Sibling rivalry: training effects, emergence of dominance and incomplete control

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Within-brood or -litter dominance provides fitness-related benefits if dominant siblings selfishly skew access to food provided by parents in their favour. Models of facultative siblicide assume that dominants exert complete control over their subordinate sibling’s access to food and that control is maintained, irrespective of the subordinate’s hunger level. By contrast, a recent functional hypothesis suggests that subordinates should contest access to food when the cost of not doing so is high. Here, we show that within spotted hyena (Crocuta crocuta) twin litters, dominants most effectively skew access to maternal milk in their favour when their aggression prompts a highly submissive response. When hungry, subordinates were less submissive in response to aggression, thereby decreasing lost suckling time and increasing suckling time lost by dominants. In a species where adult females socially dominate adult males, juvenile females were more often dominant than males in mixed-sex litters, and subordinate sisters used more effective counter-tactics against dominant brothers than subordinate brothers against dominant sisters. Our results provide, to our knowledge, the first evidence in a mammal that dominant offspring in twin litters do not exert complete control over their sibling’s access to resources (milk), and that sibling dominance relationships are influenced by sibling sex and training effects.

Keywords: sibling rivalry; spotted hyena; aggression; dominance; training effects

1. INTRODUCTION
Although siblings may provide each other with indirect fitness benefits [1], within-brood or -litter asymmetric competition may result in fitness costs to the subordinate and fitness benefits for the dominant sibling [2]. Dominants that selfishly consume the largest share of food provided by parents can benefit from increased growth and survival, whereas subordinates may suffer reduced growth and survival [3,4]. Theoretically, siblings should avoid escalated conflicts by adhering to dominance conventions based on differences in resource-holding power, unless the benefits outweigh their costs [5,6]. Competitive asymmetries may be conferred by birth order in avian species with marked asynchronous hatching [7,8], or by intrinsic factors such as fighting ability [9–11]. Alternatively, dominance may result from arbitrary historical asymmetries such as behavioural training effects, in which the experience of winning or losing a contest alters an individual’s probability of winning or losing future contests [12,13]. Few studies have investigated these effects in mammals (but see Hsu et al. [14]) and we know of no study that demonstrated this phenomenon in a free-ranging mammal.

Avian models of facultative siblicide predict that as parental food provisioning rates decline, dominant chicks should aggressively increase their share of food [2,5,6]. Such a response occurs in several bird species [7,8,12] and at least one mammal, the spotted hyena Crocuta crocuta [4], and may lead to facultative siblicide through enforced starvation or physical damage [2]. The models assume that dominants have complete control over the share of food received by subordinates, regardless of the subordinates’ hunger level. As death might result from a hungry chick’s submissiveness, selection should act against subordinates accepting complete control by dominants [15]. Extending the ‘desperado effect’ [16] idea, the ‘desperado sibling hypothesis’ [17] postulated extreme aggressiveness by subordinate chicks without survival prospects in obligatory siblicidal species. A recent hypothesis [18] suggests that in facultatively siblicidal species, subordinates should adjust their submissiveness to their survival prospects by increasing assertiveness towards dominants as the cost of subordination in terms of likelihood of starvation increases.

Here, we investigate sibling rivalry over access to maternal teats in spotted hyena twin litters. We focus on aggression by dominants to terminate their subordinate’s access to teats and the responses of subordinates to this aggression. We quantify the degree of skew dominants achieve in terms of access to teats, test whether a process akin to a trained loser effect contributed to the emergence of the within–litter dominance relationship, and explore how hunger and sex affect the competitiveness of dominants and subordinates.

2. STUDY SPECIES AND PREDICTIONS
The spotted hyena is a territorial, social carnivore living in groups termed clans, in which females socially dominate immigrant males [19,20]. Litter size is usually one or
two [4]. Cubs completely depend on nutritious maternal milk during their first six months [21], with lactation lasting up to 18 months [22]. Females have two functional teats, and as in other mammals [23], siblings in twin litters are nursed simultaneously. There is an intense rivalry between littermates [24,25], probably because dominants achieve higher growth and survival than subordinates [4,26], which may lead to facultative siblicide through enforced starvation [4,27]. Aggression between littermates begins within hours after birth as cubs are born with open eyes and teeth erupted [28], results in the establishment of dominance, and declines with age [24]. When suckling, dominants lie parallel to their mother’s belly and subordinates typically between her hind legs (see the electronic supplementary material). To stop their sibling suckling, dominants have to terminate their own milk intake. When engaged in aggressive interactions, littermates cannot suckle and thus would benefit from a dominance convention in which subordinates submit to dominants. As a corollary, aggression should cause only a short break in suckling for dominants and a longer break for subordinates. As shown for dominance hierarchies in principle [29] and for competing chicks in broods [12], trained loser effects during repeated aggressive encounters in which assertive subordinates gradually learn to submit to dominants [13] can establish such a dominance convention without requiring body size asymmetries (see the electronic supplementary material) or other differences in resource-holding power. Such training should occur when siblings are young and dominance relationships less stable. After training is established, in older litters, subordinates should adhere to dominance conventions by showing immediate submission in response to aggression.

In the Serengeti National Park, Tanzania, fluctuating prey abundance permits assessment of the effect of declining milk provisioning by spotted hyena mothers on the aggressiveness of dominants and the assertiveness of subordinates. Fluctuations in prey abundance inside clan territories drive a social-status-linked, long-distance, central-place foraging (‘commuting’) system [20,30]. With major migratory herds present, all mothers forage inside the clan territory and nurse daily [21]. When moderately sized herds are present, mothers of high-social status and some of medium-status forage inside the territory, whereas lower ranking females commute to forage on distant major herds for periods of one to several days [31]. When all migratory herds are elsewhere, all mothers commute long distances and nurse their offspring only once every few days [4,21]. As maternal absence intervals increase,hungry dominants should aggressively seek to decrease access of subordinates to maternal teats [24], whereas hungry subordinates should be less willing to adhere to dominance conventions, become more assertive [18] and resume suckling faster after aggression. In response to increased assertiveness by subordinates, hungry dominants should escalate aggression [32] that should reduce their suckling time.

In our study population, the proportion of males at three months of age, after the age at which siblicide usually occurred [27,33], showed no bias (0.52) but masked a female bias among singletons [27]. This suggests that females in both same-sex [33] and mixed-sex litters survived intense sibling rivalry more often than males and may be better at monopolizing teats than males. If so, then in mixed-sex litters, there should be a female bias among dominants, and subordinate females should reverse within-litter dominance more often than subordinate males. If dominant sisters are better competitors than dominant brothers, hungry subordinates threatened by starvation should be more assertive against dominant sisters than against dominant brothers.

3. METHODS
(a) Data collection
The study was conducted between 2007 and 2009 as part of an ongoing, long-term study on three clans in the centre of Serengeti National Park. Individuals were recognized by their spot patterns [19,20], cubs without spots by ear notches, scars or bald patches [24]. Age and sex were determined using standard methods (see the electronic supplementary material). Twin litters were observed at clan communal dens during the periods of several hours around dawn and dusk. We recorded 97 video focal samples of 15 min duration [34] at the start of the first suckling session, when aggression is highest, after a mother arrived at a den [24]. We analysed sibling behaviours in 38 twin litters from 34 mothers (mean focal samples per litter 2.6 ± 1.7, range 1–7). Litters were aged between 9 and 346 days; 50 per cent of focal samples were from litters of less than 81 days.

(b) Predictor variables
(i) Hunger level
We used three predictor variables known to significantly affect frequency of nursing and cub growth rates [21,31]: prey abundance, maternal den attendance and maternal social status (standardized rank). Standardized rank (mstatus) was calculated by evenly distributing adult female ranks between the highest (+1) and the lowest rank (−1), with the median rank being 0 [35]. Prey abundance (prey) was scored for each observation period as: low (approx. 3.3 animals km−2), medium (approx. 31 animals km−2), or high (approx. 238 animals km−2) [20]. Maternal den attendance was extracted from detailed records of all individuals within a 100 m radius of communal dens during dawn and dusk observation periods [4,21,31]. Cubs were defined as ‘fed’ when mothers were observed at the den during a 30 h period prior to the focal sample and in two focal samples during high prey abundance when cub bellies indicated they had been recently fed. Cubs were defined as ‘hungry’ when mothers were not seen at the den in the previous 30 h during medium and low prey abundance and known to be absent on long-distance foraging trips [30]. Details are provided in the electronic supplementary material.

(ii) Sibling tactics
We scored aggressive behaviour by dominants (domscore) against their suckling subordinates as: (+1) low, (+2) moderate, and (+3) high-intensity aggression. We scored the submissiveness of the subordinate’s response (subscore) during the following 5 s as: (−2) highly submissive, (−1) marginally submissive, (0) no response, (+1) marginally aggressive, and (+2) moderately aggressive (for details, see the electronic supplementary material, table S2). Dominants initiated 94.5 per cent (1053 of 1115) of agonistic interactions. We calculated for each focal sample mean scores for the dominant’s behaviours (mean.domscore) and the subordinate’s response (mean.subscore). A high mean.domscore indicated high-intensity aggression, a high mean.subscore...
assertive or aggressive responses and a low mean $\text{subscore}$ highly submissive responses.

(c) Dependent variables

(i) Lost suckling time
We measured the time (latency) elapsed after each aggressive act by the dominant until each sibling resumed suckling and calculated means per focal sample for the dominant and the subordinate (mean latencies $\text{domlat}$ and $\text{sublat}$). If a subordinate did not resume suckling within 15 min after aggression, then its latency was scored as a minimum of 900 s ($n = 5$ focal samples in five litters).

(ii) Relative delay
For each focal sample, we calculated the relative delay ($\text{rel.delay}$) between siblings as the standardized proportion of time lost suckling by the subordinate ($\text{sublat}$) relative to that of the dominant: $\text{rel.delay} = 1 - (\text{domlat}/\text{sublat})$. When $\text{rel.delay}$ tended towards $+1$, dominants had a competitive advantage because subordinates took far longer to resume suckling than dominants ($\text{sublat} \gg \text{domlat}$). In seven of 97 focal samples, $\text{domlat}$ was slightly higher than $\text{sublat}$. In these cases, we set $\text{rel.delay}$ to 0, i.e. no relative delay for the subordinate.

(iii) Sibling growth rates and suckling duration
We measured growth rates of paired dominants and subordinates in 13 twin litters aged approximately 90 days as described by Hofer & East [21]. We calculated the average duration of suckling bouts after a mother’s return from 115 suckling bouts of 45 mothers in 84 twin litters.

(iv) Loser effect
We used focal samples with a minimum of 17 interactions (20 focal samples, 14 litters; electronic supplementary material). A training period requires increased submissive-ness in subordinate’s responses ($\text{subscore}$) during a focal sample, which should produce a decrease in the value of $\text{subscore}$ and a negative slope in a linear regression of $\text{subscore}$ against time. To see whether training periods were more apparent in younger than older litters, we tested for an increase in regression slopes with age (after logarithmic trans-formation (to base 10) of age to obtain a linear relationship). An established loser effect in older litters would require that older subordinates respond submissively after the first aggressive act in a suckling bout. This should produce a decrease in the intercepts of the linear regression of $\text{subscore}$ against time with increasing litter age. To test this, we fitted a model using an exponentially declining function. The residuals of all regressions did not deviate from normal distribution ($\text{Lilliefors}$ test) and variances showed no evidence of heterogeneity (residual plots).

(v) Dominance and its reversal
Data from mixed-sex litters in study clans between 1989 and 2011 were used to test whether: (i) females were more often dominant than males, and (ii) subordinate females gained dominance more often than subordinate males during dominance reversals.

(d) Statistical analysis
Unless stated otherwise, we used R (R Development Core Team, v. 2.11.1), set the threshold for significance at 5 per cent and refer to numbers of litters as sample size. All tests were two-tailed. Statistics are quoted as means ± s.d. We calculated mean latencies from non-parametric Kaplan–Meier survivalship functions [36] in SYSTAT v. 13.0 (Systat Inc., San Jose, CA, USA) by incorporating right-censored data when subordinates did not resume suckling within at least 15 min. For each litter, we calculated mean latencies for dominants ($\text{domlat}$) and subordinates ($\text{sublat}$) from the means per focal sample to avoid pseudoreplication. We applied Wilcoxon signed-rank tests to compare mean latencies and growth rates of paired dominants and subordinates. We tested deviations from unity in the sex ratio of dominants in all mixed-sex litters using an exact binomial test. In litters where dominance reversals occurred, the sex ratio of subordinates successful in reversing dominance was also examined using an exact binomial test.

We used generalized linear-mixed models (lme4 library of R; [37]) to assess the influence of our predictors on the dependent variables: (i) $\text{rel.delay}$, (ii) $\text{domlat}$ and (iii) $\text{sublat}$ with litter identity as a random factor to avoid overrepresentation of individual litters (details in the electronic supplementary material). We used an information-theoretic approach to compare fitted models and selected those with the smallest values for the Akaike information criterion (AIC). When two models differed in their AIC values by less than 2, both can be considered competitive for interpretation [38]. In this case, we present and interpret with caution the effects of the variables included in the most complete model (when two nested models were compared) as they had a strong biological relevance (details in the electronic supplementary material).

The residuals of all presented models did not deviate from normal distribution ($\text{Lilliefors}$ test) and variances were not heterogeneous (residual plots). Electronic supplementary material, table S3 contains estimated coefficients and standard errors for the selected models.

We tested whether the assertiveness of the subordinate ($\text{subscore}$) in hungry and fed litters depended on the sex of the dominant by extending a non-parametric hierarchical mixed model [39,40] to a two-way layout for hunger level and sex of dominant sibling, with focal samples nested within litters as random factor, and implemented it in SAS v. 9.3. For a majority of litters, focal samples were available only at one hunger level. If focal samples of a litter were recorded at both hunger levels, then we included only the level where the highest number of agonistic interactions occurred to ensure independence of data points. Values of $\text{subscore}$ were ranked to obtain mean ranks for each litter. Significance threshold was adjusted to 0.025.

4. Results

(a) Lost suckling time
When dominants stopped suckling to aggressively exclude subordinates from teats, their mean latency to resume suckling was shorter than that of subordinates (all ages: dominants: $3.0 \pm 2.5$ s, subordinates: $48.2 \pm 114.1$ s, Wilcoxon signed-rank test: $V = 30$, $n = 38$, $p < 0.0001$). This difference was extreme in younger (less than 120 days: dominants: $3.3 \pm 2.7$ s, subordinates: $66.4 \pm 138.2$ s, $V = 14$, $n = 24$, $p < 0.0001$) and still apparent in older litters (more than 120 days: dominants: $2.6 \pm 2.2$ s, subordinates: $17.0 \pm 40.4$ s, $V = 3$, $n = 14$, $p = 0.003$). Without the five focal samples in which the subordinates did not resume suckling, the differences remained (all ages: dominants: $3.2 \pm 2.8$ s, subordinates: $10.0 \pm 10.1$ s, $V = 34$, $n = 38$, $p < 0.0001$) and were still apparent within both age classes (less than 120 days: $3.1 \pm 2.5$ s, subordinates: $7.8 \pm 10.7$ s, $V = 30$, $n = 38$, $p = 0.003$).
Figure 1. The relative delay (rel.delay) of dominant and subordinate siblings to return to suckling after aggression by the dominant interrupted suckling, in relation to (a) level of assertiveness of the subordinate (mean.subscore), (b) hunger level of the litter, and (c) age (days), as predicted by model 1. The relative advantage of the dominant is higher when the relative delay tends towards 1, i.e. when the dominant returned much faster to suckle than the subordinate. Tick marks inside the x-axis indicate location of individual data points, dotted lines indicate confidence intervals. Unequal spacing on the y-axis is used to obtain straight lines (see the electronic supplementary material for details on the methods used to produce figures 1–3).

Table 1. Summary of the best models with smallest Akaiake information criterion (AIC) fitted to predict variation in: (i) the relative delay between siblings (rel.delay), (ii) the suckling time lost by the dominant (domlat), and (iii) the suckling time lost by the subordinate (sublat). (ΔAIC is the difference between the AIC of the intercept model and the AIC of the candidate model. All models included litter identity as a random effect.)

<table>
<thead>
<tr>
<th>selected models (with similar AIC (2 units))</th>
<th>AIC</th>
<th>ΔAIC</th>
</tr>
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<td>time lost suckling by the dominant (domlat)</td>
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<td>(model 2)</td>
<td>108.26</td>
<td>38.65</td>
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<tr>
<td>mean.subscore, age120*, hunger</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(model 3)</td>
<td>239.60</td>
<td>111.09</td>
</tr>
<tr>
<td>time lost suckling by the subordinate (sublat)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>domlat, mean.domscore, age, mean.subscore (−1.7)*scomp2c</td>
<td>238.77</td>
<td>111.92</td>
</tr>
</tbody>
</table>
| (d) Suckling time lost by subordinates

Suckling time lost by subordinates following aggression by dominants: (i) increased as the mean suckling time lost by dominants increased (figure 3a), (ii) decreased with increasing assertiveness of subordinates (figure 3b), (iii) decreased with age (figure 3c), and (iv) increased as the mean suckling time lost by subordinates increased (figure 2a), (ii) intensity of aggression of dominants increased (figure 2b), (iii) age increased (figure 2c), and (iv) assertiveness of subordinate responses increased, especially when the subordinate was female and the dominant was male (figure 2d(ii)). Dominants lost suckling time more slowly with increased assertiveness of subordinate responses in all-female litters (figure 2d(iii)) and when the subordinate was male and the dominant was female (figure 2d(i), ‘model 2’ in table 1).

(e) Sibling growth rates and suckling duration

Mean growth rates of dominants (88.5 ± 26.3 g per day) were significantly higher ($V=84, n=13, p=0.005$) than that of their paired subordinate siblings (81.4 ± 23.8 g per day) at a mean age of 83.4 ± 3.5 days for dominants (median 84.3) and 81.8 ± 5.6 days
Subordinate assertiveness

As the sex of the dominant changed how hunger level affected the assertiveness of the subordinate (F$_{1,18.5}$ = 9.08, n = 38, p = 0.007), we performed a post hoc analysis for the effect of the sex of the dominant stratified at each category of hunger level. Within hungry litters, subordinates with a dominant sister were more assertive than subordinates with a dominant brother (F$_{1,17}$ = 6.81, n = 19, p = 0.018), whereas within fed litters, assertiveness of subordinates was independent of the sex of dominants (F$_{1,17}$ = 2.80, n = 19, p = 0.113; electronic supplementary material, figure S3).

Loser effect

All slopes of the regression of the intensity of submissive response against time per focal sample were highly significant. Intensity strongly increased during focal samples in response to repeated aggression in younger litters, resulting in strongly negative regression slopes and indicating training by a process akin to a loser effect (figure 4). With increasing age, the regression slopes of subscore against time increased (log-transformed linear regression against age, F$_{1,18}$ = 12.93, p = 0.002, adjusted r$^2$ = 0.39) and older subordinates showed higher levels of submission from the start of a suckling bout, resulting in rapidly decreasing intercept values with age (y = −1.62 + 7.04 e$^{-0.045 \text{ age}}$; electronic supplementary material, figure S4).

Dominance and reversals in mixed-sex litters

In 66.5 per cent (121/182) of mixed-sex twin litters, the dominant was female, a significant bias (exact binomial test: p = 0.0001, 95% confidence interval (95% CI): 59.1–73.3%). Dominance reversals occurred in 7.0 per cent (27/388) of litters. In mixed-sex litters, 61.5 per cent (8/13) of subordinates gaining dominance were females, and although this proportion did not deviate from chance, it was in the expected direction (p = 0.58, 95% CI: 32.7–83.4%).

5. DISCUSSION

Our results demonstrate that in spotted hyena twin litters, dominants skew access to maternal teats by using periodic aggression against subordinates during suckling bouts. Dominants achieved the highest skew when subordinates were highly submissive (figures 1–3), when litters were recently nursed (figures 1 and 3) and when young (figures 1–3). Interestingly, in this female-
dominated species, counter-tactics by assertive subordinate sisters were more effective against dominant brothers than counter-tactics by subordinate brothers against dominant sisters (figure 2). Dominant sisters were highly challenged by subordinates when hungry (electronic supplementary material, figure S3), suggesting that subordinates with dominant sisters face a greater risk of siblicide than siblings with dominant brothers [27,33]. The behaviour of competing siblings was modified by sex, age and hunger, included trained loser effects, dominance conventions and assertive counter-tactics by hungry subordinates. When parents (or other adults) frequently feed offspring with solid food items (e.g. in meerkats, Suricata suricatta; [41]), sibling competition is not fatal and may be ameliorated through begging. By contrast, in spotted hyenas, Galápagos fur seals (Arctocephalus galapagoensis) and sea lions (Zalophus wollebaeki) [42], offspring dependence on maternal milk is exceptionally long, and lactating females leave their offspring for several days during foraging trips. In such systems, low and fluctuating levels of resources result in infrequent and unpredictable nursing periods, favouring the evolution of intense sibling rivalry and facultative siblicide [2]. Subordinate spotted hyena siblings were excluded from maternal teats for substantially more time than dominants. As dominants at three months (this study) and at six months [4,26] grew significantly faster than subordinates, aggressive exclusion of subordinates is likely to reduce their milk intake below that of dominants. H. Hofer, E. Lechner, W. Golla & M. L. East 1987–2004, unpublished data show that in paired measurements (n = 16 litters, age = 229 days), milk intake rate during a suckling bout was significantly higher for dominants (9.0 ± 2.2 g min⁻¹) than by subordinates when hungry (electronic supplementary material, figure S3), suggesting that subordinates with dominant sisters face a greater risk of siblicide than siblings with dominant brothers [27,33]. The behaviour of competing siblings was modified by sex, age and hunger, included trained loser effects, dominance conventions and assertive counter-tactics by hungry subordinates. When parents (or other adults) frequently feed offspring with solid food items (e.g. in meerkats, Suricata suricatta; [41]), sibling competition is not fatal and may be ameliorated through begging. 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subordinates (5.8 ± 1.4 g min⁻¹). The average delay of subordinates to resume suckling after aggression by dominants of 6.8 s therefore implies a loss of 657 mg of milk, equivalent to 6.37 kJ on each occasion. Hence, even a small skell in lost suckling time should ultimately provide a significant increase in growth rate for the dominant.

Provided subordinates were recently fed, they responded submissively when challenged by dominants, were easily excluded from teats (figure 3a, left) and dominants achieved a higher skew in terms of access to teats (figure 1b). Four (of five) litters in which the subordinate did not resume suckling for at least 15 min after aggression had been recently nursed. These results are in accordance with the hypothesis [18] that subordinates should abide by an established dominance convention provided the cost of doing so is not too large.

To subordinates, the cost of respecting convention should rise with hunger [18]. If subordinates strictly adhered to conventions even when hungry, then despotic dominants (which may also be hungry) might consume most or all milk. If maternal input is low and mothers absent for several days, subordinates can starve [4]. Hungry subordinates responded less submissively when challenged by dominants, thereby decreasing their lost suckling time (figure 3b) and increasing that lost by dominants (figure 2d). Such responses incited dominants to use longer and more intense aggression such as bite-shakes and chases. Hence, interactions between hungry siblings developed into escalated conflicts, resulting in an increase in lost suckling times for both (figures 2a and 3a). In 7.2 per cent of focal samples, subordinates resumed suckling more quickly than dominants after aggression; in these cases, aggression failed to skew suckling in the dominant’s favour and most cases (five of seven focal samples; four litters) involved hungry litters with particularly thin cubs. The remaining two samples were recorded when prey abundance was low. In contrast to aggressive competition in some birds [7,8], our results illustrate that aggression by dominant spotted hyena siblings sometimes fails to provide clear benefits and support the idea that subordinates adjust their response to sibling aggression in relation to the costs of subordination determined by ecological conditions [18].

Young subordinates significantly increased the intensity of their submission when repeatedly attacked by dominants (figure 4). This suggests a behavioural process akin to training for a loser effect in young litters and may explain why young dominants achieved the highest skew in terms of access to teats. With increasing age, dominance relationships acquired stability because older subordinates were submissive from the beginning of a suckling bout (electronic supplementary material, figure S4). This suggests that after training is established, subordinates behave as ‘trained losers’ towards their siblings. It is unknown whether subordinates would submit in a similar way against unfamiliar opponents, as demonstrated in blue-booby chicks (Sula nebouxi) [12]. Our results are consistent with a recent model [43] that predicted more pronounced training effects in young and naive individuals, because they are unaware of, but willing to assess, their own fighting ability. It is also likely that a trained winner effect benefited dominants during interactions with their sibling because subordinates became increasingly submissive. Young and hungry dominants may escalate aggression against subordinates during sucking bouts if the subordinate’s behaviour is not sufficiently submissive—in other words, dominants ‘punish’ [32] subordinates until their response and delay to resume suckling is sufficient. When older and probably when fed, subordinates know they stand to lose less suckling time by responding appropriately to initial aggression by the dominant than prompting a series of escalating punishments by not doing so.

Owing to presumed sex asymmetries in competitiveness, it was repeatedly reported that during conflicts, females are weaker competitors than males [44]. This is clearly not the case in spotted hyena litters. Indeed, subordinate sisters were more effective than subordinate brothers in increasing suckling time lost by dominants (figure 2f). In five (of six) litters in which dominants lost more suckling time than subordinates, the subordinates were females. Hence, subordinate females may be especially effective in countering aggression, particularly by dominant brothers. In 66.5 per cent of mixed-sex twin litters, females were dominant, and subordinate females tended to reverse litter dominance order more frequently (61.5%) than subordinate males. As dominants grow faster than subordinates [4, this study] and age at parturition of adult females declined with higher cub growth rate [31], it is possible that fitness benefits of dominance are higher for female than male cubs. Subordinates with dominant sisters increased their level of assertiveness during conflicts when their hunger level increased (electronic supplementary material, figure S3), further suggesting that females are better competitors than males.

We studied sibling rivalry in a dynamic framework of interactions and addressed the roles of both dominants and subordinates in shaping the dominance relationship. During conflicts, dominants in spotted hyena litters trade off sibling aggression and suckling. Unlike the despotic control exerted by dominants on the reproduction of subordinates in species with a high reproductive skew [45], dominant spotted hyena siblings do not exert complete control over their littermate’s access to maternal teats. Instead, there is substantial variation in the degree of control and this control is a dynamic rather than static state. Dominants reared during years when overall cub growth rates were low, dispatched subordinates in 9 per cent of litters through enforced starvation [4,27]. In other litters, the long-term stability of dominance relationships was successfully undermined by (possibly assertive and hungry) subordinates and led to dominance reversals. The advantage of dominants during competition is therefore not absolute and depends on the interplay of age, maternal input, the sex of both siblings and their behavioural tactics.

All procedures were performed in accordance with the requirements of the Leibniz Institute for Zoo and Wildlife Research Ethics Committee on Animal Welfare.

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