Animal behaviour

Sibling competition and hunger increase allostatic load in spotted hyaenas

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Allostatis is the process of maintaining homeostatis through behavioural or physiological responses to challenges, and its cumulative energetic cost is termed allostatic load. The allostatic load hypothesis predicts that hunger and the mechanisms that establish and maintain social dominance should have a strong impact on allostatic load. In spotted hyaenas, dominance between twin siblings emerges during intense early competition for maternal milk and involves trained winner/loser effects. Conflict over access to teats declines with age as behavioural dominance conventions are established. In young litters, the allostatic load of subordinates measured in terms of faecal glucocorticoid metabolite concentrations (fGMCs) should be higher than that of dominants. When low milk provisioning threatens survival, hungry subordinates are more assertive, particularly when competing against a dominant sister. Dominants challenged by assertive subordinates should have allostatic loads and fGMCs above those of dominants with subordinates that adhere to dominance conventions. We show that in young litters, subordinates had significantly higher fGMCs than dominants, and dominant sisters had significantly higher fGMCs than dominant brothers. When hungry, both dominants and subordinates had significantly higher fGMCs than when fed. Our results provide evidence that hunger and sibling competition affect allostatic load in spotted hyaenas.

1. Introduction

Social status may profoundly affect how animals cope with challenges [1]. Glucocorticoids help maintain allostasis by mobilizing energy reserves and thus elevated glucocorticoid concentrations indicate allostatic load [2]. Socially subordinate individuals subject to high-level aggression by dominants should have higher allostatic loads than dominants, particularly when dominants restrict their access to food [3]. When hunger threatens their survival, subordinates are more assertive [4–6], thereby probably increasing allostatic load in dominants [3].

Within-brood/litter dominance can be established during intense early sibling competition [6]. In many bird species, subordinate siblings have higher glucocorticoid concentrations than dominants [7–9], particularly when hungry [7,10]. We present the first study of the impact of intense within-litter competition [11] on allostatic load in twins of a free-ranging mammal, the spotted hyaena (Crocuta crocuta). Dominants monopolize maternal milk, thereby obtaining higher growth rates than their subordinate siblings [5,12]. Insufficient milk provisioning results in early facultative siblicide by enforced starvation of subordinates [12,13], particularly those competing against a sister [5,13]. Within-litter dominance is established within three months of birth through trained winner/loser effects [5]. Littermates exclusively depend on [12] and intensively compete for [11] highly nutritious milk during their initial six months of life. Dependence on milk and sibling conflict decline
after this period and dominance conventions typically operate [5,11]. When hungry, subordinates competing against a sister are more assertive than subordinates competing against a brother [5]. For these reasons, we expect allostatic load measured by faecal glucocorticoid metabolite concentrations (fGMCs; [14]) to be higher in (i) subordinates than in dominants in litters younger than six months, (ii) dominant sisters than in dominant brothers and (iii) both dominants and subordinates when hungry.

2. Material and methods

(a) Study population
We studied three clans in the Serengeti National Park, Tanzania, between 2007 and 2010, which defended territories with large fluctuations in prey abundance [15]. These fluctuations profoundly affected maternal milk provisioning. When prey abundance was high, all mothers nursed their litters daily and when low only every 1–6 days [16], because they undertook long-distance foraging (‘commuting’) trips (80–140 km; [15]). At medium prey abundance, only mothers of lower social status commuted [17]. All animals were individually recognized and monitored at clan communal dens at dawn and dusk [15]. Subordinates were the most submissive siblings [11]. Cubs were sexed [18], aged [11] and categorized as ‘young’ (less than six months) or ‘old’ (between six and 24 months). Adults were older than 24 months.

(b) Faecal glucocorticoid metabolites
Faeces were collected immediately after defaecation, mixed, sub-sampled and stored frozen as previously described [19]. We quantified fGMCs as ng g\(^{-1}\) faeces using a cortisol-3-CMO enzyme immunoassay validated for spotted hyaenas [19]. Methodological pitfalls [20] associated with the measurement of fGMCs require careful consideration (see detailed discussion in the electronic supplementary material).

We measured fGMCs in 175 faecal samples for 77 twins aged 47–492 days, including 38 dominants (19 males and 19 females) and 39 subordinates (20 males and 19 females). These data (see electronic supplementary material) incorporated paired samples from both members of 23 young litters: four all-female, six all-male and 13 mixed-sex twins (eight with dominant females and five with dominant males). To verify that sex differences in fGMCs were the consequence of sibling competition and not sex differences in metabolism [20], we compared fGMCs between 29 singleton males and 23 singleton females aged 42–467 days using 132 samples.

(c) Statistics
We used R (R Development Core Team, v. 2.15.0). The threshold for significance was at 5 per cent, tests were two-tailed. Statistics are quoted as mean ± s.e.m. We used linear mixed-effects models (lme4 library) with the reciprocal square root transformation of fGMCs as the response, and mother and cub identities as scalar random effects to test whether fGMCs were affected (i) in twins by prey abundance, the
interaction between within-litter dominance status and age category and the interaction between within-litter dominance status and sex composition, and (ii) in singletons by sex and prey abundance. To assess significance of fixed factors and interactions, we used log-likelihood ratio tests ($\chi^2$). To determine significant differences between prey abundance levels, we used a post hoc analysis based on a Markov Chain Monte Carlo (MCMC) simulation (LMERConvenienceFunctions library, see electronic supplementary material).

For the within-litter comparison, we used all faeces produced by both members of the same litter when young, and calculated mean fGMCs for dominants and subordinates. To increase robustness, we first used a Wilcoxon signed-rank test ($V$) to check whether subordinates had higher fGMCs than their dominant siblings. We then tested the importance of litter sex composition on fGMCs of dominants using an ANCOVA with sex composition as explanatory variable and fGMCs of the subordinate as covariate, as we expected fGMCs of paired siblings to be positively correlated. fGMCs were transformed using a reciprocal square root transformation. Residuals of all models were normally distributed (Lilliefors test), and variances showed no heterogeneity (residual plots).

3. Results

Overall, siblings had significantly higher fGMCs during low prey periods ($\chi^2 = 7.999, p = 0.018$ (figure 1a) post hoc: low versus medium $p$(MCMC) = 0.013, low versus high $p$(MCMC) = 0.049 and medium versus high $p$(MCMC) = 0.90). When young, subordinates had significantly higher fGMCs than dominants ($\chi^2 = 4.168, p = 0.041$; figure 1b). Dominant females with a subordinate brother had higher fGMCs than dominant brothers. Dominant blue-footed booby ($Sula nebouxii$) siblings also showed marked increases in corticosterone concentrations when paired with non-submissive chicks [24]. An alternative explanation [20] that sex-specific metabolism might cause differences in glucocorticoids in a free-ranging mammal. Higher fGMCs in subordinates than dominants probably resulted from an increased allostatic load during several months of competition for and frequent aggressive exclusion from milk [5,11].

In the Serengeti, when mothers are absent on long-distance commuting trips, litters are not nursed for several days, requiring cubs to mobilize energy from body reserves [11–13]. During periods of low prey abundance with infrequent nursing, twins but not singletons had higher fGMCs than when they were nursed daily, suggesting that sibling competition had a stronger effect than hunger on allostatic load. Furthermore, the fGMCs we report from twins should be higher than those in populations where long-distance foraging is absent [22].

Dominants should have a high allostatic load when frequently challenged by subordinates [3]. In spotted hyaena litters, dominant females are more challenged by hungry subordinates than dominant males [5], possibly because subordinates with dominant sisters are more at risk of facultative siblicide than subordinates with dominant brothers [5,13,23]. Accordingly, dominant sisters had nearly four times higher fGMCs than dominant brothers. Dominant blue-footed booby ($Sula nebouxii$) siblings showed marked increases in corticosterone concentrations when paired with non-submissive chicks [24]. An alternative explanation [20] that sex-specific metabolism might cause differences in glucocorticoids in a free-ranging mammal. Higher fGMCs in subordinates than dominants probably resulted from an increased allostatic load during several months of competition for and frequent aggressive exclusion from milk [5,11].

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4. Discussion

In young twins, subordinates had higher fGMCs than dominants, and amongst dominants, females had higher fGMCs than males, particularly when their siblings were brothers. These results indicate that, as predicted [2,3], competition for dominance status and access to milk increased allostatic load.

Experimentally enlarged guinea pig ($Cavia aperea$) litters had elevated cortisol concentrations [21]. Our study is the first to demonstrate an effect of within-litter dominance on glucocorticoids in a free-ranging mammal. Higher fGMCs in subordinates than dominants probably resulted from an increased allostatic load during several months of competition for and frequent aggressive exclusion from milk [5,11].

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