



Original Article

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

Vincent A. Viblanc,<sup>a,b,c,\*</sup> Cristian Pasquaretta,<sup>a,b,\*</sup> Cédric Sueur,<sup>a,b</sup> Rudy Boonstra,<sup>d</sup> and F. Stephen Dobson<sup>e</sup>

<sup>a</sup>Département Ecologie, Physiologie et Ethologie (DEPE), Institut Pluridisciplinaire Hubert Curien (IPHC), Université de Strasbourg, 23 rue Becquerel, 67087 Strasbourg, France, <sup>b</sup>CNRS, UMR7178, 67087 Strasbourg, France, <sup>c</sup>Centre d'Ecologie Fonctionnelle et Evolutive, UMR 5175, CNRS – Université de Montpellier – Université Paul-Valéry Montpellier – EPHE, 1919 route de Mende, 34293 Montpellier, France, <sup>d</sup>Department of Biological Sciences, University of Toronto Scarborough, Toronto, Ontario M1C 1A4, Canada, and <sup>e</sup>Department of Biological Sciences, Auburn University, 311 Funchess Hall, Auburn, AL 36849, USA

Received 30 September 2015; revised 20 May 2016; accepted 1 June 2016; Advance Access publication 23 June 2016.

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 (Moorcroft 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 (Haley 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

Address correspondence to V.A. Viblanc. E-mail: [vincent.viblanc@iphc.cnrs.fr](mailto:vincent.viblanc@iphc.cnrs.fr).

\*Both are co-first authors.

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 (*Urocitellus columbianus*), a sciurid rodent species with a philopatric matrilineal social system (King and Murie 1985; 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 m<sup>2</sup> (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. 1995). Although lactating females are individually territorial (Murie and Harris 1988), 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 systems 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 conspecifics. 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 coveys of 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 1998), 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 cm<sup>3</sup>) baited with a small amount of peanut butter. Each ground squirrel was weighed to the nearest 5 g using Pesola® spring-slide 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; Neuhaus 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 polycarbonate 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 littermate kin, and pups born from the same mother but in different years as nonlittermate kin.

In Columbian ground squirrel, 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 (Viblanco 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; Neuhaus 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] =  $2.49 \pm 2.02$ ). Out-degree is the number of individuals to whom aggressions were given (mean ± SD =  $2.49 \pm 2.38$ ). 2) Strength corresponds to the sum of aggressive interactions experienced by an individual. Strength was also separated into received (in-strength; mean ± SD =  $3.92 \pm 4.08$ ) and

given (out-strength; mean ± SD =  $3.92 \pm 4.33$ ) aggressive interactions. 3) Eigenvector centrality (mean ± SD =  $0.12 \pm 0.19$ ) 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, those aggressions occur at a local level—indeed, eigenvector centrality is negatively related to individual home range ( $\rho = -0.30$ ,  $S = 38\,025$ ,  $P = 0.025$ )—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

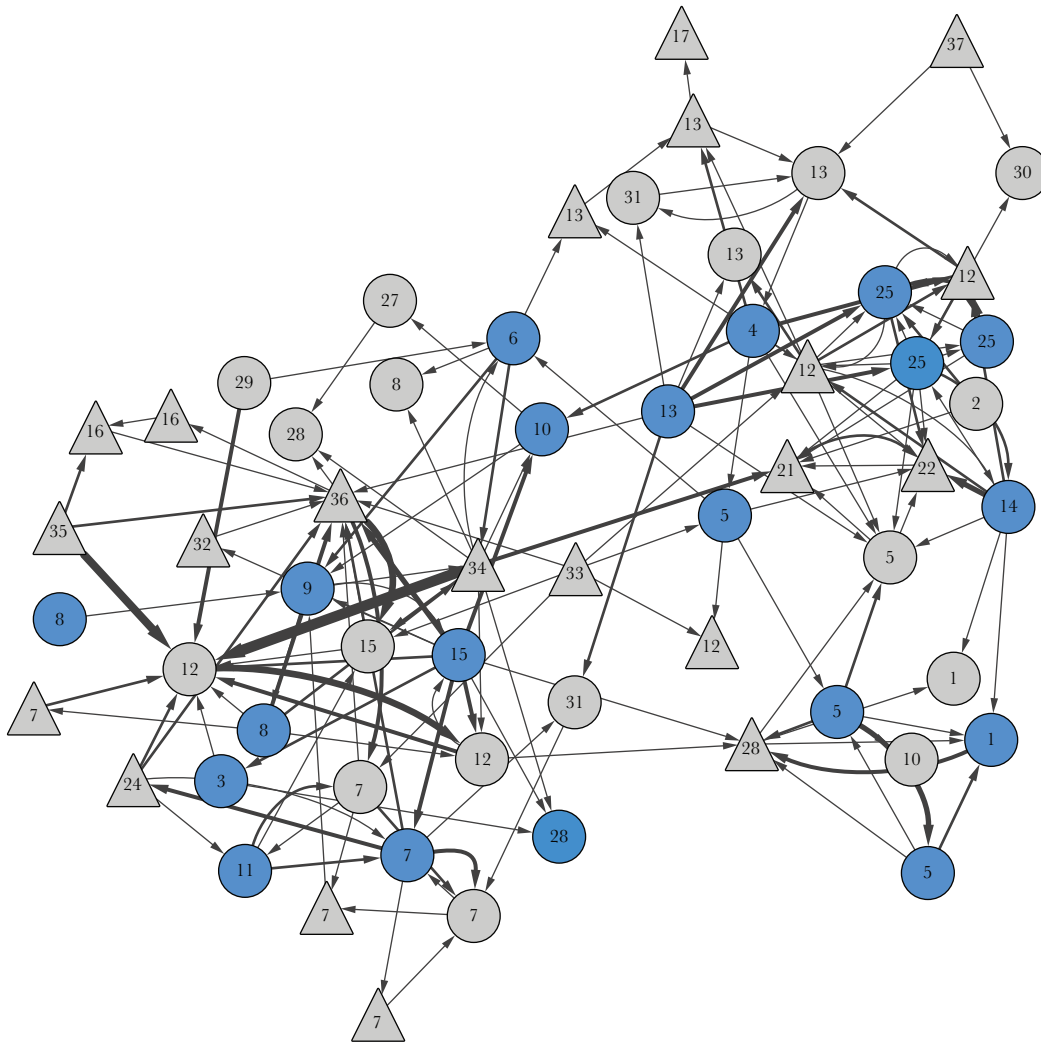
We analyzed the relationship between a matrix of dyadic aggressive interactions and a matrix of dyadic spatial distances based on the centroid of individual home ranges. We applied permutation tests for simple linear regression models for data organized in matrices of dyadic relationship among  $n$ 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



**Figure 1**

Directed, weighted, social network of aggressions during lactation in Columbian ground squirrels (*Urocyon columbianus*). Females are symbolized by circles, males by triangles. Kin individuals (regardless of sex or age) sharing the same mother are depicted by the same number. A directed aggression between 2 individuals is symbolized by an arrow pointing from the initiator toward the recipient. Arrows are weighted according to the number of aggressions exchanged. Breeding females are depicted in blue.

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](#); [Viblanç 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**

	PC1	PC2
<i>In</i> -degree	0.61	-0.11
<i>Out</i> -degree		0.67
<i>In</i> -strength	0.64	
<i>Out</i> -strength		0.68
Eigenvector centrality	0.47	0.29

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 =  $390.3 \pm 84.2$  [SD] g; range = 197–555 g), and female reproductive allocation ( $R_A$ ) as the total mass of the litter she produced at weaning (mean =  $281.7 \pm 73.5$  g; range = 123–415 g). Third, we calculated female annual fitness as  $S + 0.5 \times R$  (Qvarnström 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.

### 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

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 assorted nor disassorted by sex

( $r_{\text{sex}} = -0.10$ ;  $r_{\text{random}} = 95\%$  CI [-0.20; 0.16]) or by age ( $r_{\text{age}} = 0.11$ ;  $r_{\text{random}} = 95\%$  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

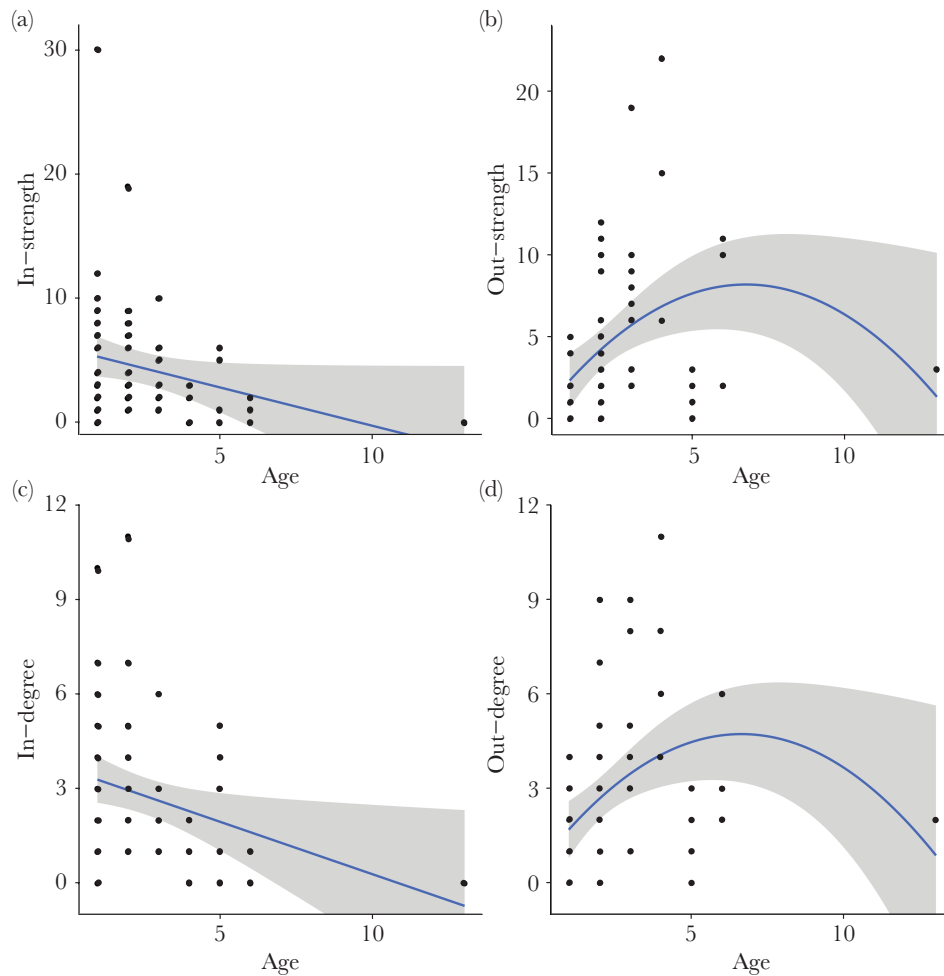
Considering the SN of female–female aggressions only, interactions were largely directed toward non-kin individuals (Figure 3a). Our estimates for the effect of kin/non-kin on *out*-degree (Figure 3b) or *out*-strength (Figure 3c) differed significantly from 1000 random estimates generated by network 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 ( $R_A$ ) (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 =  $2.15 \pm 11.80$ ,  $t = 0.182$ ,  $P = 0.858$ ; age: estimate =  $0.05 \pm 5.91$ ,  $t = 0.008$ ,  $P = 0.994$ ),  $R_A$  (kin numbers: estimate =  $29.02 \pm 19.76$ ,  $t = 1.469$ ,  $P = 0.163$ ; age: estimate =  $4.48 \pm 9.89$ ,  $t = 0.452$ ,  $P = 0.657$ ), or annual fitness (kin numbers: estimate =  $0.13 \pm 0.22$ ,  $t = 0.601$ ,  $P = 0.558$ ; age: estimate =  $-0.04 \pm 0.11$ ,  $t = -0.406$ ,  $P = 0.691$ ).

## 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 non-sexually mature individuals (most yearlings and some 2 year



**Figure 2**

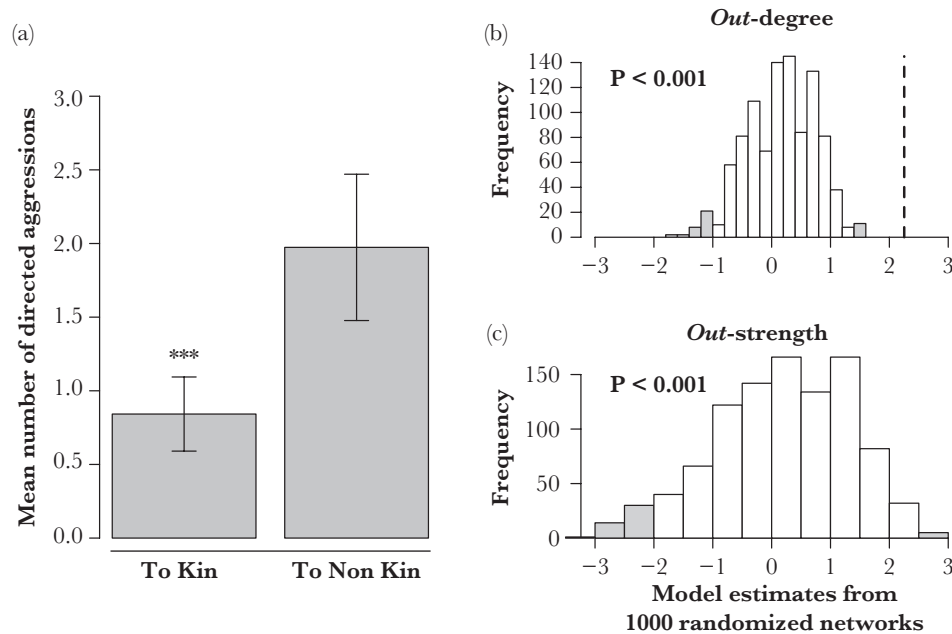
The effects of age on individual measures of strength, that is, intensity of aggressions (a) received and (b) sent—and degree, that is, number of individual contacts (c) received and (d) sent—in a social network of aggressions in Columbian ground squirrels (*Urocitellus columbianus*). Fitted lines for the best fitted model (linear or quadratic) are shown. Gray areas show the 95% CIs around fitted lines. We obtained the same results when pooling the 13-year-old female with 6-year-old individuals.

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; Viblanç 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 m<sup>2</sup> (Festa-Bianchet and Boag 1982), and kin individuals establish their nest burrows significantly closer to one another than to unrelated females (King 1989a; Viblanç et al. 2010; Arnaud et al. 2012). Close settlement near kin appears to be associated with increased individual fitness (Viblanç 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



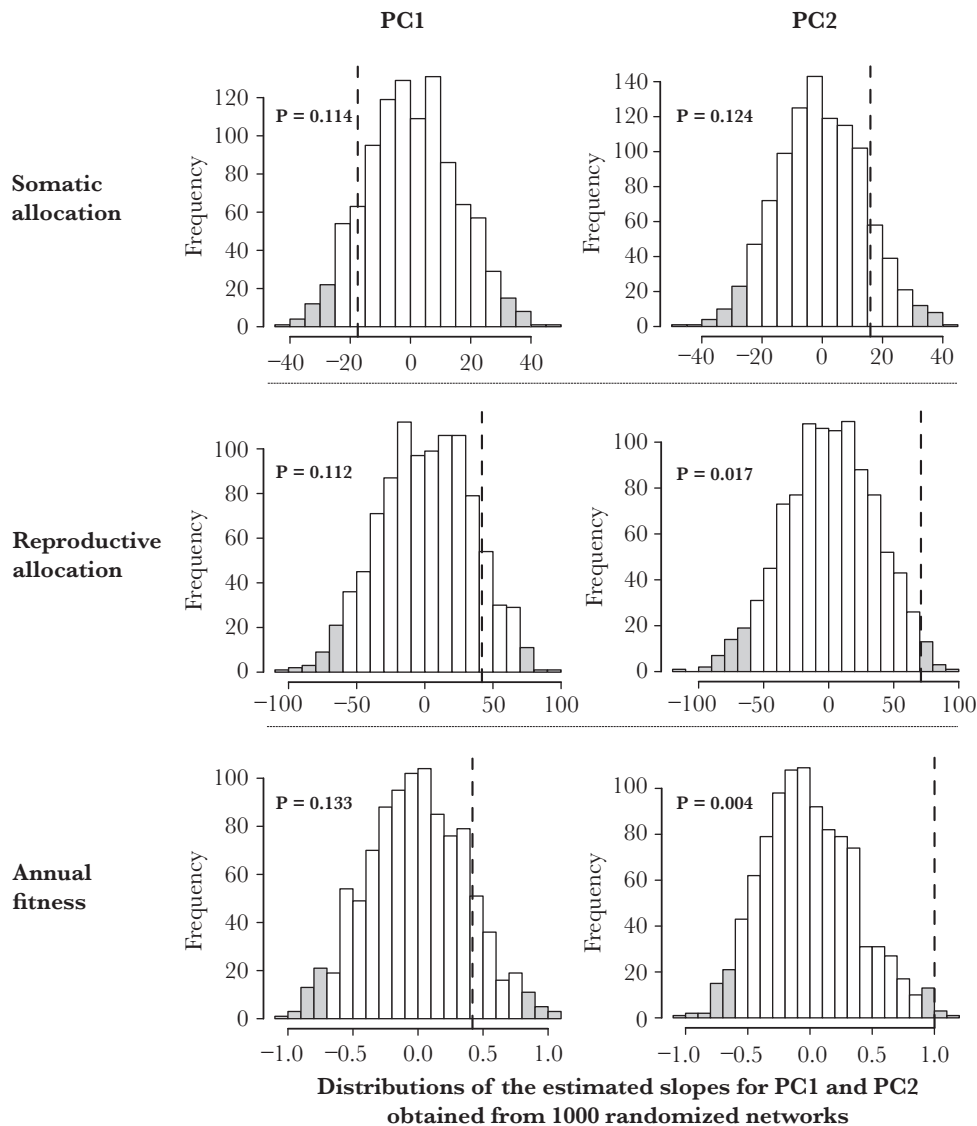
**Figure 3**

Aggregations directed toward kin or non-kin within a social network of aggressions in Columbian ground squirrels (*Urocyon 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. \*\*\* $P < 0.001$ .

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 (>200 mm rain in less than 48 h; <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 4**

Estimated effects of female–female aggression on fitness. PC1 and PC2 are principal components describing female received aggression and centrality within an aggressive environment (PC1) and female outwards aggressiveness (PC2) (see Table 1). Measures of fitness included female mass gain over the breeding season (somatic allocation, in grams); the total mass of the weaned litter (reproductive allocation, in grams), and female annual fitness that included both the production of young ( $0.5 \times$  litter size) and the survival of young and the mother until the subsequent spring (see Methods for details). Model estimates for the effects of PCs on  $S_A$ ,  $R_A$ , and annual fitness are compared against the distribution of 1000 estimates produced by permuting node attributes ( $S_A$ ,  $R_A$ , annual fitness) in randomized networks. The true estimates from the original models are figured by dashed lines. Effects falling outside the 95% CI, that is, in the gray bars, are considered significant.

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.behco.oxfordjournals.org/>

## FUNDING

This research was supported by an AXA Research Fund postdoctoral grant to V.A.V., an IPHC-DEPE grant to C.P., and a National Science Foundation grant (DEB-0089473) to F.S.D.

We are grateful to the Biogeoscience Institute (especially E. Johnson, Director; A. Cummings and J. Mappin-Buchanan, Managers; and K. Ruckstuhl, field camp responsible), University of Calgary, for providing us with field camp and laboratory facilities. We are indebted to K. Rubach, C. Klase, and



C. Bordier for their help in the field; P. Neuhaus for help in the field and scientific discussions; C. Saraux for statistical advice; and F. Criscuolo and J.O. Murie for helpful comments on the manuscript. J.O. Murie initiated the long-term study on Columbian ground squirrels and continuously inspires us through many discussions related to behavioral ecology and ground squirrel sociality. We are especially grateful to M. Silk, N. Royle, and 1 anonymous reviewer for insightful comments on a previous version of the article.

Author contributions: V.A.V., C.P. and F.S.D. designed the study; V.A.V. and F.S.D. did the fieldwork; V.A.V. and C.P. analyzed the data; V.A.V., C.P., C.S., R.B., and F.S.D. wrote the manuscript. All authors gave their final approval for publication.

**Handling editor:** Nick Royle

## REFERENCES

- Adams ES. 2001. Approaches to the study of territory size and shape. *Annu Rev Ecol Syst.* 32:277–303.
- Arnaud CM, Dobson FS, Murie JO. 2012. Philopatry and within-colony movements in Columbian ground squirrels. *Mol Ecol.* 21:493–504.
- Bartolomucci A. 2007. Social stress, immune functions and disease in rodents. *Front Neuroendocrinol.* 28:28–49.
- Beaulieu M, Mboumba S, Willaume E, Kappeler PM, Charpentier MJ. 2014. The oxidative cost of unstable social dominance. *J Exp Biol.* 217:2629–2632.
- Bejder L, Fletcher D, Bräger S. 1998. A method for testing association patterns of social animals. *Anim Behav.* 56:719–725.
- Bennett RP. 1999. Effects of food quality on growth and survival of juvenile Columbian ground squirrels (*Spermophilus columbianus*). *Can J Zool.* 77:1555–1561.
- Benus RF, Røndigs M. 1996. Patterns of maternal effort in mouse lines bidirectionally selected for aggression. *Anim Behav.* 51:67–75.
- Betini GS, Norris DR. 2012. The relationship between personality and plasticity in tree swallow aggression and the consequences for reproductive success. *Anim Behav.* 83:137–143.
- Blanchard DC, Sakai RR, McEwen B, Weiss SM, Blanchard RJ. 1993. Subordination stress: behavioral, brain, and neuroendocrine correlates. *Behav Brain Res.* 58:113–121.
- Boag DA, Murie JO. 1981. Population ecology of Columbian ground squirrels in southwestern Alberta. *Can J Zool.* 59:2230–2240.
- Boogert NJ, Farine DR, Spencer KA. 2014. Developmental stress predicts social network position. *Biol Lett.* 10:20140561.
- Boon AK, Réale D, Boutin S. 2007. The interaction between personality, offspring fitness and food abundance in North American red squirrels. *Ecol Lett.* 10:1094–1104.
- Boonstra R, McColl CJ, Karels TJ. 2001. Reproduction at all costs: the adaptive stress response of male arctic ground squirrels. *Ecology.* 82:1930–1946.
- Broussard DR, Risch TS, Dobson FS, Murie JO. 2003. Senescence and age-related reproduction of female Columbian ground squirrels. *J Anim Ecol.* 72:212–219.
- Brown GE, Brown JA. 1993. Social dynamics in salmonid fishes: do kin make better neighbours? *Anim Behav.* 45:863–871.
- Calenge C. 2006. The package ‘adehabitat’ for the R software: a tool for the analysis of space and habitat use by animals. *Ecol Model.* 197:516–519.
- Champagne FA. 2010. Epigenetic influence of social experiences across the lifespan. *Dev Psychobiol.* 52:299–311.
- Clutton-Brock TH, Albon SD. 1979. The roaring of red deer and the evolution of honest advertisement. *Behavior.* 69:145–170.
- Clutton-Brock TH, Albon SD, Gibson RM, Guinness FE. 1979. The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* L.). *Anim Behav.* 27:211–225.
- Clutton-Brock TH, Gaynor D, McIlrath GM, Maccoll ADC, Kansky R, Chadwick P, Manser M, Skinner JD, Brotherton PNM. 1999. Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. *J Anim Ecol.* 68:672–683.
- Creel S. 2001. Social dominance and stress hormones. *Trends Ecol Evol.* 16:491–497.
- Creel S, Dantzer B, Goymann W, Rubenstein DR. 2013. The ecology of stress: effects of the social environment. *Funct Ecol.* 27:66–80.
- Croft DP, James R, Krause J. 2008. Exploring animal social networks. Princeton (NJ): Princeton University Press.
- Croft DP, James R, Thomas POR, Hathaway C, Mawdsley D, Laland KN, Krause J. 2006. Social structure and co-operative interactions in a wild population of guppies (*Poecilia reticulata*). *Behav Ecol Sociobiol.* 59:644–650.
- Croft DP, James R, Ward AJ, Botham MS, Mawdsley D, Krause J. 2005. Assortative interactions and social networks in fish. *Oecologia.* 143:211–219.
- Croft DP, Madden JR, Franks DW, James R. 2011. Hypothesis testing in animal social networks. *Trends Ecol Evol.* 26:502–507.
- Csardi G, Nepusz T. 2006. The igraph software package for complex network research. *Inter J Complex Syst.* 1695:1–9.
- Dantzer B, Newman AE, Boonstra R, Palme R, Boutin S, Humphries MM, McAdam AG. 2013. Density triggers maternal hormones that increase adaptive offspring growth in a wild mammal. *Science.* 340:1215–1217.
- Dekker D, Krackhardt D, Snijders TAB. 2007. Sensitivity of MRQAP tests to collinearity and autocorrelation conditions. *Psychometrika.* 72:9016.
- Dobson FS. 1990. Environmental influences on infanticide in Columbian ground squirrels. *Ethology.* 84:3–14.
- Dobson FS, Badry MJ, Geddes C. 1992. Seasonal activity and body mass of Columbian ground squirrels. *Can J Zool.* 70:1364–1368.
- Dobson FS, Kjelgaard JD. 1985. The influence of food resources on population dynamics in Columbian ground squirrels. *Can J Zool.* 63:2095–2104.
- Dobson FS, Murie JO. 1987. Interpretation of intraspecific life history patterns: evidence from Columbian ground squirrels. *Am Nat.* 129:382–397.
- Dobson FS, Viblanc VA, Arnaud CM, Murie JO. 2012. Kin selection in Columbian ground squirrels: direct and indirect fitness benefits. *Mol Ecol.* 21:524–531.
- Enquist M, Leimar O. 1983. Evolution of fighting behavior: decision rules and assessment of relative strength. *J Theor Biol.* 102:387–410.
- Enquist M, Leimar O. 1987. Evolution of fighting behavior: the effect of variation in resource value. *J Theor Biol.* 127:187–205.
- Farine DR. 2013. Animal social network inference and permutations for ecologists in R using *asnipe*. *Methods Ecol Evol.* 12:1187–1194.
- Farine DR. 2014. Measuring phenotypic assortment in animal social networks: weighted associations are more robust than binary edges. *Anim Behav.* 89:141–153.
- Farine DR, Whitehead H. 2015. Constructing, conducting and interpreting animal social network analysis. *J Anim Ecol.* 84:1144–1163.
- Festa-Bianchet M, Boag DA. 1982. Territoriality in adult female Columbian ground squirrels. *Can J Zool.* 60:1060–1066.
- Festa-Bianchet M, King WJ. 1984. Behavior and dispersal of yearling Columbian ground squirrels. *Can J Zool.* 62:161–167.
- Gardner A, West SA, Wild G. 2011. The genetical theory of kin selection. *J Evol Biol.* 24:1020–1043.
- Grafen A. 2006. Optimization of inclusive fitness. *J Theor Biol.* 238:541–563.
- Greenwood PJ. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim Behav.* 28:1140–1162.
- Haley MP. 1994. Resource-holding power asymmetries, the prior residence effect, and reproductive payoffs in male northern elephant seal fights. *Behav Ecol Sociobiol.* 34:427–434.
- Hamilton WD. 1964. The genetical evolution of social behavior I and II. *J Theor Biol.* 7:1–52.
- Hare JF, Murie JO. 1992. Manipulation of litter size reveals no cost of reproduction in Columbian ground squirrels. *J Mamm.* 73:449–454.
- Hare JF, Murie JO. 1996. Ground squirrel sociality and the quest for the ‘holy grail’: does kinship influence behavioral discrimination by juvenile Columbian ground squirrels. *Behav Ecol.* 7:76–81.
- Harris MA, Murie JO. 1984. Inheritance of nest sites in female Columbian ground squirrels. *Behav Ecol Sociobiol.* 15:97–102.
- Isbell LA. 1991. Contest and scramble competition: patterns of female aggression and ranging behavior among primates. *Behav Ecol.* 2:143–155.
- King WJ. 1989a. Spacing of female kin in Columbian ground squirrels (*Spermophilus columbianus*). *Can J Zool.* 67:91–95.
- King WJ. 1989b. Kin-differential behavior of adult female Columbian ground squirrels. *Anim Behav.* 38:354–356.
- King WJ, Murie JO. 1985. Temporal overlap of female kin in Columbian ground squirrels (*Spermophilus columbianus*). *Behav Ecol Sociobiol.* 16:337–341.
- Krause J, James R, Franks DW, Croft DP. 2014. Animal social networks. Oxford: Oxford University Press.

- Kurvers RHJM, Krause J, Croft DP, Wilson ADM, Wolf M. 2014. The evolutionary and ecological consequences of animal social networks: emerging issues. *Trends Ecol Evol*. 29:326–335.
- Lea AJ, Blumstein DT, Wey TW, Martin JG. 2010. Heritable victimization and the benefits of agonistic relationships. *Proc Natl Acad Sci USA*. 107:21587–21592.
- Lusseau D, Newman MEJ. 2004. Identifying the role that animals play in their social networks. *Proc Biol Sci*. 271:S477–S481.
- Lusseau D, Wilson B, Hammond PS, Grellier K, Durban JW, Parsons KM, Barton TR, Thompson PM. 2006. Quantifying the influence of sociality on population structure in bottlenose dolphins. *J Anim Ecol*. 75:14–24.
- Maestripietri D. 1992. Functional aspects of maternal aggression in mammals. *Can J Zool*. 70:1069–1077.
- Manno TG, Dobson FS. 2008. Why are male Columbian ground squirrels territorial. *Ethology*. 114:1049–1060.
- Maynard Smith J. 1982. *Evolution and the theory of games*. Cambridge (UK): Cambridge University Press.
- Maynard Smith J, Parker GR. 1976. The logic of asymmetric contests. *Anim Behav*. 24:159–175.
- Mowles SL, Cotton PA, Briffa M. 2010. Whole-organism performance capacity predicts resource-holding potential in the hermit crab *Pagurus bernhardus*. *Anim Behav*. 80:277–282.
- Moorcroft PR, Albon SD, Pemberton JM, Stevenson IR, Clutton-Brock TH. 1996. Density-dependent selection in a fluctuating ungulate population. *Proc Biol Sci*. 263:31–38.
- Murie JO, Harris MA. 1978. Territoriality and dominance in male Columbian ground squirrels (*Spermophilus columbianus*). *Can J Zool*. 56:2402–2412.
- Murie JO, Harris MA. 1982. Annual variation of spring emergence and breeding in Columbian ground squirrels (*Spermophilus columbianus*). *J Mamm*. 63:431–439.
- Murie JO, Harris MA. 1988. Social interactions and dominance relationships between female and male Columbian ground squirrels. *Can J Zool*. 66:1414–1420.
- Murray CM, Mane SV, Pusey AE. 2007. Dominance rank influences space use in wild chimpanzees, *Pan troglodytes*: towards an ideal despotic distribution. *Anim Behav*. 74:1795–1804.
- Neuhaus P. 2006. Causes and consequences of sex-biased dispersal in Columbian ground squirrels, *Spermophilus columbianus*. *Behaviour*. 143:1013–1031.
- Neuhaus P, Broussard DR, Murie JO, Dobson FS. 2004. Age of primiparity and implications of early reproduction on life history in female Columbian ground squirrels. *J Anim Ecol*. 73:36–43.
- Newman ME. 2003. Mixing patterns in networks. *Phys Rev E*. 67:026126.
- Oliveira RF, Lopes M, Carneiro LA, Canário AV. 2001. Watching fights raises fish hormone levels. *Nature*. 409:475.
- Packer C, Pusey A. 1985. Asymmetric contests in social mammals: respect, manipulation and age-specific aspects. In: Greenwood PJ, Harvey PH, Slatkin M, editors. *Evolution: essays in honour of John Maynard Smith*. Cambridge (UK): Cambridge University Press. p. 173–186.
- Parker GA. 1974. Assessment strategy and the evolution of fighting behaviour. *J Theor Biol*. 47:223–243.
- Perrin N, Lehmann L. 2001. Is sociality driven by the costs of dispersal or the benefits of philopatry? A role for kin-discrimination mechanisms. *Am Nat*. 158:471–483.
- Pinter-Wollman N, Hobson EA, Smith JE, Edelman AJ, Shizuka D, De Silva S, Waters JS, Prager SD, Sasaki T, Wittemyer G, Fewell J, McDonald DB. 2013. The dynamics of animal social networks: analytical, conceptual, and theoretical advances. *Behav Ecol*. 25:242–255.
- Prentice AM, Prentice A. 1988. Energy costs of lactation. *Annu Rev Nutr*. 8:63–79.
- Qvarnström A, Brommer JE, Gustafsson L. 2006. Testing the genetics underlying the co-evolution of mate choice and ornament in the wild. *Nature*. 441:84–86.
- Risch TS, Dobson FS, Murie JO. 1995. Is mean litter size the most productive? A test in Columbian ground squirrels. *Ecology*. 76:1643–1654.
- Ros AF, Becker K, Oliveira RF. 2006. Aggressive behaviour and energy metabolism in a cichlid fish, *Oreochromis mossambicus*. *Physiol Behav*. 89:164–170.
- Rovero F, Hughes RN, Whiteley NM, Chelazzi G. 2000. Estimating the energetic cost of fighting in shore crabs by noninvasive monitoring of heartbeat rate. *Anim Behav*. 59:705–713.
- Sapolsky RM. 2005. The influence of social hierarchy on primate health. *Science*. 308:648–652.
- Silk MJ, Croft DP, Tregenza T, Bearhop S. 2014. The importance of fission-fusion social group dynamics in birds. *Ibis*. 156:701–715.
- Silk JB, Samuels A, Rodman PS. 1981. The influence of kinship, rank, and sex on affiliation and aggression between adult female and immature bonnet macaques (*Macaca radiata*). *Behavior*. 78:111–137.
- Silverin B. 1980. Effects of long-lasting testosterone treatment on freelifving pied flycatchers, *Ficedula hypoleuca*, during the breeding period. *Anim Behav*. 28:906–912.
- So N, Franks B, Lim S, Curley JP. 2015. A social network approach reveals associations between mouse social dominance and brain gene expression. *PLoS One*. 10:e0134509.
- Stevens SD. 1998. High incidence of infanticide by lactating females in a population of Columbian ground squirrels (*Spermophilus columbianus*). *Can J Zool*. 76:1183–1187.
- Sueur C, Petit O, De Marco A, Jacobs AT, Watanabe K, Thierry B. 2011. A comparative network analysis of social style in macaques. *Anim Behav*. 82:845–852.
- Sueur C, Jacobs A, Amblard F, Petit O, King AJ. 2011. How can social network analysis improve the study of primate behavior? *Am J Primatol*. 73:703–719.
- Svendsen GE. 1974. Behavioral and environmental factors in the spatial distribution and population dynamics of a yellow-bellied marmot population. *Ecology*. 55:760–771.
- Viblanç VA, Arnaud CM, Dobson FS, Murie JO. 2012. Kin selection in Columbian ground squirrels (*Urociellus columbianus*): littermate kin provide individual fitness benefits. *Proc Biol Sci*. 277:989–994.
- Viblanç VA, Sarau C, Murie JO, Dobson FS. Forthcoming. Kin effects on energy allocation in group-living ground squirrels. *J Anim Ecol*. doi: 10.1111/1365-2656.12541. <http://onlinelibrary.wiley.com/doi/10.1111/1365-2656.12541/full>.
- Viblanç VA, Valette V, Kauffmann M, Malosse N, Groscolas R. 2012. Coping with social stress: heart rate responses to agonistic interaction in king penguins. *Behav Ecol*. 85:1179–1185.
- Wascher CA, Scheiber IB, Kotschal K. 2008. Heart rate modulation in bystanding geese watching social and non-social events. *Proc Biol Sci*. 275:1653–1659.
- Wasserman S, Faust K. 1994. *Social network analyses: methods and applications*. Cambridge (UK): Cambridge University Press.
- Watson A, Moss R, Parr R, Mountford MD, Rothery P. 1994. Kin land-ownership, differential aggression between kin and non-kin, and population fluctuations in red grouse. *J Anim Ecol*. 63:39–50.
- Wey T, Blumstein DT. 2010. Social cohesion in yellow-bellied marmots is established through age and kin structuring. *Anim Behav*. 79:1343–1352.
- Wey T, Blumstein DT, Shen W, Jordan F. 2008. Social network analysis of animal behavior: a promising tool for the study of sociality. *Anim Behav*. 75:333–344.
- Wiggett DR, Boag DA. 1989. Intercolony natal dispersal in the Columbian ground squirrel. *Can J Zool*. 67:42–50.
- Wilson AJ, Nussey DH. 2010. What is individual quality? An evolutionary perspective. *Trends Ecol Evol*. 25:207–214.
- Whitehead H. 2008. *Analyzing animal societies: quantitative methods for vertebrate social analysis*. Chicago (IL): University of Chicago Press.
- Whitehead H, Bejder L, Ottensmeyer C. 2005. Testing association patterns: issues arising and extensions. *Anim Behav*. 69:e1–e6.
- Wolff JE. 1985. Maternal aggression as a deterrent to infanticide in *Peromyscus leucopus* and *P. maniculatus*. *Anim Behav*. 33:117–123.