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Original Article

Aggression in Columbian ground squirrels: relationships with age, kinship, energy allocation, and fitness

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Matrilineal kin groups are common in social mammals and often exhibit cooperative behaviors. Social interactions in such groups may have varying consequences on fitness depending on the number of kin present. We used social network analysis to study which factors (including individual spatial distribution, sex, age, and kinship) affected patterns of aggressive interactions in Columbian ground squirrels during the important breeding period of lactation. In addition, we studied how patterns of aggressive interactions affected female reproduction and fitness. Received aggressions lessened as ground squirrels aged, likely reflecting greater dominance in older individuals. Outwards aggression peaked at prime reproductive age, but decreased in older individuals. In females, outwards aggressiveness was positively related to energy allocated to reproduction and annual fitness, suggesting that highly aggressive females were either of high intrinsic quality or were able to defend high-quality territories. Finally, female–female aggression was primarily targeted toward non-kin individuals, revealing the advantage for breeding adult females of having close kin neighbors that were also breeding. Thus, breeding females that were close kin appeared to be “genial neighbors” that benefited from increased fitness, highlighting the role of kin selection in mitigating the costs (e.g., injuries, stress) of aggression.

Key words: aggressiveness, fitness, kin selection, philopatry, social network, territoriality.

INTRODUCTION

Aggressive behavior between individuals is common in social groups, allowing individuals to gain access to important resources such as territories, food, or sexual partners (Clutton-Brock et al. 1979; Isbell 1991; Adams 2001). Besides obvious benefits, aggressive interactions also carry costs, in terms of energy expenditure (Rovero et al. 2000) and stress or injuries (Boonstra et al. 2001; Viblanc et al. 2012), which can influence survival (Moore et al. 1996; Boonstra et al. 2001) and reproductive success (Lea et al. 2010; Betini and Norris 2012). Thus, aggressive interactions and territorial strategies often result from a cost/benefit fitness balance that depends on the individual attributes of opponents and the expected outcome of the conflict (Enquist and Leimar 1983, 1987). For instance, to avoid unnecessary injury costs associated with overt social aggression, animals may assess their opponents based on their likelihood of winning a contest (resource-holding power; Parker 1974; Enquist and Leimar 1983) before escalating into physical disputes (Maynard Smith and Parker 1976). Resource-holding power is often determined by resource value (Enquist and Leimar 1987), and individual attributes linked to social dominance and age (Hale 1994; Murray et al. 2007) or individual condition or quality (Clutton-Brock and Albon 1979; Mowles et al. 2010).

Individual social attributes, including aggressive behavior, might depend on the presence of kin. Specifically, kin selection...
on aggressive behavior could favor the evolution of lowered rates of aggression among close relatives. Lowered aggression between close kin may thus be seen as a form of cooperation that produces increased fitness (Viblanc et al. 2010; Dobson et al. 2012; Viblanc et al. forthcoming). Kin selection may promote the evolution of cooperative behaviors and sociality, because kin individuals share a high proportion of genes by common descent (Hamilton 1964; Grafen 2006; Gardner et al. 2011). If interacting with kin provides accrued fitness benefits to donors and recipients, decreased competition and aggression between kin individuals may be expected (Silk et al. 1981; Brown and Brown 1993; Watson et al. 1994) and kin-selected philopatry might ensue (Arnaud et al. 2012).

In this study, we examined patterns of social aggression in Columbian ground squirrels (Citellus columbianus), a sciurid rodent species with a philopatric matrilineal social system (King and Murie 1983; King 1989a; Arnaud et al. 2012). Our aim was to 1) characterize the effects of individual attributes (sex, age) and the effect of kin on social aggression, 2) assess the relationships between social aggression and maternal investment into somatic and reproductive processes, and 3) assess the overall effects of social aggression on female fitness. We did so by focusing on the period of female lactation, an energetically demanding period in mammals (Prentice and Prentice 1988), where the costs of increased aggression may be high.

Columbian ground squirrels are a hibernating species with a short (3–4 months) active season during which females come into estrus for only a single day (Murie and Harris 1982; Dobson et al. 1992). Both males and females aggressively defend individual territories, male territoriality being highest during the mating season (a few weeks between mid-April and early May; Murie and Harris 1978; Manno and Dobson 2008). During reproduction, females cluster into contiguous home ranges <1000 m² (Festa-Bianchet and Boag 1982), which are established around individual nest burrows in which they raise a litter of 3 young on average (Dobson and Murie 1987; Risch et al. 1993). Although lactating females are individually territorial (Murie and Harris 1980), an exclusive use of the home range is not achieved, and territorial overlap with neighbors may be high (Festa-Bianchet and Boag 1982). Whereas female–female aggressiveness is highest during lactation (Murie and Harris 1988), the occurrence of kin groups might allow females in matrilineal to monopolize burrow systems and resources by preferentially directing aggressiveness toward non-kin individuals (King 1989b). Such a behavioral mechanism might underlie fitness differences (increased annual litter sizes) between close kin and non-kin individuals (Viblanc et al. 2010; Dobson et al. 2012), which in turn may promote kin-selected philopatry (Arnaud et al. 2012).

Here, we used a social network (SN) analysis (Croft et al. 2008; Whitehead 2008; Krause et al. 2014) to study variation in patterns of aggressive interactions in this species. SN analysis stems from mathematical graph theory and has been used with increasing success in the field of behavioral ecology over the past 10 years (Lusseau and Newman 2004; Croft et al. 2005, 2006; Lusseau et al. 2006; Wey et al. 2008; Wey and Blumstein 2010; Sueur, Jacobs, et al. 2011; Sueur, Petit, et al. 2011; Krause et al. 2014; Kurvers et al. 2014; Silk et al. 2014). SN analysis allows capturing social complexity by considering individuals as embedded within a network of interconnected individuals (Croft et al. 2008; Pinter-Wollman et al. 2013; Silk et al. 2014; Farine and Whitehead 2015). Indeed, on top of direct interactions, individuals may also be indirectly affected by independent social interactions between conspecífics. For instance, several studies have shown how aggressive behavior between individuals may indirectly affect conspecific stress (Oliveira et al. 2001; Wascher et al. 2008; Viblanc et al. 2012), and individuals clustered within a highly aggressive social environment may pay fitness costs due to indirect relationships as well. Because female Columbian ground squirrels are known to acquire fitness benefits (through increased litter sizes) from the presence of cobreeding female kin, we expected them to act as “genial” neighbors, providing safe territory borders to close kin (Viblanc et al. 2010; Dobson et al. 2012). Infanticide at the time of juvenile weaning is relatively common in this species (Dobson 1990; Stevens 1990), and kin clusters might increase offspring survival if females are less likely to harass or kill offspring of close kin, viz. an indirect fitness benefit (Dobson et al. 2012). Thus, we predicted that fewer aggressive social interactions should be directed to close female kin. Furthermore, social aggressiveness during lactation may affect female energetics diverting time and energy away from reproduction. We expected females more involved in aggressive interactions to be able to acquire less total energy over the season (as reflected in female mass gain and mass of weaned offspring), and thus their fitness to be decreased (as reflected in the survival of females and their offspring until the next active season).

METHODS

Long-term monitoring

Columbian ground squirrels were monitored from 1992 to 2013 at the Sheep River Wildlife Provincial Park, Alberta, Canada (50°38′10″N, 114°39′56″W). The monitored population inhabits a subalpine meadow (elevation 1550 m, approximately 2.5 ha) and is clearly delimited from surrounding populations by forests and a ravine (Supplementary Material 1). Complete life histories (including age and pedigree relationships) are known for the vast majority of animals on the study site. In each year, squirrels were live-trapped within a couple of days of emergence from hibernation using live traps (Tomahawk Live Trap Co., Hazelhurst, WI; 13 × 13 × 40 cm³) baited with a small amount of peanut butter. Each ground squirrel was weighed to the nearest 5 g using Pesola® spring-silde scales and marked with numbered ear tags (Monel no. 1 National Band & Tag Co., Newport, KY) for permanent identification. In addition, each animal was given a unique dorsal mark using black human hair dye (Clairol®, Stamford, CT) for identification during field observations (see below). Throughout the mating season, we followed individual females to determine their mating day from behavioral observations and inspection of their genitalia (Murie and Harris 1982). Few females breed successfully as yearlings, and reproductive maturity is attained at 3 years for most males and 2 years for most females (Murie and Harris 1978; Neuahaus et al. 2004). Mated females were caught 22 days later, 2–3 days before expected parturition (Murie and Harris 1982), and brought to an on-site field laboratory to give birth. Females were housed in poly-carbonate cages with metal tops (48 × 27 × 20 cm), and given wood chip bedding and shredded newspaper for nest-building material. Food, including grains (a molasses-enriched horse feed), fresh apple and fresh lettuce, and water were provided ad libitum twice a day. When litters were born, mothers (nearest 5 g) and pups (nearest 0.01 g) were weighed. At birth, pups were sexed and marked with a small tissue biopsy (Hare and Murie 1992) and pups could thus be attributed to their mother. This allowed determination of kin relationships between females. Pups born in the same year and from the same mother were assigned as littemate kin, and pups born from the same mother but in different years as nonlittermate kin.
In Columbian ground squirrels, kin recognition occurs by social learning of littermates in the natal nest burrow (Hare and Murie 1996), and only littermate kin appear to have a positive effect on female fitness (Viblanc et al. 2010). Mothers and neonatal young were released approximately a day after birth into their nest burrows (known from behavioral observations prior to capture and marked with colored flags). Complete litters and the mother were caught when the young emerged from nest burrows at weaning about 27 days later, and the young were ear tagged for permanent identification and weighed to the nearest 1 g. Immigration of conspecifics occurs primarily in late June and July, late in lactation or afterwards (Boag and Murie 1981; Neuhäus 2006), so populations are stable for most of the breeding period. Emigration from the population mostly concerns yearling males (Wiggett and Boag 1989), and there is little recorded female emigration in our population.

Behavioral data

Scan sampling

During the 2013 lactation period from 10 to 27 June, behavioral observations were performed daily (08:00–12:00 and 14:00–19:00) from the top of 4-m high observation towers, excluding the hottest hours of the day when little activity was observed on the meadow. Visual scans of the meadow were performed every 10-min, recording all individuals present and their activity at that time (foraging, grooming, standing or sitting alert, loping, laying, digging, gathering nest material, rolling on the ground). During each scan, the location of each individual on a Cartesian 10 m × 10 m flagged grid was recorded to within 1 m. Scan locations (a total of 1655 location points, on average 25 per individual) were used to establish the center of activity of individual home ranges (kernelUD functions in the R package “adehabitat”; Calenge 2006) (see below).

All occurrence behavior

Scans were interrupted any time a social interaction between 2 individuals was seen, and all occurrences of dyadic aggressive interactions for which the identities of both the initiator and receiver were known with certainty were recorded (22% of all aggressive interactions were removed because only one party was known with certainty). This produced 255 known interactions between 161 dyads (38 females, 21 males). Few interactions (N = 14) were recorded between more than 2 individuals at a time, and those were excluded from the analysis. Aggressive behaviors were classified as chases (N = 216), territorial displays (N = 9), and fights (N = 30).

Social networks

Dyadic interaction matrices were used to build 2 separate social aggression networks (see below) using Cytoscape 2.8.3 (http://www.cytoscape.org), with individuals depicted as nodes and aggressive interactions as edges (Figure 1). For each individual in the networks, we calculated the following node-based metrics using the “igraph” package in R (Csardi and Nepusz 2006): 1) Degree centrality corresponds to the number of individuals with whom aggressive interactions occurred. Two separate measures of degree centrality were determined for directed aggressive interactions. In-degree is the number of individuals from whom aggressions were received (mean ± standard deviation [SD] = 2.49 ± 2.02). Out-degree is the number of individuals to whom aggressions were given (mean ± SD = 2.49 ± 2.38). 2) Strength corresponds to the sum of aggressive interactions experienced by an individual. Strength was also separated into received (in-strength; mean ± SD = 3.92 ± 4.08) and given (out-strength; mean ± SD = 3.92 ± 4.33) aggressive interactions. 3) Eigenvector centrality (mean ± SD = 0.12 ± 0.19) measures the second-order connectivity of individuals, taking into account the number of connections an individual experienced and the number of connections experienced by its neighbors (Wasserman and Faust 1994). Individuals with high eigenvector centralities thus exchange a large number of aggressions with conspecifics, and those conspecifics also exchange a large number of aggressions between themselves. For territorial ground squirrels, these aggressions occur at a local level—indeed, eigenvector centrality is negatively related to individual home range (ρ = −0.30, S = 38.025, P = 0.025)—so that squirrels with high eigenvector centralities interact within hotspots of aggressiveness.

Overall aggression network

The first network consisted of all recorded interactions (males and females) and was used to investigate the influence of individual spatial distribution, sex, and age on social aggression.

Effects of spatial distribution on social aggression

We analyzed the relationship between a matrix of dyadic aggressive interactions and a matrix of dyadic spatial distances based on the centroid of individual home ranges. We applied permutation tests for simple linear regression models for data organized in matrices of dyadic relationship among n individuals by using the “double-semi-partialing” method (Dekker et al. 2007) developed in the m rqap.dsp function from the R package “asnipe” (Farine 2013).

Assortment patterns in the network

We tested whether aggressive interactions were assorted for individuals of the same sex or age. We calculated assortativity coefficients (i.e., tendency of an individual to be connected to similar individuals; Newman 2003) and compared them with a distribution of assortativity coefficients derived from 1000 randomized interaction matrices where the number of connections was kept constant but individual characteristics randomized. Significant correlation coefficients were assigned based on the 95% confidence intervals (CIs) of their randomized distributions. Assortativity coefficients were calculated using the assortativity.discrete (sex) and assortativity.continuous (age) functions in the R package “assortnet” (Farine 2014), while randomization was coded in R v. 3.1.2.

Effects of individual attributes on social aggression

We tested whether network characteristics changed according to individual sex or age. Because network measures are usually not independent (Croft et al. 2011), we tested whether individual sex and age were significantly associated with particular positions in the network using a randomized network permutation technique. Specifically, network nodes (individuals) were permuted to create 1000 randomized networks, maintaining aggression edges constant in the network. Generic randomization methods may lead to unrealistic network configurations that bias statistical significance (Bejder et al. 1998). Thus, we stratified our randomization approach to control for individual space use (Whitehead et al. 2005). We forced permutation to occur within realistic spatial clusters, defined from a Principal component analysis (PCA) run on the distance matrix among the centroids of individual home ranges (see Supplementary Material S1). We used both linear and generalized linear models for normally and Poisson distributed network measures (i.e., linear: eigenvector centrality; Poisson: degree and strength measures, see below). From the 1000 randomized networks, we thus obtained
1000 estimates for each variable (age or sex). For age, the estimates corresponded to slopes, for sex, the estimates corresponded to mean differences between males and females (see Supplementary Materials S2 and S3). We then calculated the 95% CIs of those distributions and compared the estimates from our original dataset (dashed lines in Supplementary Materials S2 and S3) to the distributions of randomly generated estimates. Effects falling outside of the 95% CI were considered significant.

**Female aggression network**

The second network was a subset of female–female interactions only and was used to investigate the effect of kin on female aggressiveness and the effects of aggressiveness on female fitness. During lactation, territorial females defend single nest burrows in which offspring are nursed and establish those burrows closer to female kin than to nonrelated individuals (King and Murie 1985; King 1989a; Viblanc et al. 2010; Arnaud et al. 2012). The subset restricted to female–female interactions consisted of 107 interactions between 68 dyads (20 breeding and 18 non-breeding females).

**Social aggression and kinship**

We tested if aggressive interactions were preferentially directed toward kin or non-kin individuals. To do so, we calculated the total number of interactions emitted for each female in the network directed toward kin or non-kin females. As above, we used a stratified randomization procedure permuting nodes 1000 times while holding aggression edges constant in the network. We then compared the estimate of the mean difference between the number of aggressions directed to kin and non-kin in our observed data with the distribution of 1000 mean difference estimates obtained from the randomized networks.

**Social aggression and female fitness**

We investigated the effects of female–female aggression on female reproduction and fitness. First, we collapsed SN metrics into fewer measures using PCA. We created 2 major axes (PCs) describing female centrality in the aggression network that together explained over 88% of the variance observed in SN measures. Loading matrices were rotated using varimax (Table 1). The first axis (PC1)
Table 1

Rotated orthogonal axes (PC1, PC2) obtained from a principal component analysis (varimax rotation) describing social network metrics for female–female aggression in Columbian ground squirrel (Urocitellus columbianus) during lactation

<table>
<thead>
<tr>
<th>Metric</th>
<th>PC1</th>
<th>PC2</th>
</tr>
</thead>
<tbody>
<tr>
<td>In-degree</td>
<td>0.61</td>
<td>−0.11</td>
</tr>
<tr>
<td>Out-degree</td>
<td>0.67</td>
<td>0.07</td>
</tr>
<tr>
<td>In-strength</td>
<td>0.64</td>
<td>0.68</td>
</tr>
<tr>
<td>Out-strength</td>
<td>0.47</td>
<td>0.29</td>
</tr>
<tr>
<td>Eigenvector centrality</td>
<td>0.47</td>
<td>0.29</td>
</tr>
</tbody>
</table>

Effects of spatial distance on aggression rates and assortment patterns within the network

The number of interactions between individuals was negatively related to the distances between the centers of their home ranges (double-semi-partialing test: $F_{1,701} = 6.497; P < 0.01$). Individual interactions were neither assort nor disassort by sex ($r_{sex} = −0.10; r_{random} = 95\% CI [−0.29; 0.16]$) or by age ($r_{age} = 0.11; r_{random} = 95\% CI [−0.16; 0.14]$).

Effects of individual characteristics (sex and age) on individual network measures

When comparing our estimates for the effect of sex on individual network measures with the distribution of 1000 estimates generated from network permutations, we did not find any significant influence of sex on strength, degree, or eigenvector centrality (comparison with null models; see Supplementary Material S3). Individual age, however, affected received and initiated aggressive interactions. Both the intensity (in-strength) and number of individuals from whom interactions were received (in-degree) decreased linearly with age (Figure 2; Supplementary Material S2). In contrast, the intensity (out-strength) and number of individuals to whom interactions were directed (out-degree) increased with age before decreasing again in older individuals (Figure 2; Supplementary Material S2). Eigenvector centrality was not significantly influenced by age (Supplementary Material S2). We obtained the same results when pooling the oldest individual (a single 13-year-old female) with 6-year-old females.

Kin effects on female social aggressions

Considering the SN of female–female aggressions only, interactions were largely directed toward non-kin individuals (Figure 3a). Our estimates for the effect of kin/non-kin on out-degree (Figure 3b) or out-strength (Figure 3c) differed significantly from 1000 random estimates generated by network permutations. On average, the mean number of individual interactions directed toward non-kin was 2.34 times greater than that directed to kin.

Relationships between SN characteristics and female fitness

When compared with 1000 estimates generated from randomized networks, we found a significant positive relationship between PC2 (outward aggressions) and the total litter mass females weaned in the season (R$A_q$, Figure 4). Similarly, there was a significant positive association between PC2 and female annual fitness (Figure 4). In contrast, we found no effect of PC2 on female mass gain over the season ($S_A$) or any effect of PC1 (received aggressions) on $S_A$, $R_A$, or annual fitness (Figure 4). Kin numbers and female age did not significantly affect $S_A$ (Linear Mixed Model; kin numbers: estimate = 2.15 $±$ 1.30, $t = 1.62$, $P = 0.13$, age: estimate = 0.05 $±$ 0.91, $t = 1.00$, $P = 0.33$), $R_A$ (kin numbers: estimate = 29.02 $±$ 19.76, $t = 1.469$, $P = 0.15$; age: estimate = 4.48 $±$ 1.89, $t = 0.452$, $P = 0.657$), or annual fitness (kin numbers: estimate = 0.13 $±$ 0.22, $t = 0.601$, $P = 0.538$; age: estimate = $−0.04$ $±$ 0.11, $t = −0.406$, $P = 0.691$).

DISCUSSION

Because the fitness benefits of aggressive behavior generally outweigh its costs, aggressive behaviors are common in animal groups (Maynard Smith 1982). However, minimizing the costs of aggressiveness may come in the form of assessing resource-holding power as is often determined by individual attributes linked to social dominance as individual age (Festa-Bianchet and King 1984; Packer and Pusey 1985; Clutton-Brock et al. 1999). In Columbian ground squirrels, received aggressiveness decreased linearly with increasing age, consistently with the fact that nonsexually mature individuals (most yearlings and some 2 year olds) showed received interactions decreasing with age.

Ethics statement

All procedures used in this study were approved by the Auburn University Institutional Care and Use Committee (IACUC# 2012–2051). A research permit (#51774) and collection license (#51801) were obtained from Alberta ESRD Fish & Wildlife, and a research permit was obtained from Alberta Tourism, Parks and Recreation Parks Division Permit (#13-027).

RESULTS

Effects of spatial distance on aggression rates and assortment patterns within the network


described received aggressive interactions, individuals with high PC1 values receiving more interactions (high in-strength) by a greater number of individuals (high in-degree), and interacting in a highly aggressive environment (high eigenvector centrality). The second axis (PC2) described emitted aggressions, individuals with high PC2 scores emitting more interactions (high out-strength) toward a greater number of individuals (high out-degree). Second, we calculated female somatic allocation ($S_A$) as her mass gain over the breeding season from emergence out of hibernation to the end of lactation (mean = 390.3 $±$ 84.2 [SD] g; range = 197–555 g), and female reproductive allocation ($R_A$) as the total mass of the litter she produced at weaning (mean = 281.7 $±$ 73.5 g; range = 123–415 g). Third, we calculated female annual fitness as $S + 0.5 × R$ (Qvarnstrom et al. 2006), where $S$ is the female’s overwinter survival (0/1) and $R$ is the number of offspring produced in 2013 that were weaned in one summer and survived overwinter to the next spring. Finally, we ran separate linear models with the principal components as independent variables and female $S_A$, $R_A$, and annual fitness as dependent variables. In all models, we included female age and number of cobreeding close kin (mother, daughters, and littermate sisters; Dobson et al. 2012) as covariates to account for their potential effects on the dependent variables. Independent variables were mean centered and standardized. We checked for residual normality in all models using Shapiro–Wilk tests. As above, we used network randomization procedures to assess the effects of our principal components (aggression metrics) on female fitness. Node attributes ($S_A$, $R_A$, and annual fitness) were permuted 1000 times and estimates for principal components generated. We then compared our original estimates to the 1000 estimates generated from the randomized networks. Age and kin effects were estimated from conventional model outputs.
olds) are subordinate to adult breeders (Festa-Bianchet and King 1984). Interestingly, whereas outward aggressiveness initially increased with age, peaking at prime reproductive age (Broussard et al. 2003), it then decreased again in older age classes. The decrease in outwards aggressiveness observed with age could be related to the onset of senescence in older individuals (Broussard et al. 2003). Alternatively, older females may shift their home ranges to decrease local competition with conspecifics, thereby displaying overall lower rates of aggressive interactions (Arnaud et al. 2012). Furthermore, individuals in the network were not selective with regards to sex. This result highlights the principal use of aggression to defend territories during lactation, against intruders of any sex (Festa-Bianchet and Boag 1982; Murie and Harris 1988).

Kin selection has also been suggested to importantly affect aggressiveness in group-living species (Silk et al. 1981; King 1989b; Brown and Brown 1993; Watson et al. 1994). Notably, decreased aggression between close kin relatives may be an important adaptive benefit of philopatry (Greenwood 1980; Perrin and Lehmann 2001; Dobson et al. 2012). Accordingly, in Columbian ground squirrels, our results suggest that kin selection may mitigate the costs of aggression. Aggressive interactions were preferentially directed toward non-kin individuals, supporting the idea that reduced aggressiveness between cobreeding kin females is one of the mechanisms likely promoting the evolution of female philopatry (King 1989b; Viblanc et al. 2010). Those results confirm previous findings that mothers are highly tolerant of their daughters (Harris and Murie 1984) and that within-colony dispersal movements mostly occur to take advantage of the presence of close kin (Arnaud et al. 2012). During lactation, breeding females use home ranges of approximately 400–500 m² (Festa-Bianchet and Boag 1982), and kin individuals establish their nest burrows significantly closer to one another than to unrelated females (King 1989a; Viblanc et al. 2010; Arnaud et al. 2012). Close settlement near kin appears to be associated with increased individual fitness (Viblanc et al. 2010; Dobson et al. 2012). Because aggression appeared to be focused locally between individuals living in close spatial proximity—that is, was negatively related to the distance between individual home areas—this suggests that clustering with kin and breeding in a low-intensity aggressive social environment generated important benefits.

Kin groups of higher social tolerance likely provided safety for raising the young. Infanticide carried out by lactating females is
relatively common in Columbian ground squirrels (Dobson 1990; Stevens 1998) and is biased toward non-kin individuals (Stevens 1998). In addition, maintaining territorial boundaries against intruders (Festa-Bianchet and Boag 1982) likely comes with substantial costs for lactating females. These may include increased energy expenditure, decreased time devoted to foraging and energy acquisition, and increased costs of chronic stress (e.g., immunity, oxidative stress; Ros et al. 2006; Creel et al. 2013). Studying the consequences of social stimuli on individual stress and its potential transgenerational consequences on adult and offspring phenotype and future social behavior is a topic of growing importance (Champagne 2010; Dantzer et al. 2013; Creel et al. 2013; Boogert et al. 2014; So et al. 2015). In this regard, it would be interesting to test for potential differences in individual stress depending on received and elicited aggression in our system, where specific predictions can be made. For instance, if some females are chronically harassed, one might expect associations between received aggression and measures of physiological stress (e.g., higher glucocorticoid levels, depressed immune system, oxidative stress) (Blanchard et al. 1993; Sapolsky 2005; Bartolomucci 2007). Alternatively, if aggressive individuals pay a cost in terms of energy expenditure, or social dominance, one may expect positive associations between elicited aggression and metabolic rate, oxidative stress, or glucocorticoids (Creel 2001; Sapolsky 2005; Beaulieu et al. 2014).

Interestingly, we found a positive association between a female’s outwards aggressiveness and 1) the total litter mass she weaned over a season, viz. her reproductive allocation ($R_A$), and 2) her annual fitness, which included both litter size and maternal and offspring survival to the next year. Alternative hypotheses might explain those findings. First, the individual quality hypothesis suggests that high-quality individuals may perform well in a suite of correlated phenotypic traits (Wilson and Nussey 2010). For instance, female house mice (Mus domesticus) selected for high aggressiveness also appear to spend more time in maternal care (Benus and Röndigs 1996). A similar pattern might occur in Columbian ground squirrels, with high-quality females being able to conciliate the time/energy spent in territorial defense with that spent nursing the pups, achieving overall higher fitness. Nonetheless, it is important to note that we measured behavior in a single year and that the aggression-fitness relationship is likely to vary under contrasting environmental conditions. For instance, in solitary red squirrels (Tamiasciurus hudsonicus), the direction of the effect between maternal aggressiveness and offspring survival is actually opposite (positive or negative) depending on yearly environmental (good or bad) conditions (Boon et al. 2007). Thus, one might expect high aggressiveness to be advantageous in harsh environmental years when few resources are available, but disadvantageous in good years if territorial behavior trades-off with parental care (Silverin 1980).

Interestingly, our 2013 breeding season was particularly harsh in terms of rainfall (>200mm rain in less than 48h; http://agriculture.alberta.ca), virtually eliminating foraging for several days for breeding females (Dobson FS, Viblanc VA, personal observation). Such conditions may have exacerbated the impact of female aggressiveness and territoriality on fitness (after Boon et al. 2007). Thus, although the positive association between female outwards aggressiveness and fitness suggests directional selection on aggressiveness, a subtler pattern of selection may occur if aggressiveness interacts with environmental factors such as resource availability or social context (see for instance Svendsen 1974). Second, outwards aggressiveness may be particularly important for females to defend high-quality territories and prevent offspring attacks by conspecifics when they first emerge from the natal burrow. Maternal outwards aggression in rodents is indeed suggested to have an important influence in reducing infanticide (Wolff 1985; Maestripieri 1992), as is likely the case in our model species (Festa-Bianchet and Boag 1982; Murie and Harris 1988; Dobson 1990; Stevens 1998). Moreover, defending patches of higher-quality forage may translate into higher overwinter survival for both mothers

**Figure 3**

Aggressions directed toward kin or non-kin within a social network of aggressions in Columbian ground squirrel (*Urocitellus columbianus*): (a) the mean number of female–female aggressions directed to kin versus non-kin; (b) and (c) the distributions of model estimates obtained from 1000 randomized networks. The true estimates from the original model are figured by dashed lines. Effects falling outside the 95% CI, that is, in the gray bars, are considered significant. ***$P < 0.001$.**
and their offspring (Dobson and Kjelgaard 1985; Bennett 1999). In this regards, it would be interesting to estimate the quality of specific territories and test whether patch quality is associated with high territoriality.

Using a SN approach, we documented the effects of individual age on social aggression in colonial ground squirrels. In addition, our results suggested direct female fitness benefits of outwards aggressiveness and cobreeding with close kin. The recent findings that developmental (social) stress may have important consequences on offspring (Dantzer et al. 2013), including on social behavior and network patterns (Boogert et al. 2014), provides an exciting framework for studying the links between the social environment, maternal stress, and offspring phenotype in the wild.

**SUPPLEMENTARY MATERIAL**

Supplementary material can be found at [http://www.beheco.oxfordjournals.org/](http://www.beheco.oxfordjournals.org/)

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