Kin effects on energy allocation in group-living ground squirrels

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Summary

1. The social environment has potent effects on individual phenotype and fitness in group-living species.
2. We asked whether the presence of kin might act on energy allocation, a central aspect of life-history variation.
3. Using a 22-year data set on reproductive and somatic allocations in Columbian ground squirrels (Urocitellus columbianus), we tested the effects of co-breeding and non-breeding kin on the fitness and energy allocation balance between reproduction and personal body condition of individual females.
4. Greater numbers of co-breeding kin had a positive effect on the number of offspring weaned, through the mechanism of altering energy allocation patterns. On average, females with higher numbers of co-breeding kin did not increase energy income but biased energy allocation towards reproduction.
5. Co-breeding female kin ground squirrels maintain close nest burrows, likely providing a social buffer against territorial invasions from non-kin ground squirrels. Lower aggressiveness, lower risks of infanticide from female kin and greater protection of territorial boundaries may allow individual females to derive net fitness benefits via their energy allocation strategies.
6. We demonstrated the importance of kin effects on a fundamental life-history trade-off.

Key-words: energy, kin selection, life-history trade-offs, matriline, philopatry, reproductive allocation, somatic allocation

Introduction

The social environment is known to strongly affect individual behaviour, physiology and fitness. For instance, social interactions, social status and the composition of the social environment may influence individual stress levels (Creel et al. 2013), oxidative stress (Beaulieu et al. 2014), immunity (Bartolomucci 2007), longevity (Silk et al. 2010), offspring production and survival (Silk, Alberts & Altman 2003), and metabolic rate (Sloman et al. 2000). Despite these potent effects, including on energy expenditure (Viblanc et al. 2014), no study thus far has considered how the social environment might shape individual energy allocation decisions during reproduction, though some have considered how cooperation among individuals may allow alleviating workload in cooperative breeders (Reyer 1984; Komdeur 1994; Sharp, English & Clutton-Brock 2013). This is surprising given that (1) resources occur in limited amounts in nature (either in time, space or quantities), (2) energy trade-offs between functions are central to life-history theory and (3) social interactions often occur repeatedly within a season and over the years, leading to social heterogeneity in the nature and composition of social environment (e.g. age structure, nature of social bonds, number of kin) that might affect energy balance. Thus, understanding whether the social environment influences the optimal allocation of energy to the functions of growth, maintenance and reproduction appears central to an appraisal of life-history decisions in group-living species.

In particular, whereas the trade-off between somatic and reproductive functions has been long considered (Williams 1966; Hirshfield & Tinkle 1975; van Noordwijk...
Geddes 1992). During reproduction, females cluster into
only breed once (Murie & Harris 1982; Dobson, Badry &
active season of about 3
Boag 1982). They are a hibernating species with a short
Rocky Mountains (Boag & Murie 1981; Festa-Bianchet &
dense colonies in montane meadows of the northern
ensions. These semi-social sciurid rodents live in relatively
somatic (SA) or reproductive (RA) functions and then to
examine social effects on TA and the balance between SÄ and RÄ. For this, a model species is required in which
social heterogeneity that affects fitness is known to occur
both between individuals within a single breeding season,
and for single individuals over the course of several breed-
ing seasons.

Columbian ground squirrels (Urocitellus columbianus) provide a particularly good model for asking such ques-
tions. These semi-social sciurid rodents live in relatively
dense colonies in montane meadows of the northern
Rocky Mountains (Boag & Murie 1981; Festa-Bianchet &
Boag 1982). They are a hibernating species with a short
active season of about 3–4 months during which females
only breed once (Murie & Harris 1982; Dobson, Badry &
Geddes 1992). During reproduction, females cluster into
contiguous home ranges (<1000 m²) with up to seven
adjacent neighbours (Festa-Bianchet & Boag 1982). Female home ranges include an individual nest burrow
for raising a litter of about three young during lactation.
Lactating females aggressively defend their nest burrow
against intruders, although exclusive usage of the home
range is not achieved (Murie & Harris 1988). During lac-
tation, territorial overlap with neighbours may be high,
up to over 50% (Festa-Bianchet & Boag 1982). Breeding
females preferentially settle close to female kin (nest bur-
rows within 10–20 m), especially the mother, daughters or
littermate sisters (King 1989b; Viblanc et al. 2010; Arnaud,
Dobson & Murie 2012), and females typically
remain close to their natal burrows as adults (Murie &
Harris 1984).

Philopatric settlement provides breeding females with fit-
ess benefits owing to increased numbers of weaned off-
spring (but no effect on adult survival) for females with
more kin present nearby (Viblanc et al. 2010). It has been
suggested that familiarity between kin individuals may
affect patterns of social relationships, namely a reduction in
the time and energy spent in territorial defence (Murie &
Harris 1984). However, though close female kin are less
aggressive towards one another than towards distantly or
unrelated individuals (King 1989a; V.A. Viblanc, C. Pas-
quaretta, C. Sueur, R. Boonstra & F.S. Dobson, unpub-
lished data), the hypothesis that co-breeding with close kin
might allow females to acquire more total energy during
reproduction has not been tested. An alternative hypothe-
sis, not mutually exclusive, could be that the presence of
close kin provides a safer environment in which to raise
the young by decreasing the risk of offspring mortality due
to infanticide (Dobson 1990; Stevens 1998), so that females
bias energy allocation towards reproduction, with higher
chances of offspring survival, when more close kin are
present.

We tested the above alternatives using a 22-year data
set of known energy allocations and close kin number
(mother, daughters and littermate sisters) in Columbian
ground squirrels. Specifically, we tested how the number of
co-breeding female kin (that show territorial nest-bur-
row defence) and non-breeding female kin (without terri-
torial nest-burrow defence) affected breeding female litter
size at weaning (i.e. the number of offspring weaned), her
total energy available to allocate to reproductive and
somatic functions, and the balance of allocation between
both functions. Columbian ground squirrels use daily
resource acquisition to support reproduction, though ini-
tial body condition of mothers (i.e. stored resources or
initial ‘capital’) also significantly influences reproduction
(i.e. litter size and mass; Risch, Dobson & Murie 1995;
Dobson, Risch & Murie 1999; Broussard, Dobson &
Murie 2005). Whereas experimental studies do not
strongly suggest a cost of reproduction in terms of adult
survival or future reproduction in this species (Murie &
Dobson 1987; Hare & Murie 1992; Skibiel, Speakman &
Hood 2013; but see Neuhaus 2000), any substantial body
mass gained by females during a reproductive season may
be carried over into the subsequent season and positively
affect a future litter size at weaning (Rubach et al. in
press).

We calculated total energy income, and somatic vs.
reproductive energy allocation in breeding female Colum-
bian ground squirrels (van Noordwijk & De Jong 1986;
Broussard, Michener & Dobson 2006), and investigated
how kin numbers affected those parameters. If kin bene-
fits are due to breeding females being able to spend more
time feeding and less defending their territories during
reproduction, we predict a positive relationship between
female kin numbers and total energy income in this spe-
cies. In addition, as limited energy resources during a
breeding season are allocated between somatic vs. repro-
ductive functions, we considered whether the resulting
negative association of these two functions was affected
by the number of kin present in the population. As repro-
duction appears the key trait maximizing fitness (Viblanc
et al. 2010), we predicted that greater allocations into
reproduction should be made in the presence of greater
number of kin, either due to a positive effect of kin num-
bers on energy income, or if more female kin provide a
safer environment for raising the young. Thus, we tested
for an influence of kin on the balance between allocation
to current reproduction and greater chances to reproduce
in the future.

Materials and methods

GENERAL METHODS

We studied Columbian ground squirrels from 1992 to 2014 at
the Sheep River Wildlife Provincial Park, Alberta, Canada (50
Secondly, we regressed $R_A$ on $T_A$ (SA and RA). First, we calculated total energy allocation $T_A$ as the sum of reproductive and somatic allocations $T_A$ corresponded to individuals allocating relatively more into reproduction than the average, whereas negative residuals represent higher allocation to reproduction than predicted for a given total allocation and negative residuals higher allocation to the soma.

**SOMATIC VS. REPRODUCTIVE ALLOCATION**

Somatic allocation ($S_A$) was calculated as female mass change during reproduction, between emergence from hibernation and the end of lactation (mean = 99.0 ± 2.5 g; range = −50 to 225 g). Reproductive allocation ($R_A$) was calculated as the total mass of the litter at weaning, which comprised maternal allocations into both gestation and lactation (mean = 304.7 ± 4.4 g; range = 62–551 g). We then derived two different indices from $S_A$ and $R_A$. First, we calculated total energy allocation $T_A$ as the sum of reproductive and somatic allocations $T_A = R_A + S_A$. Secondly, we regressed $R_A$ on $T_A$ (slope = 0.75 ± 0.02, $F_{1,405} = 1423$, $P < 0.001$, $R^2 = 0.78$) and used the residuals as an index of balance allocation (hereafter ‘residual $R_A$’ between reproduction and somatic components. For a given $T_A$, positive residual $R_A$ corresponded to individuals allocating relatively more into reproduction than the average, whereas negative residual $R_A$ corresponded to individuals allocating relatively more into the soma than the average (Fig. 1). In other words, residual $R_A$ reflects a reciprocal change in $R_A$ and $S_A$. If residual $R_A$ is +1, then $R_A$ is higher than the average by 1 g for a given $T_A$ so that $S_A$ is lower than the average by 1 g. $T_A$ and residual $R_A$ were independent variables ($r = −0.00$, CI$_{95}$ [−0.10 to 0.10], $t = 0$, d.f. = 402, $P = 1$).

**KIN NUMBERS**

Long-term matrilineal genealogies were used to determine the number of female kin in each year of the study. In each year and for each breeding female, we determined total number of co-breeding female kin (i.e., females that successfully raised a litter) or non-breeding female kin that were present in the population. Non-breeding females mostly included females that did not attempt reproduction at all (87%; $N = 366$ cases) and a few females that gave birth to a litter but did not succeed in weaning a single pup (13%; $N = 55$ cases). We pooled those females as non-breeders, as only successfully breeding females maintain nest burrows throughout the entire period of lactation and territoriality is mostly related to the defense of nest burrow and young (Festa-Bianchet & Boag 1982; Murie & Harris 1988). The majority of breeding female kin settles in close spatial proximity (on average, 72% of close kin are established within a females’ 30-m home range; see Viblanc et al. 2010). For each female, we calculated her number of close female kin (including the presence of a mother, daughters and littermate sisters) that were either co-breeding (mean = 0.73 ± 0.04; range = 0–4), or present but non-breeding (mean = 0.70 ± 0.04; range = 0–3). We restricted kin sisters to littermates (females born in the same litter, i.e. uterine kin), as previous studies have found that kin recognition in this species occurs through familiarization in the natal burrow (Hare & Murie 1996) and only littermate kin appear to act as ‘genial neighbours’ providing direct and indirect fitness benefits (Viblanc et al. 2010; Dobson et al. 2012).

**DATA ANALYSES**

To investigate the effects of individual kin on energy allocation strategies and fitness, we performed a three-step analysis. (1) Over the 22-year data set ($n = 359$ reproductive events for $N = 138$ females), we considered the overall effect of co-breeding or non-breeding kin numbers on litter size at weaning, total energy allocation $T_A$ and the balance between somatic and
reproductive allocation (residual RA). However, if existent, effects of kin numbers on litter size, TA or residual RA could be due to interindividual differences within years, or/and to interannual differences across years for a given individual.

Thus, we tested those alternatives by running new analyses with raw data (litter size, kin numbers, SA, RA) either (2) standardized by year or (3) by female ID. Year standardization controlled for possible sources of interannual environmental variability (e.g. resource availability, climate, predation pressure) allowing an investigation of within-year differences among individuals. Female ID standardization controlled for interindividual heterogeneity allowing investigating within-individual changes across years. As a consequence, when standardizing by female ID, we only included females that were monitored for at least two breeding seasons, explaining the lower sample size of individuals in the latter analyses (n = 308 reproductive events, N = 87 females).

For instance, year-standardized SA values were calculated as $S_{A_{std,year}} = \frac{SA_{i}}{TA_{r,year}}$ and female ID-standardized values as $S_{A_{std,ID}} = \frac{SA_{i}}{TA_{r,ID}}$ and residual RA values were then recalculated from either year-standardized or ID-standardized RA and SA. In all linear mixed models (LMMs), we controlled for female age (mean = 4.07 ± 0.10; range = 1–13) as a random variable to control for age effects on reproduction (e.g. primiparity and senescence; Broussard et al. 2003; Neuhaus et al. 2004). For the overall and year-standardized models, we controlled for repeated measures on individual females by including female ID as a random variable. For the female ID-standardized models, we controlled for year effects as a random variable. For instance, for the effects of co-breeding kin on residual RA, our models would be as follows:

1. $\text{residual RA} = \text{co-breeding kin} + (1|\text{age}) + (1|\text{ID})$ [overall]
2. $\text{residual RA}_{\text{std,year}} = \text{co-breeding kin}_{\text{std,year}} + (1|\text{age}) + (1|\text{ID})$ [year-standardized]
3. $\text{residual RA}_{\text{std,ID}} = \text{co-breeding kin}_{\text{std,ID}} + (1|\text{age}) + (1|\text{year})$ [ID-standardized]

By standardizing response variables, we aimed at removing the variance associated to factors that we could not control (e.g. environmental factors that could vary across years or differences in individual quality). However, by doing so, we also removed part of the variation due to interannual or interindividual differences in the number of kin. Thus, it was necessary to also standardize the number of kin to remove any potential bias. This entails that the contrasts in kin differences on the response variables are numerically the same (from 0 to 1 kin or 2 to 3 kin for instance). Given that the non-standardized effect of kin numbers on energy allocation appeared to be linear (Fig. 2) and that models with kin as a continuous variable actually explained more of the observed variance in litter size or energy allocation than models with kin as a binary factor (presence/absence), that is AICs for models with kin as a continuous variables were lower than those of models with kin as a factor for the same degrees of freedom, this assumption appeared to be reasonable. Analyses were done in R v.3.0.2 (R Core Team 2013) and models were run using the ‘lme4 v.1.1-7’ and ‘lmerTest v2.0-20’ associated packages (Bates et al. 2014; Kuznetsova, Brockhoff & Christensen 2014). Results are reported as means ± 1 SE and considered significant for $P \leq 0.05$. Given that females bred repeatedly, the overall sample size (n) was larger than the number of individuals (N) concerned, and both are reported in the results.

![Fig. 2. Overall effect of co-breeding kin numbers on the balance between somatic and reproductive allocation (residual RA) in Columbian ground squirrels.](image)

Results

**Effects of female kin numbers on litter size at weaning**

Overall effects of kin numbers on litter size at weaning

Whereas the number of co-breeding kin (mother, daughters and littersmates) had a positive effect on females’ litter size at weaning (LMM; $\beta = 0.19 \pm 0.07$, $t = 2.75$, $P = 0.006$, $n = 359$, $N = 138$), we found no effect of non-breeding kin numbers on litter size at weaning ($\beta = -0.11 \pm 0.07$, $t = -1.64$, $P = 0.101$). To test whether the effect of co-breeding kin on litter size was direct or mediated through changes in $T_A$ or residual $R_A$, we added those as independent covariates in the model ($1.00 \leq \text{VIFs} \leq 1.03$). Not surprisingly, the variance in litter size was then explained by $T_A$ ($\beta = 0.01 \pm 0.00$, $t = 2.75$, $P < 0.001$) and residual $R_A$ ($\beta = 0.01 \pm 0.00$, $t = 16.95$, $P < 0.001$), but not longer by the number of co-breeding kin ($\beta = 0.04 \pm 0.04$, $t = 1.09$, $P = 0.274$).

**Interindividual effects of kin numbers within year on litter size at weaning**

When year-standardized, the number of co-breeding kin had a positive effect on residual $R_A$ within years, females with more co-breeding kin biased allocation strategies ($\beta = 2.83 \pm 1.00$, $t = 3.38$, $n = 338$, $P = 0.001$). Conversely, the number of non-breeding kin had no effect on $T_A$ or residual $R_A$, $P > 0.05$.

**Interannual effects of kin numbers for a given female on litter size at weaning**

When standardized by female ID, the number of co-breeding kin had a positive effect on litter size at weaning ($\beta = 0.12 \pm 0.05$, $t = 2.30$, $P = 0.022$, $n = 359$, $N = 138$) had a positive effect on litter size at weaning, whereas the number of non-breeding kin did not ($\beta = 0.02 \pm 0.06$, $t = 0.30$, $P = 0.760$). Here, controlling for year-standardized $T_A_{\text{std,year}}$ and residual $R_A_{\text{std,year}}$ in the models removed the significant effect of co-breeding kin ($\beta = 0.02 \pm 0.03$, $t = 0.77$, $P = 0.439$) on year-standardized litter size ($1.00 \leq \text{VIFs} \leq 1.01$).

**Interindividual effects of kin numbers within year on energy allocation**

Similarly, when year-standardized, the number of co-breeding kin had no effect on $T_A_{\text{std,year}}$ (LMM; $\beta = 0.09 \pm 0.08$, $t = 1.10$, $P = 0.272$, $n = 359$, $N = 138$), but a positive effect on residual $R_A_{\text{std,year}}$ ($\beta = 0.07 \pm 0.03$, $t = 2.10$, $P = 0.036$), suggesting that within years, females with more co-breeding kin biased energy allocation towards offspring production. The number of non-breeding female kin did not significantly affect $T_A_{\text{std,year}}$ ($\beta = 0.16 \pm 0.08$, $t = 1.85$, $P = 0.066$), nor residual $R_A_{\text{std,year}}$ ($\beta = -0.01 \pm 0.04$, $t = -0.21$, $P = 0.833$).

**Interannual effects of kin numbers for a given female on energy allocation**

When standardized by female ID, the number of co-breeding female kin had no effect on $T_A_{\text{std,ID}}$ (LMM; $\beta = 0.05 \pm 0.09$, $t = 0.52$, $P = 0.604$, $n = 308$, $N = 87$) or residual $R_A_{\text{std,ID}}$ ($\beta = 0.01 \pm 0.04$, $t = 0.30$, $P = 0.768$, $n = 308$, $N = 87$). The number of non-breeding female kin had no effect on $T_A_{\text{std,ID}}$ ($\beta = -0.03 \pm 0.09$, $t = -0.35$, $P = 0.730$), but was negatively associated with residual $R_A_{\text{std,ID}}$ ($\beta = -0.08 \pm 0.04$, $t = -2.08$, $P = 0.038$), suggesting that a given individual allocated less energy to reproduction when more non-breeding kin were present.

Discussion

The social environment is known to strongly affect individual behaviour, physiology and fitness. Here, we highlight novel findings of important social effects on energy allocation strategies in group-living Columbian ground squirrel females during reproduction, with ultimate consequences on fitness (female litter size at weaning).

The positive relationship between close kin numbers and female litter size at weaning is consistent with our previous results showing that direct fitness benefits for females over their lifetime occurred primarily through increases in weaned litter sizes (Viblanc et al. 2010). Interestingly, the present analyses reveal that overall kin benefits on litter size occurred both on interindividual and interannual levels. From a year-centred perspective, females with more co-breeding kin compared to others achieved larger litters. From a female-centred perspective, individual females achieved higher litters in years where they had more co-breeding kin, while years in which high numbers of non-breeding kin occurred were also years in which individual females achieved higher litters.
which litter size was relatively low, likely reflecting years where reproduction was generally poor (low numbers of breeding females and low litter sizes).

Several proximate mechanisms could explain the positive relationship between litter size at weaning and close kin numbers. For instance, reduced risks of infanticide (Dobson 1990; Stevens 1998) or net benefits in terms of energy gain owing to decreased territoriality between familiar individuals (Murie & Harris 1984) are likely to play an important role. By clustering with lowly aggressive close kin (King 1989a, b; Viblanc et al. 2010; Arnaud, Dobson & Murie 2012), breeding females may decrease the time/energy cost of maintaining territorial boundaries (Festa-Bianchet & Boag 1982; Murie & Harris 1988), which could ultimately lead to increases in net energy income (TA) or higher allocations in somatic or reproductive functions. In addition, greater offspring survival prospects around close kin (Dobson 1990; Stevens 1998) should favour a bias towards reproductive allocation (high residual RA). This appears to be supported by the fact that the overall effects of kin numbers on litter size at weaning disappeared when TA and residual RA were included in the model, suggesting that the effects of kin numbers on litter size were primarily mediated through changes in allocation strategies. Decomposing the overall kin effect indicated that the effect of kin numbers on litter size when controlling for TA and residual RA was not significant on the interindividual (within year) level, but remained significant on the interannual (within individual) level. This suggests that between individuals within a year, the greatest effect of kin numbers on litter size was indeed mediated through changes in allocation strategies. In contrast, for given females over several years, effects of kin numbers on litter size also occurred independently from effects on allocation strategies. Alternatively, the interindividual correlation between kin numbers and litter size might be explained by heritable variation among females in the population (though this alone is not sufficient to explain the significant effect of kin numbers on litter size at a within-individual level). For instance, emergence body mass is heritable in female ground squirrels (Lane et al. 2011) and females with higher body mass tend to produce larger litters (Dobson, Risch & Murie 1999; Broussard, Dobson & Murie 2005; Rubach et al. in press). Thus, female offspring of mothers that had large litters also tend to produce large litters and have greater chances of having a sibling in the population because they were born into a larger litter themselves. Teasing apart those alternatives will require further experimental work. For instance, translocation of females to novel colonies with no kin has been successfully done in the past (Wigit & Boag 1986) and may provide useful tests of kin effects on energy allocation.

For female ground squirrels that do not reproduce in a given year, a gain in body mass over a reproductive season may be carried over into the next season with positive effects on subsequent weaned litter size (Rubach et al. in press). Thus, there should be clear benefits of increased somatic allocation over the course of a season. However, the overall analysis highlights that the effect of kin numbers was not specifically on total energy (TA), but rather on the balance between reproductive and somatic allocations (i.e. residual RA), suggesting that the main benefits of co-breeding with kin were not due to increased access to food resources, but to alternative mechanisms (see below). Those findings seem to fit the life-history prediction that rodents (mammals with generally fast life-history strategies) should allocate more into current reproduction than both future reproduction and survival whenever possible (Hamel et al. 2010). Female Columbian ground squirrels may breed as yearlings (although these females virtually always fail) and prime reproductive age occurs from 2 to 7 (Neuhaus et al. 2004; Broussard, Dobson & Murie 2008) whereupon reproductive senescence occurs (Broussard et al. 2003). Given that females may wean up to six pups (average of 3) in a given year with similar chances of survival as smaller litters (Risch, Dobson & Murie 1995) and that increased reproductive investments appear to have little consequences on future survival (Murie & Dobson 1987; Hare & Murie 1992; Skibiel, Speakman & Hood 2013; Rubach et al. in press), females may indeed be expected to allocate additional resources into the current litter if they have the potential, for example because they need to spend less time on other activities such as territorial defence. It would be interesting to determine whether social influences may tilt the balance between reproductive and somatic allocations in species with slower life-history paces as well, given their relatively late sexual maturity and reproductive senescence (Jones et al. 2008).

On an interindividual (within year) level, females with more co-breeding kin biased their energy allocation towards reproduction (higher residual RA). One likely explanation for this result is that, without modifying total energy, kin individuals acted as social buffers allowing females to reduce the time and energy expended to territorial nest defence in favour of that invested into offspring. Lactating females are highly aggressive during lactation, a time when rates of aggression are related to a peak in territorial defence (Festa-Bianchet & Boag 1982; Murie & Harris 1988), and where infanticide is high (Dobson 1990; Stevens 1998). The maintenance of close nest burrows (King 1989b; Viblanc et al. 2010), greater tolerance (King 1989a; V.A. Viblanc, C. Pasquieretta, C. Sueur, R. Boonstra & F.S. Dobson, unpublished results) and less infanticide (Dobson 1990; Stevens 1998) between kin during this highly energy constraining period may allow breeding females to bias their allocation towards reproduction (e.g. increased allocation to lactation), ultimately resulting in positive effects on litter size and mass. Such kin/social effects on female energetics and allocation patterns are likely widespread in vertebrates, playing a potentially important role in the evolution of philopatry/cooperative breeding (Greenwood...
that interannual variation in RA mostly results from en-

it ditory traits from being maximally expressed (Fisher 1930; Arnaud, Dobson & Murie 2012; Dobson et al. 2012).

Because lactating females are typically more territorial (around their nest burrows) than non-lactating females (Murie & Harris 1988), it is not surprising that kin benefits on energy allocation arose essentially from co-breeding kin.

On an interannual level (for a given female over several years), the number of co-breeding kin was no longer associated with residual RA. Again, those results likely reflect that interannual variation in RA mostly results from environmental sources of variation other than kin (e.g. climate conditions, predation). For instance, Columbian ground squirrels are mainly income breeders that are highly sensitive to food resources (Dobson & Kjelgaard 1985; Brous-
sard, Dobson & Murie 2005; Rubach et al. in press).

Indeed, inclement weather conditions during breeding, such as late snow falls and heavy rainfall preventing breeding females from feeding, may have strong consequences on female litter size and breeding success (Neuhaus, Bennett & Hubbs 1999; Lane et al. 2012). This is further confirmed by the negative effect of non-breeding kin on residual RA at the intraindividual level suggesting that for a given female, in years where a large number of female kin was non-breeding, individual females also allocated less to reproduction. Nonetheless, it is noteworthy that the effects of kin numbers on litter size were not mediated only through effects on energy allocation strategies but also by direct effects on offspring survival (positive association between co-breeding kin numbers and litter size at the intraindividual level).

Energy is usually the limiting factor preventing life-his-
tory traits from being maximally expressed (Fisher 1930; Hirshfield & Tinkle 1975; Reznick 1985; Stearns 1992; Brown et al. 2004), and kin/social effects on energy allocation patterns are likely widespread in birds and mammals. For instance, energy benefits of breeding with kin have been highlighted in house mice (Mus musculus domesticus) where mothers communally nursing with kin are able to allocate more time to foraging or territorial defence without impairing maternal care to the offspring (Auclair et al. 2014), and wean larger litter sizes (König 1993; Dobson, Jacquot & Baudoin 2000). In cooperatively breeding meerkats (Suricata suricatta), mothers with (not necessarily related) helpers are able to reduce the energy cost paid for lactation (Scantlebury et al. 2002), highlighting direct social effects on maternal energy expenditure. Comparative data in social carnivores also suggest that the energy costs of reproduction may underlie reproductive suppression and the evolution of communal breeding (Creel & Creel 1991). Social influences on resource acquisition and allocation may also help explain the occurrence of philopatry/cooperative breeding in environments where resources are unpredictable and energy budgets limited (Greenwood 1980; Ebensperger 2001). In Siberian jays (Perisoreus infaustus) for instance, individuals in kin groups have greater access to high quality resources and greater energy intake under increased predator exposure compared to individuals with no kin (Nystrand 2007). In yellow-bellied marmots (Marmota flaviventris), the formation of kin matrilines facilitates resource acquisition and decreases aggression within the group (Armitage 1991, 1998).

The extent to which kin and the social environment at large play a direct role (e.g. via helping in reproduction, monopolizing high quality resource patches) or indirect (e.g. via decreased territoriality) roles in shaping animal energy budgets and the trade-off between reproductive and somatic allocations, is based on the cost of reproduction hypothesis (Williams 1966; Hirshfield & Tinkle 1975), offers an exciting hypothesis for the evolution of sociality by kin selection.

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Author contribution

V.A.V. conceived and designed the study, collected field data, did the statistical analyses and wrote the paper. C.S. co-ran the analyses and participated in paper writing. J.O.M. initiated the long-term study, collected field data and commented on the paper. F.S.D. co-designed the study, collected data in the field and participated in paper writing. All authors gave final approval for publication.

Data accessibility

The data related to this publication are archived at the Dryad Digital Repository http://dx.doi.org/10.5061/dryad.50hk0 (Viblanc et al. 2016).

References


