported in mammals, for instance a recent study in spotted hyenas (*Crocuta*

crocuta) showing that physiological stress is reflected in allostatic load (Benhaiem et al. 2013).

One way to assess body condition and physiological stress during development in birds is to measure 'stress bars', which are expressed on feathers and are quantifiable through ptilochronology (Grubb 1991, 2006, Grubb & Yosef 1994). In an earlier study, Braziotis et al. (2017) quantified body mass and morphological traits in female and male lesser kestrel *Falco naumanni* nestlings from a lowland Greek breeding population. They found that differences in the growth rate of body mass, tarsus and bill length, were substantially greater among nests than amongst siblings, implying differences in parental quality between nests and an even distribution of parental care amongst siblings. Similar results were also obtained for American kestrels (*Falco sparverius*) in which the impact of disparities of sibling egg size on post-natal size continued throughout the nesting period (Anderson et al. 1997). This response potentially provides parents with a means by which they can influence body size in their offspring (Anderson et al. 1997). Thus, we hypothesized that although Braziotis et al. (2017) concluded that parental care was evenly distributed amongst siblings in a brood, differences in body condition would be greater among siblings in larger broods. We tested the hypothesis that there are physiological disparities between the dominant and subordinate individuals in a brood and predicted that biometrics (wing chord length, body mass), and ptilochronology of the rectrix (Grubb 1989) would provide evidence of competition between siblings based on body size resulting in physiological stress and increased allostatic loads (Goymann & Wingfield 2004). This hypothesis was based on the principle that initial differences in nestling size after hatching are exacerbated by sibling competition during the time spent in the nest, with the primary factor mitigating these differences is the way parents allocate food among siblings. We further wished to test whether the sex of nestlings (Blanco et al. 2006, Tryjanowski et al. 2011), as well as hatching order influenced body condition (Braziotis et al. 2017).

Material and Methods

Study area
The study was conducted at a lesser kestrel colony of 120 nest boxes in the village of Armenio (39°29′07″ N, 22°41′39″ E), Central Greece, which is characterized by a flat terrain surrounded by

mountains. In the study period, only 61 nest boxes were occupied. The altitude ranges from 48 to 52 m and the climate is characterized as thermo-Mediterranean. In this area, land use around the villages is mostly non-intensive agricultural land (cereal), intensive agricultural land (cotton) and pasture on hill slopes (Vlachos et al. 2004, 2015, Braziotis et al. 2017).

Fieldwork and data collection

The lesser kestrel is a colonial breeder that readily adapts to nest boxes. Data were collected during the 2017 breeding season, in late June. During this period most of the broods are ready to fledge and we undertook an expedition to ring all the nestlings. We measured 206 nestlings from 61 broods (range 2-5 nestlings), and in the case of young < 18 days (n = 198, 96.1% of the total) we also measured the length of feathers. Since we have followed the colony since its inception in 1999, and know the reproductive dates of each pair in the colony, while ringing each brood we noted the age (days) and sex, measured the 8th Primary (P8), wing chord (±1 mm) and weighed (digital ± 0.1 g) each chick. Sex of nestlings was determined in the field based on their plumage, which is similar to that of Eurasian kestrels (cf. Village et al. 1980). Female nestlings have a uniform brown and striated plumage while males have grey feathers on the rump. The age of nestlings for which the hatching date was not already known was calculated based on the equation AGE = 10.44 + 0.14 LENGTH (P8) (cf. Donazar et al. 1991), and we determined hatching asynchrony on the same basis. Since within-clutch asynchrony is small (Bustamante & Negro 1994), the length of P8 was measured at the time of ringing the brood. We also clipped/collected the central right rectrix for ptilochronology (Grubb 1989).

Ptilochronology is a technique based on the evaluation of the width of feather growth bars. Growth bar width indicates an individual's relative nutritional condition and can also reflect corticosterone levels (cf. Yosef et al. 2013). Feather growth as an index of body condition is based on natural selection, as birds need to regenerate lost feathers as rapidly as possible. Birds in better nutritional condition regenerate feathers faster than individuals in poor condition (Grubb 1991, 2006). Thus, feather quality is a relatively accurate indicator of an individual's nutritional condition. On each feather, 10 growth bars centred on a point two-thirds of the distance toward the tip of the feather were measured by Reuven Yosef, who was blind to all other measurements (Grubb & Yosef 1994, Gombobaatar et al. 2009, Maciorowski et al. 2018).

Data processing and analyses

Body mass and wing length were highly correlated (all $P < 0.01$) and thus both variables could not be included in the analysis (Quinn & Keough 2002). Instead the residuals of the linear regression between mass and wing length were used as a measure of body condition (Starck & Ricklefs 1998). Growth bar width was not correlated with any biometric variable so was used as a second independent measure of body condition. We used a General Linear Mixed Model (GLMM) with a Gaussian error structure where the response variables were: (1) body condition (BoC), and (2) average growth bar width (GBW). Four additional covariates; brood size, nestling age, nest ID (as a random factor) and standardized dominance rank (SDR), were used as explanatory variables. SDR is based on hatching order standardized for brood size and expressed as a rank from 0 to 1 i.e. when brood size is 4, standardized dominance rank is 0, 1/3, 2/3, and 1).

Sex was determined for only 98 nestlings, thus to determine the influence of sex on allostatic loads we used two additional GLMMs, one for body condition index (BoC) and one for average growth bar width (GBW), with sex included as an additional predictor to the four independent variables mentioned above.

In all cases, the most parsimonious models were selected using the Akaike Information Criterion (mgcv library in R; Wood 2013) with the lowest AIC score (Burnham & Anderson 2002). We analysed all possible models (2n, where n = the number of variables), using the MuMIn library in R (Bartoń 2016). The probability of including a variable in the most parsimonious model was estimated as the relative importance (RI) by summing the Akaike weights of all candidate models in which the variable was included (Burnham & Anderson 2002). As the measure for the best model, we used the evidence ratio (Burnham & Anderson 2002).

Results

General information on population

The mean (±SD) number of nestlings per nest was 3.7 ± 1.2 (range 1-5, n = 61); 4 nests (6.6%) had one nestling, 8 (13.1%) had 2, 18 (29.5%) had 3, 23
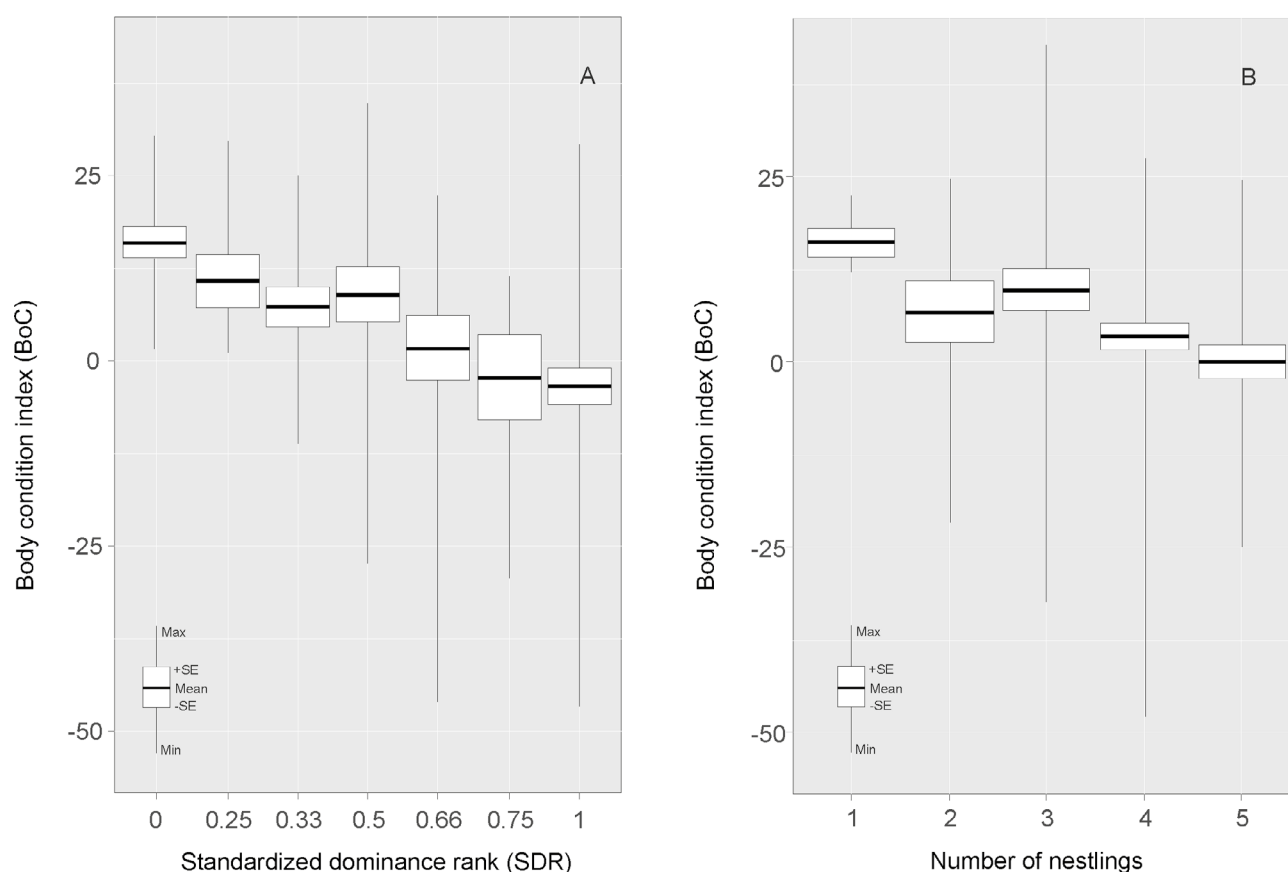
Fig. 1. Differences in the body condition index (BoC) of nestlings predicted by; (A) dominance rank and; (B) number of siblings. BoC is expressed as the residuals of the linear regression describing the relationship between body mass and wing length. Thus, values on the y-axis indicate deviation from the average BoC of the population, which is 0.

(37.7%) had 4, and 8 (13.1%) had 5 nestlings. Mean (±SD) hatching asynchrony was 3.0 ± 1.2 (range 0-9) days and was not significantly affected by number of nestlings ($F_{4,57}$ = 2.24, P = 0.073). We successfully sexed 98 nestlings based on their plumage and found a ratio of 63 females to 37 males; a sex ratio of 1:1.7 in favour of females. It is of interest to note that all of the youngest nestlings in 5-brood nests were female (n = 8).

Factors affecting body condition (BoC)
Of the five GLMMs fitted, four were supported by information-theoretic criteria, showing AIC weights > 0 (Table 1a). The R^2-coefficient for the most parsimonious model for the standardised body mass index (SBM) (Table 1a) was 21.3 % and was slightly better than the second model (evidence ratio 3.58) in our candidate set. Model selection identified four predictors with relative importance RI > 0, but only 3 were included in the best-supported model (Table 1a). Wald statistics showed that BoC was predicted by standardized dominance rank (SDR, Fig. 1A) and brood size (Fig. 1B); body condition (BoC) decreased incrementally from the dominant (first) sibling to

the most subordinate in the brood (Table 2) and BoC was also negatively predicted by the number of siblings in the nest. The age of nestlings was not a significant predictor of BoC (Table 2).

Factors affecting growth bar width (GBW)
Of all the models, only three GLMMs supported the information-theoretical criteria, showing AIC weights > 0 (Table 1b). In this case, the R^2-coefficient was 11.7 % and was better than the second model (evidence ratio 23.2) in our candidate set. Model selection procedures allowed us to identify 4 predictors with relative importance RI > 0, but only 1 was included in the best-supported model. The Wald statistic for factors included in this model was significant (Table 2) and showed that GBW decreases with an increased number of siblings (Fig. 2).

Factors affecting BoC and GBW with sex as an additional predictor
In this case, out of all GLMMs for BoC and GBW where sex was used as an additional predictor, four models in both were supported using information-theoretic criteria, showing AIC weights > 0. The

Table 1. Comparison of GLMM models for body condition (BoC), average growth bar width (GBW) with and without sex as an additional predictor (null and all where Akaike weights > = 0.001). Most parsimonious model given in bold.

Model	Independent variables	LogLink	AIC$_C$	ΔAICc	ω
(a) body condition (BoC)					
1	null	–57.92	156.0	14.81	0
2	SDR + Age	–56.55	147.4	6.18	0.030
3	SDR + Siblings + sex	–56.90	144.4	3.22	0.131
4	SDR + Age + Sex	–56.66	143.8	2.55	0.183
5	**SDR + Age + Siblings**	**–56.07**	**141.2**	**0**	**0.656**
(b) factors affecting growth bar width (GBW)					
1	null	–49.70	105.6	14.21	0.001
2	SDR + Siblings + Sex	–44.70	99.2	7.8	0.001
3	SDR + Siblings	–43.62	97.7	6.30	0.036
4	SDR + Age	–42.48	95.4	4.01	0.114
5	**Siblings**	**–41.54**	**91.4**	**0**	**0.849**
(c) factors affecting BoC with sex as an additional predictor					
1	null	–74.92	56.0	14.81	0
2	Age + SDR	–69.55	47.4	6.18	0.030
3	SDR	–65.90	44.4	3.22	0.131
4	Siblings + SDR	–66.66	43.8	2.55	0.183
5	**Siblings + Age + SDR + Sex**	**–62.07**	**41.2**	**0**	**0.656**
(d) factors affecting GBW with sex as an additional predictor					
1	null	–47.94	112.9	21.57	0
2	Age	–49.70	105.6	14.21	0.001
3	Siblings + SDR	–44.69	102.0	10.62	0.005
4	SDR + Age	–43.62	97.7	6.30	0.041
5	**Siblings**	**–41.54**	**91.4**	**0**	**0.954**

R^2-coefficient for the most parsimonious model was 19.2 % for BoC and 12.4 % for GBW and was a better predictor of variation in BoC and GBW than the second model (evidence ratio respectively: 3.58 and 23.2) in our candidate set. Model selection allowed us to identify four predictors for BoC, (Table 1c) and three for GBW (Table 1d) with relative importance RI > 0, but only three (for BoC) and one (for GBW) were included in the best-supported model. Wald statistics for the BoC model showed that SBM is affected by the number of siblings while age of nestlings, standardised dominance rank and sex were not significant (Table 2). Wald statistics for the GBW model (Table 2) showed that GBW decreased with an increase in the number of siblings, while sex was not a significant predictor.

Discussion

Our prediction that differences in body condition, and potentially also in allostatic load, between siblings is a consequence of the number of siblings in the nest was supported by this study. None of the measured parameters showed any significant differences between the sexes; body mass index was influenced by order of hatching and dominance rank, while growth bar width was dependent only on the number of siblings. Thus, the dominant sibling had a higher body condition index than the subordinate siblings with the latter predicted to have an increased allostatic load. Similar results were found in other studies on the similar-sized American kestrel (*Falco sparverius*; Negro et al. 1994) and common kestrel (Dijkstra et al. 1990) as well as the common buzzard in Hungary (*Buteo buteo*; Fehervari et al. 2014) and the upland buzzard in Mongolia (*Buteo hemilasius*; Gombobaatar et al. 2010).

Several theories have been advanced to explain this phenomenon (e.g. Lack 1954, Mock 1984). Hussell (1972) suggested the 'peak load hypothesis', which attempts to explain mitigation of allometric load as a result of the parents supplying food at differential rates to the young. Hahn (1981) forwarded the 'sibling rivalry reduction hypothesis' suggesting that energetic demands upon the parents could be reduced if the subordinate siblings, right from the
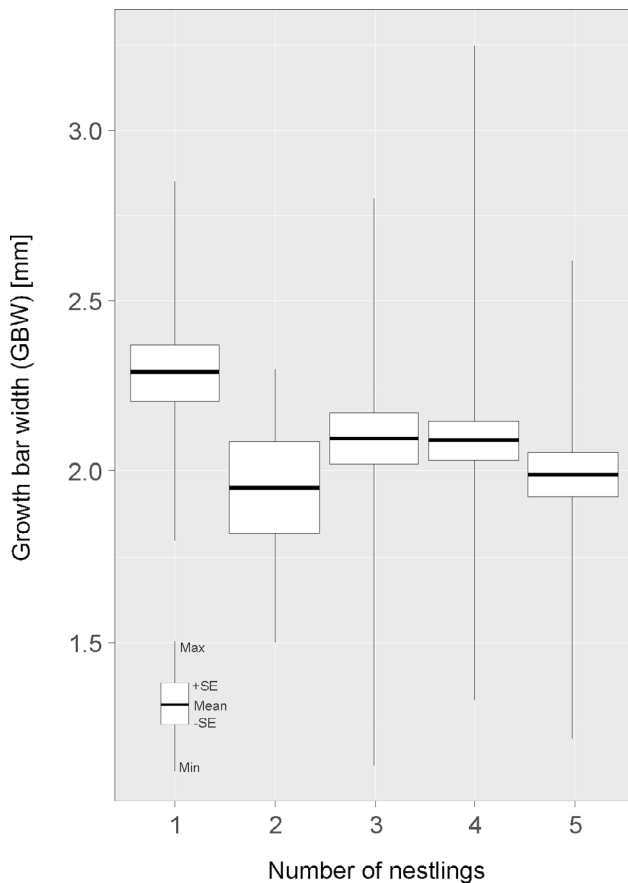
Fig. 2. Differences in average feather growth bar width in nests with different numbers of siblings.

moment of hatching, were exposed to a hierarchy in the brood that resulted in reduced attempts to

access food. However, Massemin et al. (2003), who studied asynchronous broods of Eurasian kestrels *Falco tinnunculus*, contended that these hypotheses are not necessarily mutually exclusive as different explanations may apply at different stages of the hatching and brooding process. Without food supplementation, daily energy expenditure (DEE) in first hatched nestlings was 35% higher than the last hatched, suggesting substantial competition. With food supplementation, DEE declined and the difference between the first- and the last-hatched nestling disappeared, suggesting that sibling competition supported a third 'food amount hypothesis'. This study also found support for the 'sibling rivalry reduction hypothesis' since once energy expended in competition by the smallest chicks declined, a result was lower total brood energy requirements and reduced parental food delivery rates in asynchronous compared to synchronous broods.

Our results showed the dominant sibling had a higher body condition index than subordinate siblings. The fact that the first and the second hatched siblings showed similar nutritional condition (according to the body condition index) suggests that in our case the 'food amount hypothesis' was best supported and that the colony of lesser kestrels had access to ample prey (Nilsson & Gårdmark 2001, Vlachos et al. 2015,

Table 2. The most parsimonious GLMM for body condition (BoC) and average growth bar width (GBW) with and without sex as an additional predictor. Statistically significant variables in bold.

	Estimate ± SE	df	t	P	RI
(a) factors affecting body condition (BoC)					
Intercept	0.14 ± 12.92	75.1	0.01	0.995	-
SDR	**−4.37 ± 2.28**	**126.92**	**−1.91**	**0.012**	**1**
Age	0.50 ± 0.46	78.02	1.10	0.276	0.869
Siblings	**−2.41 ± 1.59**	**52.95**	**−1.51**	**0.013**	**0.787**
(b) factors affecting growth bar width (GBW)					
Intercept	2.20 ± 0.057	61.05	38.03	0.001	-
Siblings	**−0.24 ± 0.050**	**105.15**	**−4.75**	**0.001**	**1**
(c) factors affecting BoC with sex as an additional predictor					
Intercept	−0.08 ± 12.9	74.1	−0.007	0.996	-
Siblings	**−2.42 ± 1.58**	**36.1**	**−2.08**	**0.031**	**0.839**
Age	0.49 ± 0.46	77.13	1.06	0.294	0.686
SDR	−4.34 ± 2.31	124.7	−1.88	0.069	0.970
Sex	−0.005 ± 2.63	127.91	−0.002	0.999	0.656
(d) factors affecting GBW with sex as an additional predictor					
Intercept	2.20 ± 0.057	61.05	38.03	0.001	-
Siblings	**−0.24 ± 0.05**	**105.15**	**−4.75**	**< 0.001**	**0.959**

Braziotis et al. 2017, Kotsonas et al. 2017). It should be also noted that a previous study on the same population of lesser kestrels (Braziotis et al. 2017) found that body mass of females was significantly greater than that of fledgling males of the same dominance rank, which is inconsistent with our results. However, the former study averaged biometric parameters between clutches taking a more holistic approach to nestling growth rate and did not isolate individual growth rates.

In conclusion, our study shows that body condition, and potentially allostatic load, are inversely proportional to the dominance rank and number of nestlings. The highest body condition index was found for the oldest chicks with the lowest number of siblings. We speculate that this relationship arises from accessibility to food sources, although we have not demonstrated this directly. We also propose that sibling competition may drive physiological developmental stress for the youngest siblings, reflected in decreased body condition and an increased allostatic load. A prediction is that the probability of survival of the youngest individuals in a brood will be reduced as a result of increased pressure from older siblings which, in accordance with the 'food amount hypothesis' may derive from limited food resources.

Acknowledgements

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