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Prairie dogs increase fitness by killing interspecific competitors

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Interspecific competition commonly selects for divergence in ecology, morphology or physiology, but direct observation of interspecific competition under natural conditions is difficult. Herbivorous white-tailed prairie dogs (*Cynomys leucurus*) employ an unusual strategy to reduce interspecific competition: they kill, but do not consume, herbivorous Wyoming ground squirrels (*Urocitellus elegans*) encountered in the prairie dog territories. Results from a 6-year study in Colorado, USA, revealed that interspecific killing of ground squirrels by prairie dogs was common, involving 47 different killers; 19 prairie dogs were serial killers in the same or consecutive years, and 30% of female prairie dogs killed at least one ground squirrel over their lifetimes. Females that killed ground squirrels had significantly higher annual and lifetime fitness than non-killers, probably because of decreased interspecific competition for vegetation. Our results document the first case of interspecific killing of competing individuals unrelated to predation (IK) among herbivorous mammals in the wild, and show that IK enhances fitness for animals living under natural conditions.

1. Introduction

Interspecific competition—i.e. reciprocal negative effects of one species on another [1]—commonly leads to divergence among species in ecology, morphology, behaviour or physiology, with reduced competition the outcome ([2–5]; but see [6]). This divergence sometimes allows us to infer the 'ghost of competition past' [7], but direct contemporary observation of competition, especially in non-experimental natural systems, can be difficult [6–10]. One way that ongoing interspecific competition can manifest itself is through physical combat and, in extreme cases, the killing of interspecific competitors [11]. Usually at a low frequency, interspecific killing of competing individuals unrelated to predation (IK) has been observed for a variety of both vertebrates and invertebrates [11–15]. When IK is common and becomes an important cause of mortality, it can substantially affect not only the ecology and demography of the killing and victimized species [16–19], but also the community structure of ecosystems in which these species live [20–22].

Especially when killers are larger than their interspecific competitors, the cost of attempted and successful killings (e.g. risk of injury) is probably small for killers [11–14,22], but the cost (e.g. death) can be enormous for victims. In these cases, the frequency of IK probably will decrease or disappear because of natural selection within victimized species to reduce interspecific competition via divergence (character displacement) in ecology, morphology, physiology or behaviour [2–5,23]. The continued occurrence of non-predatory IK in species that differ markedly in size is therefore difficult to explain.

In research over 6 years under natural conditions, we documented IKs of herbivorous Wyoming ground squirrels (Sciuridae: *Urocitellus* [*Spermophilus*] *elegans*, hereafter 'ground squirrels') by herbivorous white-tailed prairie dogs (Sciuridae: *Cynomys leucurus*, hereafter 'prairie dogs'). IK presumably reduced the number of nearby interspecific competitors for vegetation, and here we evaluate whether IK

Table 1. Percentage of white-tailed prairie dogs ($n = 114$) and Wyoming ground squirrels ($n = 87$) that consumed the six plants most common in the diets of both species. These data are from observations of foraging individuals at Hutton Lake National Wildlife Refuge near Laramie, Wyoming, USA (from [24], with conversion to percentages), about 110 km from our study site at the Arapaho National Wildlife Refuge near Walden, Colorado.

six most common plants consumed by both prairie dogs and ground squirrels	percentage of prairie dogs that consumed this plant	percentage of ground squirrels that consumed this plant
western wheatgrass, *Agropyron smithii*	23	21
needle and thread grass, *Stipa comata*	18	14
plains pricklypear, *Opuntia polyacantha*	16	10
blue grama, *Bouteloua gracilis*	14	15
Indian ricegrass, *Oryzyopsis hymenoides*	7	10
prairie junegrass, *Koleria cristata*	5	13

increased prairie dog fitness. Our research is the first systematic study of IK and its consequences on fitness among herbivorous mammals.

2. Material and methods

(a) Study animals and study site

Prairie dogs are medium-sized (500–1100 g for adults, more than nine months after weaning), colonial, diurnal, burrowing, sciurid rodents that inhabit the western USA [24,25]. A prairie dog of either sex typically has a burrow (the 'home-burrow') where it spends every night, and it defends a small territory (the 'home-territory', radius approx. 10 m) around the home-burrow from conspecifics and ground squirrels [24,25]. Females rear their offspring in the home-burrow during the 5.5 weeks of lactation, and the offspring obtain most of their nutrition from plants in the territory around the home-burrow (their natal burrow) for four to five weeks after they first appear above-ground at weaning in late May or early June [24–26]. Smaller than prairie dogs, ground squirrels (200–500 g for adults, more than nine months after weaning) are also colonial, diurnal, burrowing, sciurid rodents [27–29]. Ground squirrels often live in the same meadows with prairie dogs, occasionally occupy prairie dog burrows, and frequently forage in close proximity to prairie dogs. Both prairie dogs and ground squirrels are primarily herbivorous [24,25,27,28,30], and their diets are similar (table 1).

We studied prairie dogs and ground squirrels at the Case Ranch (40.6634° N, 106.3210° W, elevation approx. 2500 m a.s.l.) of the Arapaho National Wildlife Refuge (ANWR) near Walden, Jackson County, CO, USA. This area is characterized by short-grass prairie, with substantial annual fluctuation in temperature and rainfall [31]. Both prairie dogs and ground squirrels at ANWR were protected from recreational shooting, poisoning and other forms of human disturbance. Further, we detected no evidence of bubonic plague [24,32,33] or other epidemic diseases among the prairie dogs or ground squirrels at ANWR during our research.

(b) Designating colonies, wards and clans

Prairie dog groups exist on three spatial scales. *Colonies* can contain hundreds of adults of both sexes, with individuals distributed over areas as large as 100 ha [24–26]. Unsuitable habitat such as a hill, tall vegetation, a stream or a road sometimes divides a colony into two or more *wards* (or subcolonies) [25–26,34]. Residents of one ward usually can see or hear residents of an adjacent ward, but movements, behavioural interactions and communications between wards are uncommon.

Wards contain territorial, contiguous family groups called *clans*, which typically contain one sexually mature male, 2–5 sexually mature females, 1–2 yearling adult males that have not reached sexual maturity and (in May and June) 5–10 juveniles (less than two months after weaning) [24–26]. Over 95% of social interactions among prairie dogs are with members of the home or adjacent clans.

Our study-colony at ANWR occupied approximately 30 ha, and in May of each year (2007–2012) contained a mean ± s.d. of 17.7 ± 6.89 adult male prairie dogs, 30.2 ± 4.17 adult females, and 115.2 ± 45.5 weaned juveniles. Each year the study-colony had eight wards (each with 6.69 ± 3.48 adults per year), and 16–20 clans (each with 3.11 ± 1.65 adults per year). Ground squirrels were common at all wards and within all clan territories, and no ward or clan territory had any sections that contained prairie dogs with no ground squirrels (or vice-versa).

(c) Field methods

J.L.H. and three to four assistants per year studied prairie dogs and ground squirrels at ANWR from early March through early July of 2007–2012 [25,35]. We initiated research each year as the prairie dogs were emerging from hibernation and before the onset of the mating season in March, and we remained until approximately two weeks after marking the last weaned juvenile in June. From five 2-m towers, we began observations with binoculars every day when the prairie dogs were first emerging from their home-burrows shortly after sunrise, and we continued observations until the last prairie dog had submerged into its home-burrow shortly after sunset. When necessary, we interrupted observations for live-trapping and marking. Around each tower were 2–5 clans with 10–15 adult prairie dogs that used about 100 burrow-entrances and could be easily observed (less than 150 m away).

From our towers, we recorded chases and fights involving prairie dogs with ground squirrels and other prairie dogs [26]. Because our objective was to record all aggressive interactions of all prairie dogs, we did not do observational sub-sampling of the individuals being watched. We also recorded predations on ground squirrels (electronic supplementary material, table S1) and prairie dogs. Our 6 years involved more than 30 000 person-hours of research. Before we discovered IK, we also studied prairie dogs at ANWR in 1974–1976 [26] and in 2006 [25]. All animals in the study-colony were live-trapped, ear-tagged and marked with Nyanzol black fur dye for behavioural observations (as described in [35,36]). The combination of eartags and Nyanzol enabled us to identify the same prairie dogs within and across years, and we therefore obtained an exact count of prairie dogs within every ward and clan each year; we also obtained accurate estimates of litter size at weaning every year.

(d) Statistical analyses

For every adult female prairie dog in the study-colony each year, we measured the following response variables: whether she survived until the next mating season in March; her litter size (range = 0–8) when her weaned offspring first appeared above-ground in May or June; her annual fitness, defined as the sum of (i) her survivorship until the next mating season (0 or 1) and (ii) 50% of the current year's offspring that survived for at least nine months (i.e. to adulthood) after weaning (sensu [37,38]); and her lifetime fitness (or lifetime reproductive success [39,40]), defined as the cumulative number of offspring over her lifetime that survived for at least nine months after weaning (i.e. yearlings). We focus on females, because we do not have rigorous information on paternity for males at our study-colony, and therefore cannot do analyses of fitness comparable to those for females; further, killing was more common among females (see Results).

For every adult female prairie dog each year or over her lifetime, we documented the following predictor variables (fixed effects): annual and lifetime number of ground squirrels she killed; her age (in years); her body mass when her weaned juveniles first appeared above-ground; her clan size (number of adult prairie dogs that lived in her home-territory); her ward size (number of adult prairie dogs that lived in her home-ward); the study-colony's annual rate of aggression, defined as the mean number of aggressive interactions per day among prairie dogs for the entire study-colony during the period when IKs occurred; the female's annual rate of aggression to other prairie dogs, defined as her mean number of aggressive interactions per day with other prairie dogs during the period when IKs occurred; and the female's rate of aggression to ground squirrels, defined as her mean number of aggressive interactions per day with ground squirrels during the period when IKs occurred. For our analysis of lifetime fitness for each female, we used the cumulative number of ground squirrels that she killed over her lifetime as a predictor variable; for every other predictor variable, we used the mean of the annual estimates for that variable over the female's lifetime. All these variables were deemed a priori to potentially affect the number of ground squirrels a female might kill, her annual fitness or her lifetime fitness. For analyses of annual fitness, we did not include animals that we could not capture for body mass. For analyses of lifetime fitness, we used only females for which we had information from birth until disappearance (and death, presumably) from the study-colony; most females that survived for at least nine months after weaning lived for only 1–3 years (mean ± s.d. = 1.80 ± 1.15, $n = 55$), but one female lived for 6 years.

We used linear mixed models [41], as constructed in SAS [42] with PROC Mixed or Proc GLIMMIX, to examine the fixed effects on our response variables. We used individual identity as a random effect in all analyses involving data from the same marked females in consecutive years. Residuals for all dependent variables closely approximated a normal distribution with homogeneous variances, and thus all models had a normal error structure. Little correlation occurred among independent variables: 27 of 35 of the pairwise correlations were non-significant ($p > 0.050$), and only two of the significant correlation coefficients exceeded 0.40. Thus, we considered our dataset as generally meeting the assumptions inherent in mixed-model analyses [43]. Our modelling approach for each response variable was to begin with a global model containing all relevant fixed effects (see above). We used backward stepwise regression to progressively remove the independent variable with the highest p-value at each step, with $p \leq 0.157$ as the criterion for inclusion in the final model (sensu [44]). P-values reported in the text are those for the final model (or the step at which a non-significant variable was removed). Beta coefficients (β) are presented ±1 s.e.; numbers in the text are means ± 1 s.d. Sample sizes vary for different analyses because all information was not always available for every IK.
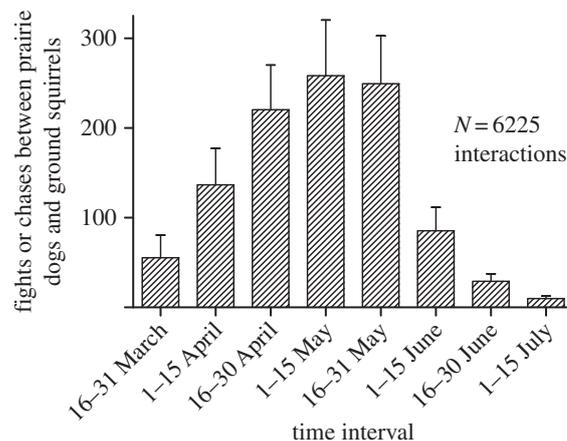

Figure 1. Mean ± s.e. number of fights or chases between prairie dogs and ground squirrels during different times of the year. For 93% of aggressive interactions (5767/6225), the prairie dog initiated the fight or chase; for the other 7%, the ground squirrel initiated the aggression. Means are from 6 years for each time-period except early July, for which means are from 3 years.

Figure 2. One-year-old female prairie dog that has just killed a ground squirrel juvenile via a series of bites to the neck. (Online version in colour.)

3. Results

(a) Natural history of interspecific killing

Prairie dogs frequently chased ground squirrels that entered the home-territory (figure 1), and we watched every chase until it was over. The prairie dog captured and fought with the ground squirrel after about 5% of chases, and capture sometimes led to IK. We observed at least two IKs at all eight wards from 2007 through 2012 (12.6 ± 10.0 IKs per ward, range = 2–30), with a total of 101 IKs (16.8 ± 7.78 per year, range = 10–32) by 47 marked prairie dogs (11 males and 36 females). In a typical IK, the prairie dog repeatedly bit the ground squirrel in the head, neck or thorax over a period of 1–3 min until

4

death (figure 2), and then abandoned the carcass and resumed foraging on nearby vegetation.

After 35 of the 101 observed IKs, most commonly within 120 min after the killing, an avian scavenger landed near the fresh carcass, seized it with its beak and then flew away with it (electronic supplementary material, table S2). We observed 58 additional cases of an avian scavenger picking up and flying away with a fresh carcass (electronic supplementary material, table S2) and four more cases of a recently killed (un-scavenged) carcass above-ground with wounds similar to those after an observed IK. These latter 62 cases likely involved IKs for which we did not observe the actual killing. If these inferences of IK are correct, the total number of IKs at the study-colony from 2007 through 2012 was $101 + 62 = 163$.

In 87% of the 101 observed IKs, no consumption of the victim by prairie dogs occurred; for the 13% of IKs that did involve consumption, the killer ate less than 5% of the victim. In 3 of 6 years, IKs at the study-colony were more common than the cumulative number of predations on ground squirrels by American badgers (*Taxidea taxus*), Swainson's hawks (*Buteo swainsoni*) and 13 other species of predators (electronic supplementary material, table S1 and electronic supplementary material, figure S1). We never observed a prairie dog kill another adult or juvenile prairie dog, and we also never observed a ground squirrel kill an adult or juvenile prairie dog.

Lactating females were responsible for 79% of the 101 observed IKs, males for 17% and non-lactating females for 4%. Ninety-six per cent of 101 observed IKs occurred less than 20 m from the killer's home-burrow, and 96% of ground squirrel victims ($n = 163$) were juveniles. Most killers ($n = 28$) slew a single ground squirrel, but 19 serial killers slew two or more ground squirrels. One female killed six ground squirrels over 5 years, another female killed nine over 4 years and a third female killed seven juveniles from the same litter in a single day. Of the 101 observed IKs, most involved capture after a chase as described above, but six involved slow stalking before attack; four involved digging out a juvenile from its home-burrow and two involved waiting near a ground squirrel's home-burrow before assaulting a juvenile as soon as it appeared above-ground.

Of the 53 adult female prairie dogs for which we have rigorous information on both lifetime fitness and number of IKs, 30.2% killed at least one ground squirrel over their lifetimes. The mean percentage of females that killed at least one ground squirrel per year was $26.0 \pm 8.68\%$ (range = 17.6–40.0%).

The number of ground squirrels killed by a female in a year was significantly predicted by her rate of aggression with ground squirrels ($p < 0.001$, $t_{36} = 9.79$, $\beta = 1.568 \pm 0.160$), but not by her age, her body mass, clan size, ward size, her aggression towards other prairie dogs or the study-colony's annual rate of aggression ($p \geq 0.33$ for all; electronic supplementary material, table S3). Because a female's rate of aggression to ground squirrels was so strongly correlated with the number of victims she killed ($r = 0.71$, $p < 0.001$), we did not include a female's rate of aggression to ground squirrels for analyses of annual and lifetime fitness, and used only the number of victims killed (next section).

(b) Benefits of interspecific killing

The number of ground squirrels killed by a female was the only significant predictor of annual prairie dog fitness at
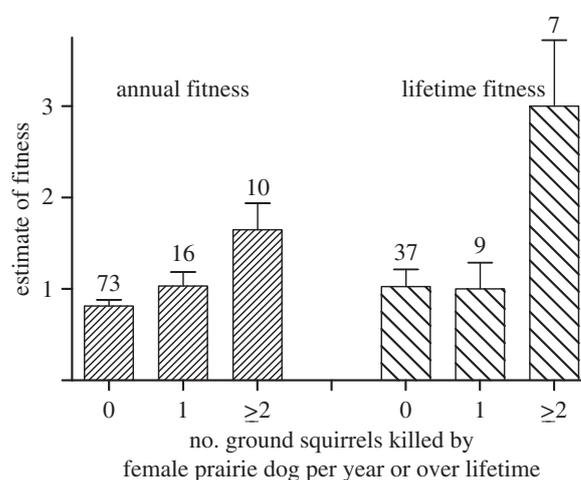
Figure 3. Mean ± s.e. annual fitness and mean ± s.e. lifetime fitness for female prairie dogs versus the number of ground squirrels they killed. Both measures of fitness increased significantly with the number of victims ($p \leq 0.001$; see Results). Number of ground squirrels killed is the number per year for annual fitness and the cumulative number over a female's lifetime for lifetime fitness; see text for definitions of annual and lifetime fitness.

our study-colony ($p = 0.001$, $t_{38} = 3.57$, $\beta = 0.181 \pm 0.050$). Mean annual fitness was two times higher for serial killers (those killing two or more ground squirrels) than for non-killers (figure 3). A female's age, her body mass, her level of aggressiveness with other prairie dogs, clan size, ward size and the study-colony's annual rate of aggression were not significant predictors of annual fitness ($p \geq 0.39$ for all; electronic supplementary material, table S4).

A female's annual litter size increased with the number of ground squirrels she killed ($p = 0.001$, $t_{26} = 3.61$, $\beta = 0.704 \pm 0.194$), whereas her annual survivorship tended to decrease with the number of ground squirrels she killed ($p = 0.054$, $t_{38} = -1.99$, $\beta = -0.540 \pm 0.271$). A female's body mass at weaning had a significant positive effect on her litter size ($p = 0.010$, $t_{26} = 2.75$, $\beta = 0.007 \pm 0.002$), while a female's rate of aggression with other prairie dogs was negatively associated with litter size ($p = 0.021$, $t_{26} = -2.45$, $\beta = -1.197 \pm 0.489$). No other variables significantly predicted litter size or annual survivorship ($p \geq 0.68$ for all; electronic supplementary material, tables S5 and S6).

The number of ground squirrels a female killed over her lifetime was the only significant predictor of her lifetime fitness ($p < 0.001$, $t_{51} = 4.50$, $\beta = 0.418 \pm 0.093$); the effects of the other predictor variables (above) were non-significant ($p \geq 0.21$ for all; electronic supplementary material, table S7). Mean lifetime fitness was almost three times higher for serial killers than for non-killers (figure 3). For this analysis of lifetime fitness, we also included a female's lifespan (maximum known age), which was not a significant predictor ($p = 0.21$; electronic supplementary material, table S7).

(c) Parent–offspring resemblance in interspecific killing

For females known to be killers, 19% of their 47 male and female offspring survived for at least nine months after weaning and later became killers; for non-killing females, 29% of their 58 male and female offspring survived for at least nine months after weaning and later became killers. This difference was not significant ($\chi_1^2 = 1.44$, $p = 0.230$). An analysis of daughters only that survived for at least nine

months after weaning also showed little parent–offspring resemblance (25% and 38% of daughters became killers for killers and non-killers respectively, $n = 28$ daughters versus $n = 37$, $\chi_1^2 = 0.1.20$, $p = 0.273$).

4. Discussion

White-tailed prairie dogs commonly kill Wyoming ground squirrels, and killing enhances both annual and lifetime fitness for female prairie dogs. This is the first demonstration that IK increases fitness for animals living under natural conditions. The number of IKs by a female prairie dog was the only significant predictor of both her annual and lifetime fitness that we could identify during our long-term study. Killing was a stronger predictor of lifetime fitness than even longevity, which is the major factor that affects lifetime fitness for many species [36,39,40,45,46]. In general, the benefits of killing increased with the number of ground squirrels slain, with female serial killers accruing higher annual and lifetime fitness than one-time killers. Our results are surprising, because both prairie dogs and ground squirrels are herbivorous and differ substantially in size [24,25,28,30], and because all previous cases of IK among mammals have involved predatory carnivores [12,14,18,19,47,48].

In what way(s) does killing of ground squirrels benefit prairie dogs? The most likely possibility is that IK reduces interspecific competition for food (vegetation) near the killer's home-burrow. Prairie dogs and ground squirrels have similar diets. Indeed, the six most commonly consumed plant species for prairie dogs and ground squirrels were identical (table 1). The removal of at least one ground squirrel in a prairie dog mother's territory leads to more vegetation for the mother herself and for her weaned offspring. Especially when mothers are pregnant or lactating in late March through May in years when spring is late and snow is still deep at colony-sites, food is probably limiting for prairie dogs [24]. The larger litter size at weaning for killers is consistent with their having access to more resources than non-killers, and this effect of larger litters is probably the primary reason why both annual fitness and lifetime fitness are higher for killers. Because of the negative association between killing and a female's annual survivorship, IK by prairie dogs seems to represent a classic life-history trade-off, with negative effects on survivorship and positive effects on reproduction [36,39,40,45]. However, despite a net increase attributable to IK in both annual and lifetime fitness for female prairie dogs, we found no indication that the behaviour is heritable.

In other mammalian species, individuals that kill interspecific competitors sometimes consume their victims, and distinguishing between IK and predation therefore can be difficult [12,14,18,47,48]. Prairie dogs, however, rarely fed on ground squirrels they killed; when they did, they consumed less than 5% of the carcass. Sustenance from consuming ground squirrels is thus unlikely to be a benefit of IK, or a reason for its occurrence.

An alternative interpretation of the link between fitness and IK is that some prairie dogs inhabit higher quality home-territories (e.g. those containing more high-quality vegetation), which attract more ground squirrels. With more ground squirrels present, IK probably becomes more likely simply because encounters with ground squirrels are more frequent. In this scenario, the higher fitness of killers results from high-quality

vegetation *per se* rather than from IKs *per se*. We have no information about the quality of vegetation within home-territories. Further, we did not collect systematic data on the numbers of ground squirrels in different prairie dog home-territories, but we did not notice obvious heterogeneities in ground squirrel distribution throughout the study-colony. However, if killers consistently live in home-territories of higher quality, then the killers also might be in better body condition and better able to support larger extended families (clans). We found that a female's body mass and her clan size were unrelated to the number of ground squirrels she killed, so quality of the home-territory—at least as reflected in these metrics—does not seem to vary consistently among killers and non-killers.

Increases in annual and lifetime fitness presumably would result if prairie dogs killed other prairie dogs rather than ground squirrels, and such intraspecific killing occurs in many species of ground-dwelling squirrels [49–51]. However, we did not detect a single killing of an adult or juvenile conspecific by a prairie dog, perhaps because potential conspecific victims near a female's home-burrow are almost always close kin [25,35].

IKs sometimes resulted from strategies (e.g. slow stalking of juveniles) beyond simply catching a ground squirrel at the end of a chase. In response to the threat of IKs, ground squirrels have four behavioural defences. They run faster than prairie dogs, as evidenced by more than 5500 cases in which a fleeing ground squirrel escaped a chasing prairie dog. A ground squirrel mother sometimes chases or rams into a prairie dog that is within 5 m of her above-ground offspring (40 such chases/ attacks observed), and the offspring then safely submerge into a burrow. A ground squirrel mother occasionally attempts to lure a prairie dog away from the ground squirrel's above-ground offspring by repeatedly running up to the prairie dog and then trotting away—as though inviting a chase (30 such interactions observed). Finally, in rare cases after IK of some of her offspring, a ground squirrel mother transfers her remaining live offspring to a new home-burrow away from the killer's home-territory (three transfers observed).

Despite these defences, the danger to ground squirrel mothers and their offspring from IK remains high. So why do ground squirrels continue to inhabit the same meadows as prairie dogs? Offsetting the risk of IK are at least three potential benefits. First, if prairie dogs live in meadows with high-nutrition vegetation, then inhabiting the same meadows gives ground squirrels access to the same vegetation. Second, ground squirrels frequently use burrows excavated by prairie dogs for either short periods (e.g. temporary refuge from predators) or longer periods (e.g. spending the night, or rearing offspring from birth until weaning at four weeks). Third, similar to other animals that respond to heterospecific alarm calls [52–54], ground squirrels react to the alarm calls of prairie dogs by increasing vigilance or submerging into a burrow, and thereby improve their safety from capture by 15 avian and mammalian predators (electronic supplementary material, table S1). Living with prairie dogs thus involves a compromise for ground squirrels: they incur higher mortality from IK, but they probably incur lower mortality from predation. Consequently, ground squirrels probably receive a net benefit from living with prairie dogs, and perhaps for this reason natural selection has not led to clear character displacement that would reduce competition with prairie dogs.

Because IKs at our study-colony were so quick, subtle and unanticipated, we studied prairie dogs for 4 years before we detected the first case—even though IKs were likely occurring. After discovering IK in 2007, however, we documented 163 cases over the next 6 years. Our results should help other ecologists to realize that IK might be happening frequently but covertly right before their eyes, with animals they know well, and with significant consequences for fitness.

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