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Behavioural responses of red foxes to an increase in the presence of golden jackals: a field experiment

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The golden jackal, *Canis aureus*, and the red fox, *Vulpes vulpes*, are two common canids in Israel. Although the two species have similar diets, the jackal is about three times larger than the red fox. The current evidence for interspecific competition between these two canids is circumstantial and indirect. In this study we aimed to measure experimentally the response of red foxes to increasing exposure to the presence of the golden jackal. Our field experiments comprised three stimuli: urine as a scent stimulus, a mounted specimen and urine as a static animal-image stimulus, and a caged pet animal as a live animal stimulus. The treatment and control were placed near food trays, and the behaviour of foxes around these trays was documented by video recorders. In most cases, the presence of scent or cast of a golden jackal did not alter the behaviour of the foxes. However, foxes avoided the test arena when a live jackal was present. This finding provides strong evidence that red foxes fear jackals, and shows that foxes are more concerned when a live jackal is present. The possible implications of the observed fox behaviour for the understanding of large-scale competitive exclusion among canid species are discussed.

The Gause principle states that two species with identical ecological demands cannot coexist, and one of them will be outcompeted by the other (Gause 1934; Schoener 1982). Thus, it is generally assumed that closely related sympatric species compete, and the fitness of at least one of the competitors will be negatively affected (Krebs 2001). Hutchinson (1959) suggested that the frequently observed constant size ratio between species in a feeding guild is a result of such interspecific competition, and it reduces competition by resource partitioning. However, resource partitioning is rarely complete, and species within a feeding guild frequently compete with each other to a certain degree. Within a predator guild, such competition may take the form of intraguild predation (Holt & Polis 1997) and a recent review shows that predation is common (Palomares & Caro 1999). Controlled experiments are rare, but several studies have shown that

accidental removal of one carnivore species had a significant effect on other species of predators. For example, the removal of the grey wolf, *Canis lupus*, from large areas in North America was followed by an increase in coyote, *Canis latrans*, populations (Peterson 1995), the removal of coyotes was related to changes in populations of other carnivores in these areas (Henke & Bryant 1999), and a decline in populations of the red fox in Scandinavia was followed by an increase in the population of the pine marten, *Martes martes* (Lindstrom et al. 1995). Stealing of prey by larger or more numerous carnivores is a common phenomenon frequently observed in Africa. For example, African hunting dogs, *Lycaon pictus* (Cooper 1991; Carbone et al. 1997), and cheetahs, *Acinonyx jubatus*, often lose their prey to lions, *Panthera leo*, and spotted hyaenas, *Crocuta crocuta* (Creel & Creel 1996; Vucetich & Creel 1999). Potential competitors may avoid each other, as do genets, *Genetta genetta*, and Egyptian mongooses, *Herpestes ichneumon*, in the presence of the Iberian lynx, *Lynx pardina* (Palomares et al. 1995), and South American grey foxes, *Dusicyon griseus*, avoid their congeneric competitors, *D. culpaeus* (Johnson & Franklin 1994). However, interactions between two competing species may take various forms, ranging from tolerance to predation, as

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seen in coyotes and red foxes, *Vulpes vulpes* (Gese et al. 1996) and in wolves and coyotes (Thurber et al. 1992; Peterson 1995).

Most research on interspecific competition deals with resource competition within a guild, but studies on predator guilds, including canids (Canidae), deal also with interference competition (Diamond 1978). Interference competition, including killing or competitive exclusion of one species by another (generally the smaller by the larger), has been described for several canid guilds. For example, Arctic foxes, *Alopex lagopus*, were excluded by red foxes (Elmhagen et al. 2002), red foxes by coyotes (Voigt & Earle 1983; Harrison et al. 1989), and coyotes by wolves (Thurber et al. 1992).

Avoidance behaviour by smaller species seems to be common. For example, survival rates of coyotes in Alaska were higher where they avoided wolves (Thurber et al. 1992), and red foxes in Maine and Dakota were rarely predated upon by sympatric coyotes, apparently because of avoidance (Sargeant et al. 1987; Harrison et al. 1989). Indeed, interaction between two potentially competing species does not have to involve aggression, especially during periods of high food availability or when the competitors specialize on different foods (Theberge & Wedeles 1989; Paquet 1992; Gese et al. 1996).

The canid guild in Israel is composed of five species: the wolf, the golden jackal, *Canis aureus*, and three species of foxes, genus *Vulpes*. Dayan et al. (1992) found a constant size ratio in the carnassials of these species, and claimed that this ratio indicates interspecific competition. The golden jackal and the red fox are common canids in Israel, where they feed on a large variety of animal and plant food, as well as being commensal with people. Both species have been studied in Israel (Golani & Keller 1974; Macdonald 1979a; Assa 1990) and elsewhere. They are known to use olfactory marking in their home ranges or territories, using faeces, urine or secretions from various skin glands (summarized in Mendelssohn & Yom-Tov 1999). The red fox is smaller than the golden jackal (mean body weight 2.6 and 8.5 kg, respectively), and when jackals became very abundant, population size of foxes decreased significantly in such areas, apparently because of exclusion by jackals (Ilani 1979; Mendelssohn & Yom-Tov 1999). However, only anecdotal observations of red foxes being chased by jackals are available (Ilani & Shalmon 1985; Macdonald 1987). A study of the diet of these two species in Hungary revealed no differences (Lanszki & Heltai 2002), and Kingdon (1997) claimed that in North Africa golden jackals are more numerous than red foxes, apparently because of the inferior position of the foxes in the food hierarchy.

Most evidence for interspecific competition between carnivores is circumstantial and indirect, and as far as we know there is little experimental evidence on how potentially competing carnivores react to the presence of each other. Our aim in this study was to test experimentally how the red fox reacts to the presence of the golden jackal in the field. Specifically, which particular jackal stimuli cause a reaction in foxes?

For our field trials we had two types of control: a treatment-specific control (e.g. water for the scent stimulus) and the stimulus of red fox. Lack of a behavioural response between fox and jackal stimuli would suggest that the red foxes in the field view a jackal as another individual fox and not as a larger predator. On the other hand, stressful response to the jackal stimulus, relative to the fox stimulus, would imply that foxes view the jackal as a potential predator or competitor.

METHODS

Study Area

The study was based on five sites, where the local red foxes frequently fed and were habituated to the equipment used in the experiments (see below). These feeding sites were situated in the northern Arava Valley (30°46′N, 35°18′E), between two villages (Hatzeva and En Yahav) 12 km apart. To minimize the possibility that individual foxes from one site would visit another site in the same experimental session, we set up two feeding sites at opposite ends of each village, and a fifth between the villages. We selected sites where human activity is rare to minimize interference during the experiments. A permit for this research was granted by the Nature and Parks Authority of Israel.

The study area is an extreme desert. Precipitation averages 42 mm/year, and most rainfall is restricted to the few thunderstorms that occur in this area during November–February. Mean summer and winter temperatures are 38°C and 22°C, respectively (Bitan & Rubin 1994). During the night, temperature drops considerably. Isolated trees (*Acacia tortilis*, *Acacia raddiana*, *Tamarix aphylla*) and small bushes (*Anabasis articulata*, *Hammada salicornica*, *Haloxylon persicum*) along creekbeds dominate the flat scenery, a set-up of wide visibility. Golden jackals are rare in this area, but red foxes are abundant.

Experimental Design

We conducted each trial by placing in the field a pair of plastic trays (60 × 40 cm and 15 cm deep) filled with local gravel and fox bait for 4 h. We used local gravel to reduce alien factors (e.g. strange smells) that might interfere with our treatments. For bait we obtained dead frozen chicks from the Tel Aviv University Zoo. These chicks are used for animal feed and supplied dead to the zoo by breeders. Five thawed chicks were placed in each tray, one at each corner and one in the centre, and covered with gravel. Thus, for each pair of trays we used 10 chicks, about 400 g, which is the daily requirement of one 3.5-kg fox (Macdonald & Barrett 1993). We anticipated that this quantity would be an incentive, and not a surfeit, for foxes to participate in our experiment. More food in a single tray might have reduced motivation of the foxes to seek food from both trays, consequently biasing our experiment.

Each session comprised two trials conducted simultaneously at two randomly selected sites. At each site, we placed two trays 150 m apart, a distance that allowed the visiting foxes to detect the food in both trays. One,

randomly selected, tray served as the control and the other as the treatment. A Sony camcorder (Sony TR728E), capable of recording under infrared (IR) light, and an IR spotlight (Sony HVL-IRC) were placed 3 m from each tray, and continuously recorded all events during the 4-h experimental session. To habituate the foxes to the presence of the equipment, using the above tray set-up, we prebaited all the sites for 1 week before the trials. We also placed a dummy camcorder by each tray to acclimatize the foxes to its presence and food and dummy cameras at the sites not used in a particular session to encourage local foxes to keep visiting these locations and to reduce the chances of individuals wandering between sites.

We tested six stimuli in a form of two-way factorial design. We used urine as a scent stimulus, a mounted specimen and urine as a static animal-image stimulus, and a caged pet animal as a live animal stimulus. Each stimulus was tested for the effect of jackal and of red fox. Trials with each stimulus were done in comparable pairs (one with jackal and the other with fox stimuli) over a short period (1–2 months). Below we provide a detailed description of each set of trials.

(1) Scent stimulus: scent marking in canids is a key communication route among individuals and foxes tend to urinate 2–20 ml at each spot they mark (Macdonald 1979b). To conduct scent trials we collected golden jackal and red fox urine from two zoos. For each species, urine from several individuals was mixed together, divided into 4-ml portions, and kept frozen until use. We conducted all scent trials over 20 evenings during August–September 2001. In each session, two sites were randomly selected and the feeding trays were placed as noted above. In the middle of one shorter side of each tray we placed a cotton pocket (5 × 10 cm), mounted on a metal spike 25 cm high. At one of the sites, the cotton on the treatment tray was soaked with 4 ml of jackal urine, while on the control tray it was soaked with 4 ml of water. At the other site, the cotton on the treatment tray was soaked with 4 ml of fox urine and on the control tray with 4 ml of water. Simultaneous trials at both sites were conducted for 4 h starting at darkness.

(2) A mounted specimen and scent stimulus: this treatment combined scent and mounted specimens of a jackal and a fox. Pelts of a golden jackal and of a red fox were obtained from hunters and mounted on plaster casts. These models looked like real animals but were solidly designed to prevent chewing damage by the animals in the field. We repeated the exact design of the above scent trials during January–February 2002, but added a jackal or a fox model to the corresponding scent, and placed it adjacent to the scent spikes on the treatment trays. At the control trays we added a 10-litre plastic bucket, which was placed by the scent-free, water-soaked spike. All model and scent trials were conducted at the four feeding sites around Hatzeva and En Yahav.

(3) Live animal stimulus: male pups of the golden jackal and red fox were obtained from zoos in Israel during spring 2001, and reared to adulthood as pet animals by S. Scheinin. We selected males to eliminate the variance in behaviour associated with sex. These two animals were habituated to living in a house, to human handling, walking on a leash, and to transport in a dog cage. During April–May 2002, we repeated the scent trials but replaced the scent spikes with double-steel mesh cages (120 × 50 cm and 50 cm high) with sufficiently thick mesh to prevent any possible injury from the animals visiting the trays. The cage at the treatment tray contained either a jackal or a fox, according to the corresponding site, while cages at the control trays were empty. Both the pet jackal and the pet fox were relaxed inside their cages throughout the trials. These pet animals were reared in the presence of dogs and cats, and showed no distress when other foxes approached their cage. After the study, both pet animals were returned to the zoo of origin. Live animal trials were conducted at four feeding sites: two near the village of Hatzeva, one near the village of En Yahav, and one between these villages.

For all trials we counted and recorded the position of chicks left at each tray at the end of each session. The videos taken at all trays were observed and we recorded (1) the number of foxes at the tray, (2) the total amount of time foxes were observed, (3) the minimal distance of foxes from the scent spike or cage, (4) the position of the first chick taken, (5) the position and frequency of scent marking, (6) aggressive behaviour towards the treatment or control and (7) the duration and type of vocalization.

Overall, we conducted three sets of trials, each set comprising 20 4-h sessions that were distributed among four sites. For each set of trials, the same individual foxes may have participated in more than one session at a site. Since the foxes were not individually marked and could not be individually identified on the videos, we had to consider all sessions at a site as a single independent cluster, and performed the statistical analysis accordingly. Thus, for each site, we used the means of the various measurements as independent observations. This conservative approach successfully deals with the possibility of pseudoreplication. Taking into consideration the distance between sites, and that the trials were conducted at different times and seasons (hence enabling a turnover in the participating fox population), site-specific trials and treatments were each considered to be independent. To test differences in the measured variables between treatment and control we used two-tailed paired t tests. Two-way ANOVAs were used to evaluate the effect of the stimulus (scent, model and scent, and a live animal), the species (jackal or fox), and their interaction on the following variables: the mean difference between the number of chicks taken from the treatment and control trays; the mean difference in the minimal distance from the stimulus of foxes feeding at the treatment and control trays; the mean difference in the distance from the stimulus when the first chick was taken from the treatment and control trays; and the mean difference between the rate of scent marking at the treatment and control trays.

A Euclidean distance matrix was calculated from relative frequencies of vocalization, aggression and marking behaviour for the live animal experiment. Based on these characters, sites and species combinations were clustered

by Ward's method of squared Euclidean distances and minimum variance amalgamation (Ward 1963).

RESULTS

Scent Trials

Jackal and fox scents had no significant effect on either the mean number of chicks taken (paired t test, treatment minus control: jackal: $t_3 = 0.66$, $P = 0.56$; fox: $t_3 = 1.44$, $P = 0.25$) or the minimal distance from the scent spike (jackal: $t_3 = 0.49$, $P = 0.66$; fox: $t_3 = 0.00$, $P = 1.00$). The first chick was picked up closer to the jackal-scent spike relative to the control ($t_3 = 3.52$, $P = 0.04$); an opposite, but nonsignificant trend, was observed when the treatment was a fox-scent spike ($t_3 = 2.29$, $P = 0.11$). As expected, scent-marking frequency tended to increase in the vicinity of treated trays (paired t test: $t_3 = 2.90$, $P = 0.06$) and on the scent spike ($t_3 = 2.93$, $P = 0.06$) when fox scent was introduced. Jackal scent had less effect on scent marking by foxes (marking near trays: $t_3 = 1.00$, $P = 0.39$; marking on scent spike: $t_3 = 2.35$, $P = 0.10$).

Model and Scent Trials

At one site, the local foxes completely ceased visiting after we placed the models, hence the effect of the treatment (and control) could not be evaluated. Therefore, we provide the results only from the three sites where foxes continued to participate in our trials. We did not detect significant effects on the mean number of chicks taken (paired t test: jackal: $t_2 = 1.00$, $P = 0.42$; fox: $t_2 = 1.23$, $P = 0.34$), minimal distance from the scent spike (jackal: $t_2 = 1.43$, $P = 0.29$; fox: $t_2 = 2.89$, $P = 0.10$) and location of the first chick taken (jackal: $t_2 = 1.98$, $P = 0.19$; fox: $t_2 = 0.00$, $P = 0.99$). Marking frequency in the vicinity of the trays did not increase significantly (paired t test: jackal: $t_2 = 1.60$, $P = 0.25$; fox: $t_2 = 0.85$, $P = 0.48$) nor did marking on the scent spike (jackal: $t_2 = 0.65$, $P = 0.58$; fox: $t_2 = 2.00$, $P = 0.18$). A decrease (although not significant) was observed in most of the marking comparisons. In addition, at one site we observed an aggressive attack on the fox model that lasted several minutes and involved mounting the cast and repeated biting on the neck area. These attacks were observed at this site on three different occasions. The jackal model at this site, however, was never attacked.

Live Animal Trials

The presence of a live animal generated a profound response, relative to the previous treatments. Foxes reduced by half the number of chicks taken (paired t test: $t_3 = 3.48$, $P = 0.04$) and increased the minimal distance ($t_3 = 3.73$, $P = 0.03$) when a live jackal was present at the trays. When a live fox was the treatment, the number of chicks taken from the tray was not significantly different from that at the control ($t_3 = 1.38$, $P = 0.26$), but foxes kept further from the caged animal than expected ($t_3 = 4.12$, $P = 0.03$). The position of the first chick taken was not different from that observed at the control for both jackal and fox treatments (jackal: $t_3 = 0.61$, $P = 0.58$; fox: $t_3 = 0.78$, $P = 0.49$). The frequency of scent marking at the site and near the cage did not differ between the treatment and the control for the caged jackal (at site: $t_3 = 1.26$, $P = 0.30$; near cage: $t_3 = 1.00$, $P = 0.39$) and the caged fox (at site: $t_3 = 1.10$, $P = 0.35$; near cage: $t_3 = 0.79$, $P = 0.49$). Digging by the cage ($N = 8$) and aggressive behaviour towards the caged animal ($N = 12$) were observed only when a caged fox was present.

Differences Between Stimuli

Overall, we observed in each session the same number of foxes at both the treatment and the control trays. The minimum numbers of different individual foxes that participated in the scent, model and scent, and live animal trials were seven, nine and eight, respectively. The minimum number of foxes observed per session (range 1.15–1.87 individuals) did not differ between treatment and control trays during scent (jackal: $t_3 = 1.65$, $P = 0.20$; fox: $t_3 = 0.38$, $P = 0.73$), model and scent (jackal: $t_2 = 0.38$, $P = 0.74$; fox: $t_2 = 0.98$, $P = 0.43$), and live animal (jackal: $t_3 = 0.32$, $P = 0.77$; fox: $t_3 = 0.68$, $P = 0.55$) trials. We also did not detect significant differences in the frequency of scent marking at the control trays between the three sets of trials (i.e. seasons; Kruskal–Wallis test: jackal: $H_2 = 0.84$, $P = 0.66$; fox: $H_2 = 0.15$, $P = 0.93$). These results confirm that the reported differences found between the control and treatment trays were not associated with either variance in visit rate to one type of tray compared to the other or season.

To examine differences in response to the presence of fox or jackal across increasing stimulus treatments we used two-way ANOVA. The difference in number of chicks taken in the treatment versus the control was smallest in the presence of urine and greatest when a live animal was present ($F_{2,16} = 5.13$, $P = 0.02$; Fig. 1a). Scheffé post hoc tests indicated that the number of chicks taken in the presence of a live animal was significantly lower than in the other two treatments ($P \leq 0.05$). No significant difference was detected between the jackal and fox treatments ($F_{1,16} < 0.01$, $P = 0.99$), but the interaction was marginally significant ($F_{2,16} = 3.38$, $P = 0.06$). As the stimulus increased, from urine to live animal, foxes tended to take food from a more distant position on the food tray relative to the control ($F_{2,16} = 8.93$, $P < 0.01$; Fig. 1b). This trend was similar for the jackal and fox treatments ($F_{1,16} < 0.01$, $P = 0.99$). The distance between the first chick taken from the tray and the object at the treatment (i.e. scent spike, model or live animal) did not differ between stimuli ($F_{2,16} = 0.38$, $P = 0.69$), but differed significantly between jackal and fox treatments ($F_{1,16} = 6.43$, $P = 0.02$). The foxes tended to take the first chick from a closer position (relative to the control) in the presence of jackal urine, but from a further position (relative to the control) when fox urine was present (Fig. 1c). We did not detect differences in rate of scent marking either between stimuli or between species treatments (stimuli: $F_{2,16} = 1.37$,
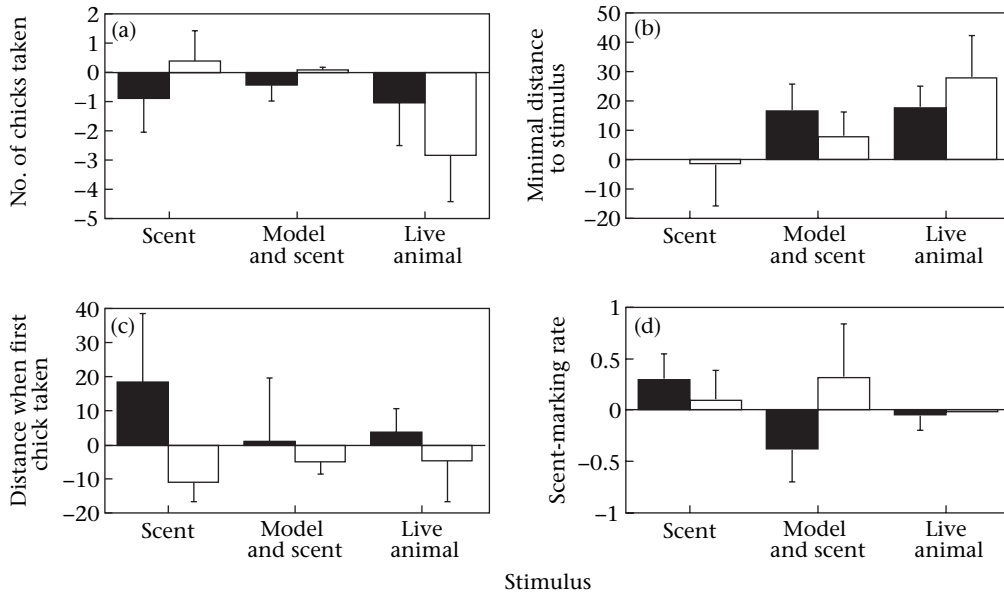
Figure 1. The mean difference ±SD in (a) the number of chicks taken, (b) the minimal distance from stimulus when feeding, (c) the distance from stimulus when first chick was taken and (d) the rate of scent marking between treatment and control trays at three jackal (□) and fox (■) stimuli (scent, model and scent, and live animal).

$P = 0.28$; species: $F_{1,16} = 1.75$, $P = 0.20$). However, the interaction between these factors was significant ($F_{2,16} = 3.87$, $P = 0.04$; Fig. 1d). Rate of scent marking at the treatment trays was highest when fox urine was applied and lowest when a live fox was present. This effect was not observed with the jackal treatment. Last, an inverse correlation was detected between stimulus level and frequency of scent marking (Spearman rank correlation: jackal: $r_S = -0.57$, $t_9 = 2.07$, $P = 0.06$; fox: $r_S = -0.62$, $t_9 = 2.39$, $P = 0.04$).

Relative frequencies of vocalization, aggression and marking behaviour differed according to the species in the cage (Fig. 2). When the fox treatment was present (as a model or live), the foxes approached in an aggressive posture and growled or took a submissive stand and uttered a greet cry towards the caged pet fox. None of the foxes were aggressive towards the jackal; instead, they displayed nervousness and occasionally barked an alarm (for
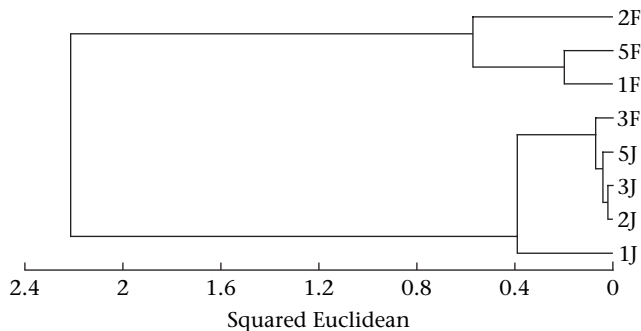
posture and vocal types see Macdonald 1987). The foxes at all sites behaved similarly towards a caged jackal. When a live fox was used as treatment, foxes at sites 1, 2 and 5 behaved similarly but their behaviour was markedly different towards the caged jackal. However, the foxes at site 3 treated the caged fox similarly to the jackal.

DISCUSSION

In this experimental study, foxes continued to use the food trays despite the presence of the scent or model of a golden jackal. However, when a live jackal was present, the foxes avoided the treatment trays. This finding provides clear evidence that red foxes fear jackals, and display greater concern when the latter are present. Indeed, the foxes avoided the food tray where the live jackal was present, even though it was completely calm and non-aggressive while in the cage. Considering the poor food availability of the desert environment where the trials were conducted, giving up such a food resource as fresh dead chicks serves to emphasize the impact of the jackal's presence upon the foxes. On the other hand, when a live pet fox was present by the treatment tray, foxes arriving at the site were attracted to it and on a few occasions tried to attack it. The contrasting responses generated by the presence of a live pet fox and jackal indicate that the foxes clearly distinguished between the two species treatments. The caged animal stimulus is of course not identical to a stimulus generated by a free-ranging fox or jackal, which would probably have generated an extreme response by the visiting foxes. However, such field experiments may lead to severe aggression and therefore were not attempted.

Figure 2. Ward's minimum-variance tree for relative frequencies of vocalization, aggression and marking behaviour in the live animal stimulus experiments. F: fox treatment; J: jackal treatment. The numbers designate experimental sites.

The three series of trials were conducted at different periods, which coincided with an increase in food stress. The scent trials were conducted during the nonbreeding period when food stress is minimal because the young are already independent at that time. The model and scent trials were done during the mating season, a period of much activity but when only mated pairs occupy their territory. Finally, the live animal trials were done during peak breeding when energy demand is greatest. This design ensured that during the live animal experiments the incentive for foxes to obtain the food at the tray would be maximal because of their breeding state. Consequently, their avoidance of such a rich food source (i.e. dead chicks) at this critical time of the year further validates our conclusions.

The effect of scent was most notable for distance between the first chick taken from the tray and the object at the treatment. The foxes were attracted to the jackal urine but remained distant from the fox urine. This trend was opposite to that expected, and may have to do with the scent of jackal being an uncommon smell for the foxes in our study area. The model and live animal stimuli did not produce different responses between species. Because a significant difference between species was observed only for scent, the least level of stimulus, we concluded that attraction between foxes and jackals is present when only urine is involved. Foxes avoided both the static image and live jackal; this avoidance was also reflected in their behaviour and vocalizations when visiting the trays, which showed marked differences between jackal and fox treatments (Fig. 2).

Frequency of scent marking decreased with the increase in stimulus, an indication of reduced visit rate to the treatment tray when the model or live animal was present. However, although scent-marking rate (marks/min) between the stimuli was similar, we detected a significant interaction between fox and jackal treatments. The increase in stimulus did not change the rate of scent marking for the jackal treatments, but decreased the rate for the fox treatments. Foxes are known to scent-mark more frequently in their own territory, and mark over any scent of strangers (Macdonald 1979b; Gorman & Trowbridge 1989). Our observations showed an intense response to scent of strange foxes, but not to the scent of the jackal.

Although our independent data come from only four locations, we were able to show significant behavioural responses associated with the stimuli of jackal in free-ranging red foxes. It is possible that the jackal's presence affected all the behavioural responses we examined, but our statistical power, owing to the sample size of four sites, was too low to enable firm statistical conclusions. To test the responses to fox stimuli of free-ranging golden jackals we conducted a limited number of trials at Emek Hefer (32°22′N, 34°55′E), an area densely populated by jackals. Information on how jackals (the larger species) view red foxes (the smaller species) is important for understanding competition among canids. Unfortunately, the jackals were not as cooperative as the foxes, and seldom visited our food trays.

We concluded, based on our field manipulations, that foxes are not concerned by the presence of jackals in their area (that is, by urine) but avoid direct contact with them. How is this tied into the process of competitive exclusion? Below we provide a novel hypothesis that attempts to combine individual behavioural response, productivity and interspecific interactions into a single theoretical framework that explains the mechanism behind competitive exclusion in canids. We have shown that the response to the stimulus treatments gradually increases, being weakest with scent, more profound when model and scent are provided, and extreme when a live animal is present. In other words, jackal scent caused minor anxiety in foxes, but a live jackal produced a severe reaction expressed as the complete avoidance of a very rich food patch.

Kleptoparasitism has been suggested as the main mechanism enabling lions and hyaenas to exclude African hunting dogs and cheetahs from an area (Creel & Creel 1996; Gorman et al. 1998). In contrast, because small carnivores usually feed on widely scattered and small prey such as invertebrates, small vertebrates and fruit (Carbone et al. 1999), they consume prey on the spot or cache it. It is impractical to kleptoparasitize small prey items since the cost of such an effort is undoubtedly much higher than the gain. Hence, the mechanism of competitive exclusion between small canid species is still unclear. For example, exclusion of the Arctic fox by the red fox in Scandinavia may be achieved by predation on adults and juveniles of the smaller species (Polis et al. 1989; Tannerfeldt et al. 2002) and active monopolization of breeding dens (Frafjord 2003) and food patches (Hersteinsson & Macdonald 1992; Frafjord 2000).

Our results imply that one canid can be excluded by a larger species with no further aggression, after an initial stage of intraguild predation. In places where two competitive canid species coexist, selection favours the individuals of the smaller species that fear the larger species. Observations on canids being killed by a larger species are common (e.g. grey wolves and coyotes: Arjo & Pletscher 1999; coyotes and kit foxes, *Vulpes velos*: Ralls & White 1995; Cypher & Spencer 1998; red and arctic foxes: Tannerfeldt et al. 2002), but predation alone is not the cause of the complete local exclusion of one canid species by another. However, such interspecific predation eliminates the 'bold' individuals (i.e. those that get too close to the larger species and get killed) and leaves behind a population of 'timid' animals that fear the congener and avoid it. Studies on canid foraging behaviour and anecdotal observations on interspecific predation have shown that larger canids do not actively seek the smaller canid species (Thurber et al. 1992; Cypher & Spencer 1998; Clark et al. 2005). Most interspecific predation occurs around a carcass or at a favourable food patch. In a 'timid' population, appearance of a congener (i.e. the larger competitive species) at the food patches used by 'timid' individuals would cause them to avoid these areas and use less productive patches. This process requires no aggression from the larger competitor, only its presence. In our experiment, one pair of foxes completely avoided our arena after the introduction of the jackal model which shows that boldness varies between individuals within populations. The proposed process of competitive exclusion depends on productivity. In a rich environment, the smaller species

can use less productive patches that are not visited by the larger congener; hence both species can coexist. However, in a poor environment suitable food patches are more limited. Avoidance of the larger species at the available food patches may mean eviction from that area and moving elsewhere. For example, red foxes that penetrated the lower tundra in Scandinavia might have initially been able to kill the 'bold' portion of the Arctic fox population, and the remaining 'timid' population may have moved to a higher elevation and decreased in number as a result of food deprivation. The outcome of such a process is the removal of the smaller species from a vast area with little effort (i.e. killing the boldest individuals) by the larger competitor. Who are the 'timid' and the 'bold' individuals in a population? Boldness can be genetically determined or related to age. In other words, intraguild predation may be directed largely towards the young and naïve, which are often the 'bold' individuals. Specific data on intraguild predation are required to support the above ideas.

We are aware that the proposed hypothesis is speculative, but it is based on behavioural interactions observed between competitive canids. Most studies on competitive exclusion describe only the final outcome and, in some cases, the rate of decline of one species as a function of population or range increase in the other. However, these studies lack direct observations on the players in this process. Realization that the behavioural component is a key feature in understanding competitive exclusion among canid species is important if we ever wish to control or counteract it.

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References

Arjo, W. M. & Pletscher, D. H. 1999. Behavioral responses of coyotes to wolf recolonization in northwestern Montana. *Canadian Journal of Zoology*, **77**, 1919–1927.

Assa, T. 1990. The biology and biodynamics of the red fox (*Vulpes vulpes*) in the Northern Arava Valley, Israel. M.Sc. thesis, Tel Aviv University (in Hebrew).

Bitan, A. & Rubin, S. 1994. *Climate Atlas for Physical and Environmental Planning in Israel*. Tel Aviv: Ramot.

Carbone, C., Du Toit, J. T. & Gordon, I. J. 1997. Feeding success in African wild dogs: does kleptoparasitism by spotted hyenas influence hunting group size? *Journal of Animal Ecology*, **66**, 318–326.

Carbone, C., Mace, G. M., Roberts, S. C. & Macdonald, D. W. 1999. Energetic constraints on the diet of terrestrial carnivores. *Nature*, **402**, 286–288.

Clark, H. O., Warrick, G. D., Cypher, B. L., Kelly, P. A., Williams, D. F. & Grubbs, D. E. 2005. Competitive interactions between endangered kit foxes and nonnative red foxes. *Western North American Naturalist*, **65**, 153–163.

Cooper, S. M. 1991. Optimal hunting group size: the need for lions to defend their kills against loss to spotted hyaenas. *African Journal of Ecology*, **29**, 130–136.

Creel, S. & Creel, N. M. 1996. Limitation of African wild dogs by competition with larger carnivores. *Conservation Biology*, **10**, 526–538.

Cypher, B. L. & Spencer, K. A. 1998. Competitive interactions between coyotes and San Joaquin kit foxes. *Journal of Mammalogy*, **79**, 204–214.

Dayan, T., Simberloff, D., Tchernov, E. & Yom-Tov, Y. 1992. Canine carnassials: character displacement in the wolves, jackals and foxes of Israel. *Biological Journal of the Linnean Society*, **45**, 315–331.

Diamond, J. M. 1978. Niche shifts and the rediscovery of interspecific competition. *American Scientist*, **66**, 322–331.

Elmhagen, B., Tannerfeldt, M. & Angerbjorn, A. 2002. Food-niche overlap between arctic and red foxes. *Canadian Journal of Zoology*, **80**, 1274–1285.

Frafjord, K. 2000. Do arctic and red foxes compete for food? *International Journal of Mammalian Biology*, **65**, 350–359.

Frafjord, K. 2003. Ecology and use of arctic fox *Alopex lagopus* dens in Norway: tradition overtaken by interspecific competition? *Biological Conservation*, **111**, 445–453.

Gause, G. F. 1934. *The Struggle for Existence*. Baltimore: Williams & Wilkins.

Gese, E. M., Stotts, T. E. & Grothe, S. 1996. Interactions between coyotes and red foxes in Yellowstone National Park, Wyoming. *Journal of Mammalogy*, **77**, 377–382.

Golani, I. & Keller, A. 1974. A longitudinal field study of the behavior of a pair of golden jackals. In: *The Wild Canids: Their Systematics, Behavioral Ecology and Evolution* (Ed. by M. W. Fox), pp. 303–325. New York: Van Nostrand Reinhold.

Gorman, M. L. & Trowbridge, B. J. 1989. The role of odor in the social lives of carnivores. In: *Carnivore Behavior, Ecology and Evolution* (Ed. by J. L. Gittelman), pp. 57–88. London: Chapman & Hall.

Gorman, M. L., Mills, M. G., Raath, J. P. & Speakman, J. R. 1998. High hunting costs make African wild dogs vulnerable to kleptoparasitism by hyaenas. *Nature*, **391**, 479–481.

Harrison, D. J., Bissonette, J. A. & Sherburne, J. A. 1989. Spatial relationships between coyotes and red foxes in eastern Maine. *Journal of Wildlife Management*, **53**, 181–185.

Henke, S. E. & Bryant, F. C. 1999. Effects of coyote removal on faunal community in western Texas. *Journal of Wildlife Management*, **63**, 1066–1081.

Hersteinsson, P. & Macdonald, D. W. 1992. Interspecific competition and the geographical distribution of red and arctic foxes *Vulpes vulpes* and *Alopex lagopus*. *Oikos*, **64**, 505–515.

Holt, R. D. & Polis, G. A. 1997. A theoretical framework for intraguild predation. *American Naturalist*, **149**, 745–764.

Hutchinson, G. E. 1959. Homage to Santa Rosalia, or why are there so many kinds of animals? *American Naturalist*, **93**, 145–159.

Ilani, G. 1979. *Zoogeographical and Ecological Survey of Carnivores in Israel and Administered Areas*. Tel Aviv: Nature Reserves Authority (in Hebrew).

Ilani, G. & Shalmon, S. 1985. On jackals and foxes. *Teva va-Aretz*, **27**, 37–38 (in Hebrew).

Johnson, W. E. & Franklin, W. L. 1994. Spatial resource partitioning by sympatric grey fox (*Dusicyon griseus*) and culpeo fox (*Dusicyon culpaeus*) in southern Chile. *Canadian Journal of Zoology*, **72**, 1788–1793.

Kingdon, J. 1997. *The Kingdon Field Guide to African Mammals*. London: Academic Press.

Krebs, C. J. 2001. *Ecology.* San Francisco: B. Cummings.

Lanszki, J. & Heltai, M. 2002. Feeding habits of golden jackal and red fox in south-western Hungary during winter and spring. *Mammalian Biology*, **67**, 129–136.

Lindstrom, E. R., Brainerd, S. M., Helldin, J. O. & Overskaug, K. 1995. Pine marten–red fox interactions: a case of intraguild predation? *Annales Zoologici Fennici*, **32**, 123–130.

Macdonald, D. W. 1979a. The flexible social system of the golden jackal, *Canis aureus. Behavioral Ecology and Sociobiology*, **5**, 17–38.

Macdonald, D. W. 1979b. Some observations and field experiments on the urine marking behaviour of the red fox, *Vulpes vulpes. Zeitschrift für Tierpsychologie*, **51**, 1–22.

Macdonald, D. W. 1987. *Running with the Fox*. London: Unwin Hyman.

Macdonald, D. W. & Barrett, P. 1993. *Collins Field Guide: Mammals of Britain and Europe*. London: Harper Collins.

Mendelssohn, H. & Yom-Tov, Y. 1999. *Mammalia of Israel*. Jerusalem: Israel Academy of Sciences and Humanities.

Palomares, F. & Caro, T. M. 1999. Interspecific killing among mammalian carnivores. *American Naturalist*, **153**, 492–508.

Palomares, F., Gaona, P., Ferreras, P. & Delibes, M. 1995. Positive effects on game species of top predators by controlling smaller predator populations: an example with lynx, mongooses, and rabbits. *Conservation Biology*, **9**, 295–305.

Paquet, P. C. 1992. Prey use strategies of sympatric wolves and coyotes in Riding Mountain National Park, Manitoba. *Journal of Mammalogy*, **73**, 337–343.

Peterson, R. O. 1995. Wolves as interspecific competitors in canid ecology. In: *Ecology and Conservation of Wolves in a Changing World* (Ed. by L. N. Carbyn, S. H. Fritts & D. R. Seip), pp. 315–323. Alberta: Canadian Circumpolar Institute.

Polis, G. A., Myers, C. A. & Holt, R. D. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics*, **20**, 297–330.

Ralls, K. & White, P. J. 1995. Predation on San-Joaquin kit foxes by larger canids. *Journal of Mammalogy*, **76**, 723–729.

Sargeant, A. B., Allen, S. H. & Hastings, J. O. 1987. Spatial relations between sympatric coyotes and red foxes in North Dakota. *Journal of Wildlife Management*, **51**, 285–293.

Schoener, T. W. 1982. The controversy over interspecific competition. *American Scientist*, **70**, 586–595.

Tannerfeldt, M., Elmhagen, B. & Angerbjorn, A. 2002. Exclusion by interference competition? The relationship between red and arctic foxes. *Oecologia*, **132**, 213–220.

Theberge, J. B. & Wedeles, C. H. R. 1989. Prey selection and habitat partitioning in sympatric coyotes and red fox populations, southwest Yukon. *Canadian Journal of Zoology*, **67**, 1285–1290.

Thurber, J. M., Peterson, R. O., Woolington, J. D. & Vucetich, J. A. 1992. Coyote coexistence with wolves in the Kenai Peninsula, Alaska. *Canadian Journal of Zoology*, **70**, 2494–2498.

Voigt, D. R. & Earle, B. D. 1983. Avoidance of coyotes by red fox families. *Journal of Wildlife Management*, **47**, 852–857.

Vucetich, J. A. & Creel, S. 1999. Ecological interactions, social organization, and extinction risk in African wild dogs. *Conservation Biology*, **13**, 1172–1182.

Ward, J. H. 1963. Hierarchical grouping to optimize an objective function. *Journal of the American Statistical Association*, **58**, 236–244.