

Kin selection in Columbian ground squirrels: direct and indirect fitness benefits

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Abstract

Empirical and theoretical studies have supported kin selection by demonstrating nepotism or modelling its conditions and consequences. As an alternative, we previously found that female Columbian ground squirrels had greater direct fitness when more close kin were present. Extending those results, we used population matrix methods to calculate minimum estimates of individual fitness, estimated direct and indirect components of fitness, estimated inclusive fitness by adding the direct fitness (stripped of estimated influences of the social environment) and indirect fitness components together, and finally looked for inclusive fitness benefits of associations with close kin who seem to be 'genial neighbours'. We examined the estimated fitness of a sample of 35 females for which complete lifetimes were known for themselves, their mothers and their littermate sisters. Six of these females had no cosurviving adult close kin, and their direct fitness was significantly lower than 29 females with such kin ($\lambda = 0.66$ vs. $\lambda = 1.23$). The net fitness benefit of the presence of close kin was thus 0.57. The estimated indirect component of fitness through benefits to the direct fitness of close kin was 0.43. Thus, estimated inclusive fitness for females with cosurviving close kin ($\lambda = 1.09$) was significantly greater than that for females without surviving close kin (viz., $\lambda = 0.66$). The presence of closely related and philopatric female kin appeared to result in considerable fitness benefits for female ground squirrels, perhaps through the behavioural mechanisms of lowered aggression and other forms of behavioural cooperation.

Keywords: cooperation, direct fitness, group-living, inclusive fitness, indirect fitness, individual fitness, kin selection, matrix models, *Urocitellus columbianus*

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Introduction

Hamilton (1964) developed the theory of kin selection to explain what appeared to be cases of altruistic helping behaviour, in which some individuals in a population forgo personal fitness components (e.g. reproduction in the case of sterile ant workers) in favour of aiding another individual's fitness (e.g. the reproduction of the 'queen' colonial ant). Hamilton solved the seeming dilemma by formalizing genetic nepotism, analogous to cases in which close human rel-

atives (kin) or friends are favoured via the gift of position with little or no regard for merit. The basic idea is that traits that promote kin might be favoured by natural selection because close relatives have a high probability of sharing genes underlying 'kin promotion' through descent. Hamilton provided an accounting procedure for dealing with the influence of the social environment in terms of fitness, including the ideas of indirect and inclusive fitness. Of course, the benefits and any costs of such helping behaviour are important, and these were incorporated into 'Hamilton's inequality': $rb > c$, where r is the coefficient of relatedness, b the benefit of helping behaviour and c the cost of helping, both b and c measured in fitness terms. When the

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inequality is met, natural selection should favour the evolution of helping behaviours, given the heritability of the behavioural traits. This form of natural selection is termed 'kin selection' (Maynard Smith 1964).

With the publication of Wilson's (1975) tome 'Sociobiology' and an influential review by West Eberhard (1975), kin selection became a central focus in the growing field of behavioural ecology, a field that studies the evolution of behavioural traits and in particular social behaviours. Further modifications and improvements to kin selection theory have been made, such as defining relatedness in different ways (Hamilton 1970; Grafen 1985) and the use of matrix population models to measure fitness (Oli 2003). Modelling studies of kin selection are legion (e.g. Lehmann & Keller 2006; Grafen 2007, 2009; Lehmann *et al.* 2007; Lehmann & Rousset 2010; Mathot & Giraldeau 2010; Taylor & Grafen 2010; and references therein). Many empirical studies have demonstrated nepotistic helping behaviour in social species and used this as suggestive evidence of a behavioural basis for kin selection (e.g. reviews by Clutton-Brock 2009; Hatchwell 2009; Silk 2009).

We recently took an alternative approach of testing for fitness differences among individuals that did and did not share time and space with close kin (Viblanco *et al.* 2010). We found that philopatric female Columbian ground squirrels (*Urocitellus columbianus*) that had more close kin available to cooperate through lowered rates of aggression (King 1989a) also had greater direct individual fitness (i.e. a difference based on their own reproduction) than females without such close relatives. Such a difference based on the presence of cooperative kin neighbours implies a net benefit of the social environment in terms of fitness and thus suggests that indirect benefits to inclusive fitness should also occur (Grafen 1982; Queller 1996). This does not demonstrate ongoing kin selection, but it indicates one of the necessary conditions for kin selection, namely fitness differences that favour cooperating close kin, perhaps through the behavioural mechanism of being 'genial neighbours' via lowered rates of aggression. However, the magnitude of indirect fitness advantages of cooperation compared to direct fitness in the absence of cooperation could indicate the relative strength of kin selection.

Our study (Viblanco *et al.* 2010) used matrix models to estimate the individual fitness (after McGraw & Caswell 1996; Oli & Armitage 2008; but see Brommer *et al.* 2004). We modified our estimate of individual fitness to take into account changes in population size over the lifetime of individual females. First, individual fitness estimates were obtained using a population projection matrix applied to an individual. Fitness is thus modelled as the finite growth rate of a population of individuals with the

same life cycle as the individual under study. This rate is an estimate of fitness for the individual female, over her lifetime. Second, a similar matrix model for each female was used, but using population growth rates from year to year as values of fertility. Finally, the individual fitness values were regressed on the estimate of population change during the lifetime of the females, and residuals were used as a measure of individual fitness that was adjusted for population size.

Our earlier study (Viblanco *et al.* 2010) only examined direct fitness. In other words, cooperation between close kin was favoured by a fitness difference in the mothers' own production of offspring. If kin selection contributes to the evolution of cooperation, behavioural traits should also be favoured by the indirect fitness benefit to relatives. This indirect component can be calculated from the net fitness benefit for relatives of receiving help, devalued by the coefficient of relatedness (Grafen 1982; Creel 1990; Lucas *et al.* 1996; Queller 1996; Oli 2003). The purpose of the present study was to estimate the indirect component of fitness, devalued not only by the degree of kinship, but adjusted for changes in population size as well. We estimated the net fitness benefit for kin by subtracting the direct fitness of females that did not have helpful kin nearby when they were reproducing from those that did have kin present. We tested whether direct fitness was greater for individuals that lived with kin present. When direct fitness is greater for kin that cooperate, each female will also acquire a positive indirect fitness component from her close kin neighbours. And as more kin neighbours are present, the indirect fitness component should be enhanced.

We calculated the difference in direct fitness for mothers with and without successfully reproducing close kin during their lifetimes, to estimate the net benefit of the social environment and produce a fitness estimate that was stripped of this benefit. We further estimated the degree to which the indirect component of fitness complemented the stripped direct fitness estimate. Then, we added these two components together to produce an estimate of inclusive fitness for 'genial neighbour' cooperation. Importantly, female Columbian ground squirrels act as though they only recognize individuals that they share a nest burrow with at the time of their birth (viz., littermate sisters and their mother; King 1989a; Viblanco *et al.* 2010; but see King & Murie 1985). Thus, our evaluation of indirect fitness benefits of geniality to neighbours only extended to these 'close kin' and whether a focal female had an opportunity to influence their fitness (i.e. whether the females cosurvived and thus had a chance to provide 'genial neighbour' social benefits). Finally, we tested the 'genial neighbour' idea by examining whether littermate sisters were more tolerant of proximity of nest burrows than

were nonlittermate sisters during the lactation period when females hold individual territories.

Methods

We studied a colony of Columbian ground squirrels on about 1.8 ha of contiguous subalpine meadow in the Sheep River Provincial Park of Alberta, Canada (50° N, 118° W; elevation 1500 m). Our ground squirrel population was monitored from 1992 to 2008, and thus several generations of matrilineal genealogies were known from mother-offspring associations at about the time of weaning. In addition, analyses of microsatellite DNA identified paternity patterns from 2005 to 2008 (Raveh *et al.* 2010). Ground squirrels were captured in live traps (13 × 13 × 40 cm³, Tomahawk Co., WI, USA) baited with peanut butter. Individuals were examined for sex and reproductive condition, weighed to the nearest 5 g using a Pesola™ spring-slide balance, and zygomatic arch breadth measured to the nearest 0.1 mm with dial callipers. Each individual received a pair of numbered metal ear tags (Monel #1 National Band & Tag Co.) and a unique black dye mark on the dorsal pelage (Clairol® human hair dye). All ground squirrels were captured in mid-April to mid-May, within 3 days of their emergence from the 9-month period of annual hibernation. Females usually mated 3–7 days after spring emergence. Later in mid-June to early July (51 days after mating), weaning litters and their associated mothers were live trapped as the young emerged for the first time from their natal burrows.

We estimated individual fitness of 70 mothers for which we had complete lifetime records of survival and reproduction, using individual transition matrices (after McGraw & Caswell 1996; Oli 2003; Oli & Armitage 2008; Viblanc *et al.* 2010). The size of these matrices depends on the mother's lifetime, and these ranged from 2 to 10 years (mean = 4.87 years, $N = 70$). Lifetime reproductive success and individual fitness are alternative estimates of the fitness of mothers (Brommer *et al.* 2004). We chose the latter to make adjustments for changes in population size (after Viblanc *et al.* 2010). Mothers that live during periods of increasing population will, on average, have higher estimated individual fitness than mothers that live during periods of decreasing populations. Fitness depends on an individual 'matrix population model' growth rate (basically, a population growth rate, λ , but calculated for an individual mother) relative to other females in the population. It was necessary to adjust the matrix estimate of fitness for changes in population size. Thus, for each of the 70 mothers, we used the proportional change in population size between years to construct a 'population' fitness matrix for years that she survived. We then

regressed individual fitness on population fitness and used the residuals as an estimate of relative individual fitness. Hereafter, we drop the terms 'relative individual' from our estimate of fitness.

Our estimate of fitness was calculated for each mother as a measure of the direct component of inclusive fitness (Oli & Armitage 2008; Viblanc *et al.* 2010). To estimate the indirect component of inclusive fitness, it was necessary to estimate the coefficient of relatedness for mother-daughter and sister-sister dyads, multiply this value times the net fitness benefit to their relatives and sum the values over relatives that survived to successfully reproduce (Queller 1996; Oli 2003). We estimated the net indirect fitness benefit by subtracting the mean direct fitness of mothers that had no surviving adult close kin from the direct fitness of mothers that had surviving close kin and multiplying this value times the coefficient of relatedness between the focal mother and the relative. In three cases, two littermate sisters shared a dam, and the indirect fitness benefit of cooperative behaviour towards the dam was divided equally between the sisters to avoid double accounting. In 10 cases, females were multiple relatives of other kinds (e.g. both a sister and a daughter), and the fitness benefits of each of these females were divided equally among their relatives. All other indirect fitness benefits were within dyads, so that fitness benefits of cooperative traits were counted only once for each individual. Mothers were related to daughters by 0.50 on average. Because of multiple paternity in Columbian ground squirrels (Murie 1995), the degree of relatedness among littermate siblings was estimated from paternity analyses (related by 0.39 on average, $n = 110$ litters; from Raveh *et al.* 2010), and we used this value as an estimate of the relatedness of littermate sisters. Alternative procedures for measuring indirect fitness benefits are given by Creel & Waser (1994), Oli (2003), and Oli & Armitage (2008).

We used Wilcoxon tests (z-approximations) to compare the direct fitness estimates for mothers with and without cosurviving close kin and inclusive fitness of cooperation vs. noncooperation (estimated from mothers that could and could not have cooperated). Estimates of direct fitness compared to 1.0, the indirect component of inclusive fitness of cooperation compared to 0.0 and inclusive fitness of cooperation compared to 1.0 were made with *t*-tests. Close kin (*viz.*, adult mother-daughter and sister-sister dyads) were assumed to be genial neighbours, as King (1989a) showed that they have lower aggression rates than less related dyads and nonlittermate sister dyads, and because they have closer nest burrows than less related dyads when nearest neighbours are compared (Viblanc *et al.* 2010). To further test this assumption, we compared the

distance between nest burrows for littermate and nonlittermate sisters using a Wilcoxon test (z-approximation). Statistics were calculated in VASSARSTATS (<http://faculty.vassar.edu/lowry/VassarStats.html>), and one-tailed tests were applied where a priori predictions were tested.

Results

Our estimate of direct fitness over the lifetimes of 70 mothers approximately followed a normal distribution (Fig. 1). We added 1.0 to our residuals of λ values for mothers regressed onto estimates of population λ during their lifetimes to produce an unbiased estimate (i.e. negative values are possible). Of these females, 35 had complete reproductive histories known for their mother and any littermate sisters. The direct fitness of these females ($\lambda = 1.13 \pm 0.12$ SE, $N = 35$) was somewhat >1.0 , but not significantly ($t = 1.12$, d.f. = 34, $P = 0.27$). Of the 35 females with complete lifetime records, 29 had close kin that cosurvived with them to reproductive age and six had no cosurviving close kin. Females with cosurviving close kin when both were adults had significantly greater direct fitness ($\lambda = 1.23 \pm 0.13$ SE, $N = 29$) than those that had no cosurviving close kin as adults ($\lambda = 0.66 \pm 0.20$ SE, $N = 6$), leaving a considerable and significant difference of 0.57 (Fig. 2; Wilcoxon test, $z = 1.95$, $P = 0.03$). We used 0.66 as our estimate of direct fitness stripped of the net benefit of the social environment, because females without cosurviving close kin could not have benefited by having genial neighbours.

This same 'net benefit of the social environment' provides a starting point for our estimates of indirect fit-

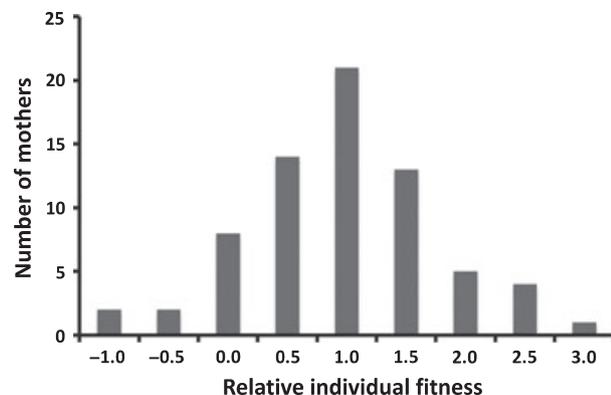


Fig. 1 The distribution of an unbiased estimate of relative individual fitness (our estimate of direct fitness): from the individual fitness measure, a population fitness estimate and the regression of the former on the latter. See Methods and Viblanc *et al.* (2010) for details. The mean is 1.00 and the variance 0.659, for a sample of 70 mothers.

ness. To estimate the indirect fitness that a female gains by her genial behaviour towards her close kin, we used the mean direct fitness of females without cosurviving close kin as an estimate of fitness in the absence of 'genial neighbour' helping and subtracted it from the direct fitness of close kin individuals to estimate the net fitness benefit of cooperation for them. We then multiplied this value by the coefficient of relatedness and summed over close kin. Twelve focal females had only their mothers cosurvive with them, so that both were of reproductive age; two females had only a littermate sister cosurvive; two females had only a daughter cosurvive; seven females had their mother and one or more daughters cosurvive; five females had both their mother and a littermate sister cosurvive; and one female had her mother, a sister and a daughter cosurvive. The indirect fitness component estimated from these 29 females was substantial and significantly different from zero (0.43 ± 0.08 SE, $t = 5.71$, d.f. = 28, $P < 0.0001$). The sum of direct and indirect components of fitness (the 1st 'stripped' of effects of the social environment, the 2nd based on these very effects) was used to estimate the inclusive fitness of the 'genial neighbour' trait for all 35 females in our sample, and this estimate was not significantly different from 1.0 ($\lambda = 1.02 \pm 0.07$; $t = 0.24$, d.f. = 34, $P = 0.82$). The inclusive fitness for 'genial neighbour' cooperation was significantly greater than for noncooperation (respectively, $\lambda = 1.09 \pm 0.08$ SE, $N = 29$; $\lambda = 0.66 \pm 0.20$ SE, $N = 6$; Fig. 3; Wilcoxon test, $z = 1.90$, $P = 0.03$). As the number of cosurviving close kin increased, so did the estimated inclusive fitness value (Fig. 4; $r = 0.425$, d.f. = 33, $P = 0.005$).

To further test the difference in 'genial neighbour' behaviour between known and unknown kin, we examined the distance between nest burrows for littermate

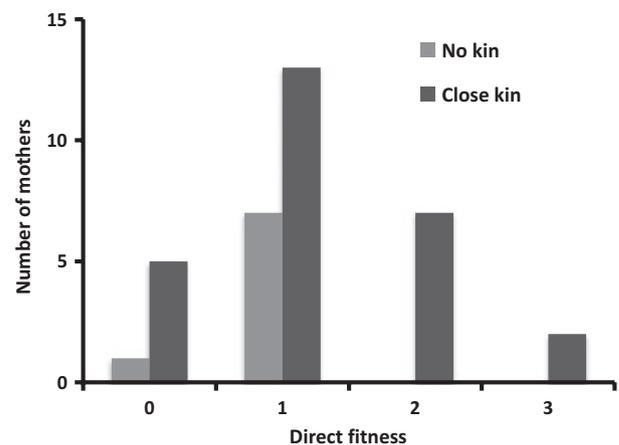


Fig. 2 The distribution of direct fitness estimates for females with and without close kin (viz., mother and littermate sisters) that cosurvived to be reproductive adults at the same time.

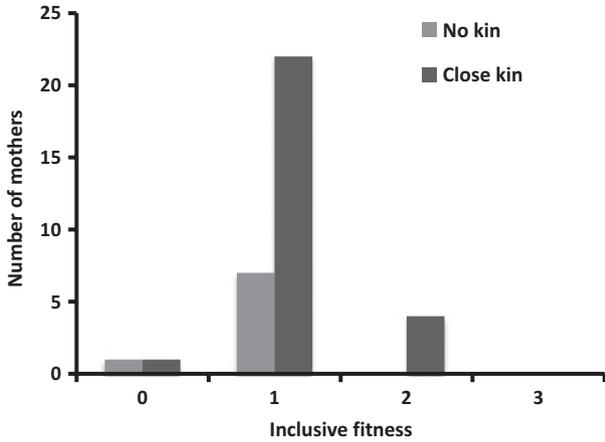


Fig. 3 The distribution of inclusive individual fitness of ‘genial neighbour’ cooperation, estimated from females with and without close kin (viz., mother-daughter and littermate sisters) that cosurvived to be reproductive adults at the same time (see Methods).

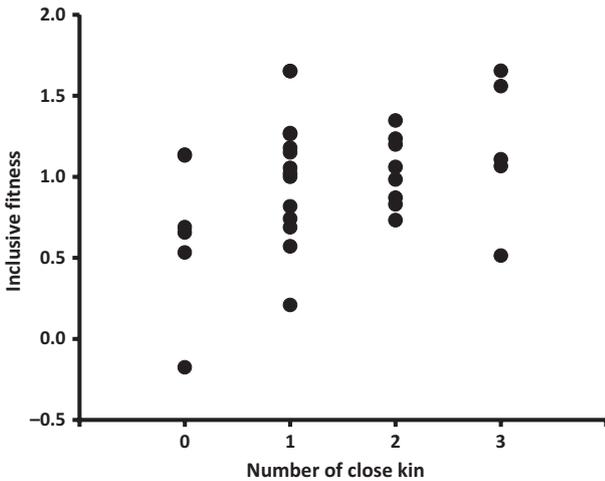


Fig. 4 Estimated inclusive fitness and number of cosurviving close kin (mother-daughter and littermate sister dyads) that were both of reproductive age (2 years old and older) or actively reproducing at the same time.

sisters and nonlittermate sisters (Fig. 5). Both types of sisters should settle near their mothers and thus be in close proximity. Nest burrows are constructed by lactating females a few days before birth, have a single entrance and no connection with the extensive burrow systems that are used by many individuals. Mothers suckle their dependent young during lactation in these burrows. Littermate sisters maintained nest burrows that were significantly closer than the nest burrows of nonlittermate sisters (littermate sister median = 19.7 m, inter-quartile range = 14.3–33.2 m, $N = 27$; nonlittermate sister median = 30.1 m, inter-quartile range = 15.2–83.1 m, $N = 72$; Wilcoxon $z = 1.80$, $P < 0.04$).

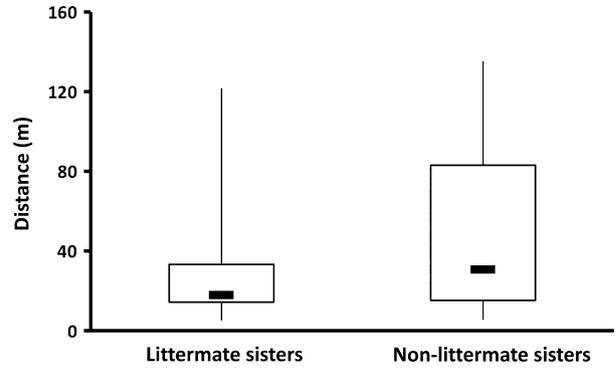


Fig. 5 The distance between nest burrows of littermate and nonlittermate sisters. Boxes show quartile distributions, and whiskers indicate the range of extreme values. The bold horizontal bars give the medians (not that the distributions are far from normality).

Discussion

Our purpose was to evaluate direct and indirect components of fitness among nepotistic kin female ground squirrels. We had previously found direct fitness differences between females with close natal kin that could provide ‘genial neighbour’ cooperation and those with only more distantly related females in the population (Viblanco *et al.* 2010). Thus, there appeared to be a fitness advantage for cooperation that should be complemented by an indirect component. Here, we used the direct fitness of females with complete lifetime records for themselves and their nearest relatives to evaluate the possible fitness benefits of ‘genial neighbour’ behaviours. Hamilton (1964) described how personal fitness should be stripped of components due to an individual’s social environment to reveal the individual’s personal contribution to inclusive fitness (e.g. Grafen 1982; Creel 1990; Lucas *et al.* 1996; Queller 1996; Oli 2003). The amount stripped because of the social environment then reflects any net benefit of that environment. We estimated this amount by looking at the direct fitness difference between females that had cosurviving close kin that could be genial neighbours and females that did not share this advantage. These ‘stripped social effects’ were very similar in magnitude to the direct fitness of females that had no possibility of help from close relatives (viz., $\Delta\lambda = 0.57$ vs. $\lambda = 0.66$, respectively). This suggests the possibility of a strong effect of the social environment on direct fitness.

We also estimated the indirect component of inclusive fitness for cooperation with surviving adult kin by multiplying the coefficient of relatedness times the direct fitness benefit and summing appropriate terms (see Methods). This was a substantial and significant augmentation of mean cooperative trait fitness (an average

of 0.43 units of λ) and suggests that any 'geniality' towards related neighbours significantly augments fitness. Finally, we added this augmentation to the direct fitness estimates (stripped of the net benefit of the social environment) to estimate the inclusive fitness of cooperation. Of course, females without the benefit of cosurviving 'genial neighbour' close kin were not augmented. The result was an average fitness for the sample of 35 females that was around 1.0, but a significant fitness advantage for cooperation. Our estimates of direct, indirect and inclusive fitness all show a strong advantage to the presence of nearby close kin. As the number of co-occurring close kin increased, so did the estimate of inclusive fitness. The idea that these neighbours might be genial is an indirect inference from behavioural and spatial evidence. We also suggest the indirect inference that matrilineal philopatry facilitates the fitness advantage of genial neighbours by keeping close kin together.

Our results are correlative rather than experimental. Thus, we cannot rule out the possibility that females in matrilineal cosurvive together and have greater fitness because they possess richer territories. Covariance between the social and ecological environment, however, provides an ecological explanation for the results that we found, not an alternative to the fitness benefits of the presence of close kin. This ecological hypothesis and perhaps others might be tested in future. Another curiosity from our results was a considerable difference between the estimated influence of the social environment that needed to be stripped away from direct fitness, and the summed influences of a female's presence as an adult on her female close kin (*viz.*, the estimated indirect component of fitness), as the former was somewhat larger than the latter. The accuracy (our sample sizes were limited) and meaning of this difference might also be the subject of future research. Finally, we estimated fitness based on offspring at weaning, but Hamilton (1964) specified the production of *adult* offspring; future analyses should focus on this period in the life cycle as more data become available.

The ground squirrels have a comparatively weak form of social cooperation that is exhibited among close female kin, lessened aggression compared to unrelated individuals (King 1989a). Female Columbian ground squirrels that are close kin (*viz.*, mother-daughters and littermate female siblings) cooperate by having a lower rate of fights and chases with one another than they do with other females who live adjacent to them, including non-littermate sisters and unrelated individuals. The lower rates of aggression appeared independent of proximity of adult females, because the ranges of kin and nonkin neighbours did not differ significantly in spatial overlap (King 1989b). However, we documented greater proximity of nest burrows of close kin compared to more dis-

tantly and unrelated individuals (Viblan *et al.* 2010; Arnaud *et al.* 2011), and greater proximity of nest burrows of littermate sisters than nonlittermate sisters (results above). In sum, current evidence suggests that close kin are genial neighbours that cooperate via greater tolerance of and perhaps proximity to one another.

This mild form of cooperation might also be associated with kin-biased alarm calling (MacWhirter 1992) as described for other ground squirrels (e.g. Armitage 1962; Sherman 1977, 1985; Carey & Moore 1986; Hanson & Coss 2001; Hare & Atkins 2001), but it does not appear to extend to advantages with respect to vigilance behaviour (Fairbanks & Dobson 2010). Furthermore, nepotistic cooperation in this species is constrained by the mechanism of recognition, because only those females that have shared a natal burrow act as though they recognize one another as close kin (King 1989a; Viblan *et al.* 2010). This produces an interesting situation where a mother may cooperate with two daughters born in different years, but the daughters might not cooperate. This possible constraint of the recognition system (perhaps through some form of social learning; e.g. Hoogland 1995; Hare & Murie 1996) on kin-selection deserves further research. Nonetheless, there appear to be fitness benefits to the presence of close and recognized relatives that very likely have a behavioural basis.

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Date accessibility

Field data: Excel file of demographic records available as the online Supporting information material.

Supporting information

Additional supporting information may be found in the online version of this article.

Data S1 Demographic records.

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