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Abrupt spatial and numerical responses of overabundant foxes to a reduction in anthropogenic resources

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Summary

1. Carnivore overabundance that results from exploitation of human derived resources can have numerous detrimental effects on local human populations and ecological communities. Experimental studies on the responses of overabundant carnivores to reductions of such resources are necessary to understand the effectiveness and impacts of resource reduction.

2. We conducted controlled experiments in two villages in which we drastically reduced the availability of anthropogenic food sources in half of each village. Spatial and numerical responses of radio-collared red foxes *Vulpes vulpes* were recorded and contrasted with those of radio-collared foxes in three similar untreated villages and pristine areas in the region. In total, we looked at survival rates of 134 foxes.

3. Prior to the resource manipulation, home range sizes (0·47 and 0·56 km^2) and population densities (30 and 36 foxes km^{-2}) in the two villages were comparable to documented low and high-end values, respectively.

4. Fast and distinct spatial responses were observed in response to the resource manipulation, and were manifested in either increased home range size or home range shifts. In one village, foxes exposed to reduced resource availability more than doubled their home range size.

5. Survival rates of individuals in the treated areas were drastically reduced. Actual fox mortality in the two treated areas reached 100% and 64% within 12 months of the onset of resource manipulation. Estimated monthly survival in the two treated areas declined from 0·96–0·98 and 0·98–0·99 (~0·69 and 0·78 derived annual survival) before treatment to 0·80–0·83 and 0·92–0·94 ($\sim < 0{\cdot}01$ and 0·42 derived annual survival) after treatment, respectively. By contrast, average monthly survivorship in pristine areas was nearly 0·97 (~0·69 annual survival) and in the untreated areas and other non-treated villages was 0·95–0·99 (~0·54–0·89 annual survival).

6. *Synthesis and applications*. This study demonstrates that sound waste disposal measures are very effective in controlling populations of overabundant carnivores. Contrary to common notion, the response of foxes to reduced resources was fast, manifested more by reduced survival than by successful dispersal into adjacent pristine areas. The results offer support to the Resource Dispersion Hypothesis regarding both home range size and density (suggested by the sharp decrease in survival) as a function of the spatial and temporal dispersion of resource.

Key-words: carnivore overabundance, kernel utilization distribution, MARK, radio tracking, red fox, Resource Dispersion Hypothesis, resource manipulation, survival

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Introduction

Supported by anthropogenically derived resources, canid densities near human settlements can be as much as 15 times higher than those in pristine areas (Cavallini 1996; Adkins & Scott 1998; Fedriani, Fuller & Sauvajot 2001; Panez & Bresinski 2002). High canid densities can have numerous detrimental effects on local human populations and ecological communities (Sillero-Zubiri & Switzer 2004), including increased livestock depredation and damage to farming infrastructure (Asheim & Mysterud 2004; Michalski *et al.* 2006; Holmern, Nyahongo & Roskaft 2007), elevated risk of disease outbreaks (Anderson *et al.* 1981; Daszak, Cunningham & Hyatt 2000; Yakobson 2007), and disruption of trophic cascades (Yom-Tov & Mendelssohn 1988; Dickman 1996; Newton 1998; Saltz *et al.* 2002). As invasive species, carnivores when uncontrolled can pose a substantial threat to native species, driving many to extinction (Saunders *et al.* 1995; Dickman 1996). Consequently, the management and control of carnivores in human-dominated landscapes is of major concern (Treves & Karanyh 2003; Sillero-Zubiri & Switzer 2004) for both economic and conservation reasons. However, active reduction of canid densities by shooting or poisoning commonly raises public objections and is often ineffective due to the high recruitment rates of canids, their nocturnal behaviour, and lack of species specificity (Sillero-Zubiri & Switzer 2004). Improved sanitation procedures, on the other hand, are considered to be effective only in the long-term as a result of an assumed delayed response. This has raised concerns over the possibility of individuals from a treated area spilling over into the surrounding natural environment and causing a 'crowding the ark' effect (Meffe & Carroll 1997). To date, studies examining carnivore responses to reduced resources have sought correlations between relevant variables (Baker 2000; Gilchrist & Otali 2002; Johnson *et al.* 2002; Pereira, Fracassi & Uhart 2006), so that planned experimental studies on the responses of overabundant carnivores to resource reduction remain to be done.

Israel's Galilee and northern periphery is characterized by a large number of small villages that rely economically on family farms. Often, these villages lack any organized means of husbandry waste disposal, and carcasses from poultry cultivation and other wastes are dumped in the open. As a result, these villages are transformed into hotspots for many wild canids, mainly the red fox *Vulpes vulpes* and golden jackal *Canis aureus* (Dolev *et al.* 2004; Dolev 2006), both native to the region. Existing conditions offer a unique opportunity to study the responses of canids when improved sanitation procedures are implemented.

In this work, we examined the short-term effects of reducing anthropogenic resources on foxes scavenging near poultry farms in two Israeli villages by eliminating poultry carcasses. We contrasted the survival and spatial responses of foxes to the sudden decrease in anthropogenic resources with those of foxes in three untreated villages and in the region's pristine areas. We focused our study on fox survival and spatial responses to the sudden decrease in resources.

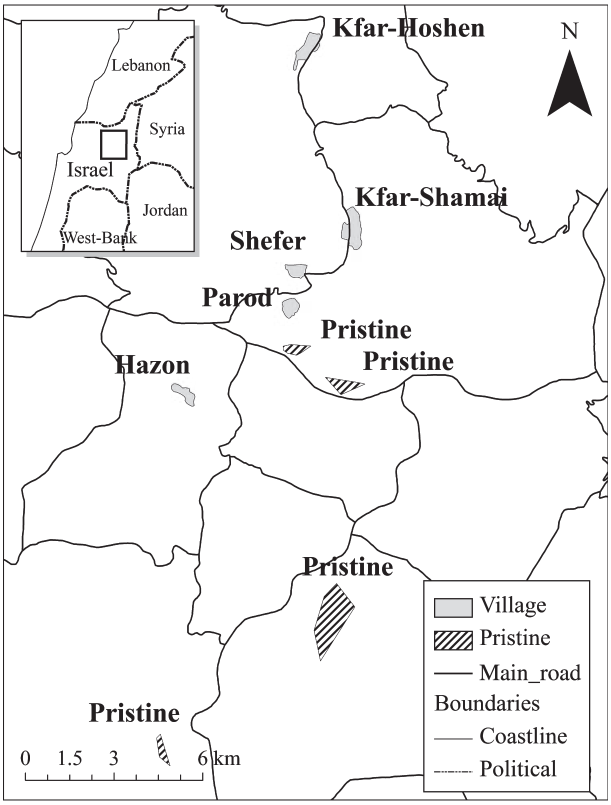

Fig. 1. The study area and five villages and pristine areas where a total of 134 foxes were radio-collared and tracked. Pristine areas are represented as the 100% Minimum Convex Polygon of captured animals.

Materials and methods

STUDY AREA

The study area was centred in northern Israel's eastern Galilee and was conducted within and around five typical peripheral villages: Kfar-Shamai (KS) and Kfar-Hoshen (KH), Parod, Shefer, and Hazon, covering an approximate area of 600 km^2 (Fig. 1). Surroundings consist predominantly of agricultural lands (mainly vineyards and orchards) and Mediterranean woodland. Residential areas covered approximately 0·5 km^2. A major source of agricultural income in the villages is poultry farming, producing either eggs or meat.

TRAPPING AND RADIO-TRACKING

Due to logistic limitations and varying survival of animals and radio transmitters, we radio-collared and tracked foxes in the different areas over varying time spans starting in spring 2002 and ending in spring 2009 (Fig. 2). Foxes were captured with padded foothold traps. Traps were set within and along the outer edge of the five villages as well as in pristine regions. Traps were checked every 4 h for the duration of the night. After sedation, captured animals were fitted with a radio-collar equipped with a mortality sensor. For each animal we recorded sex, weight, morphological measurements (tarsus and neck width), and age (juvenile or adult). Aging was based on weight,

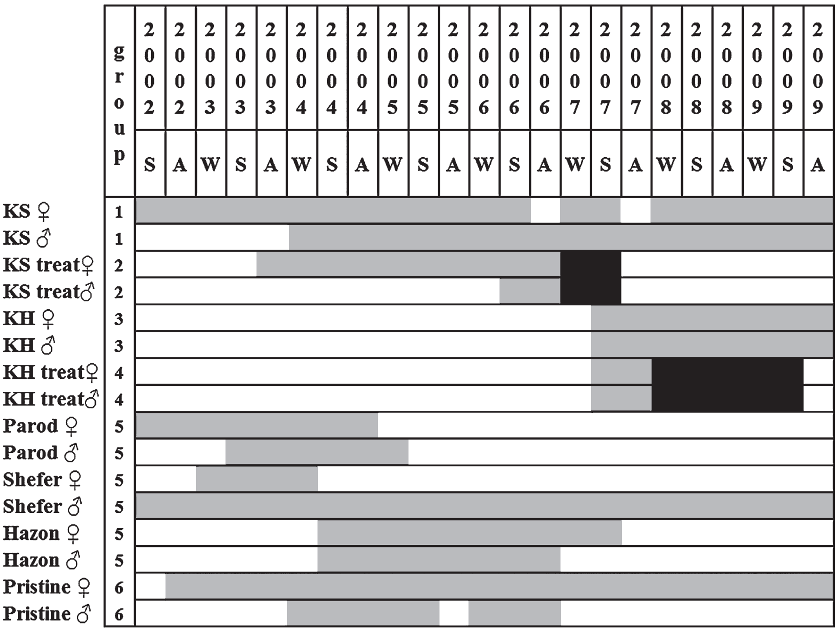

Fig. 2. The presence of radio-collared adult foxes during each season (S-spring, A-autumn, and W-winter) in each of the areas, stratified according to gender. No shading represent absence, grey shading represent presence, and black shading represent presence during the resource manipulation period.

dentition, and muscle condition. A relatively small individual with white, undamaged or deciduous teeth was considered juvenile. Development of robust muscle tissue was associated with adults. Animals were released the same night they were trapped.

Telemetry readings in KS and KH were made using a three element Yagi hand-held antenna. We located radio-collared animals through ground triangulation at short range (< 300 m). Triangulations were carried out by a single person, while keeping the time interval between two consecutive bearings to a minimum ($\bar{X}$ < 3 min in KS and $\bar{X}$ < 18 min in KH), and recording both the azimuth and the location of the receiving site. Accuracy of radio-telemetry was determined by placing radio transmitters in unknown locations for the radio-tracker and was found to be at approximately 25% of the distance from the radio transmitter. As most telemetry readings were taken 100 m away from animals, the deviation between the estimated and true location of the transmitter was approximately 25 m. In order to minimize errors, triangulation angles were kept over 30º (Saltz 1994). We had two radio-tracking protocols, the first (KS) being intensive telemetric following of foxes within the village and surroundings throughout the night. During each tracking night, we initially located all animals and then continued cycling through the frequencies and relocating the animals while keeping the time interval between rotations no shorter than 1 h. In total we carried out 64 whole night tracking sessions in KS. Due to a limited budget, the second radio-tracking protocol (KH) was carried out at low intensity with a single telemetry reading of each radio-collared individual taken once per night. Triangulations were carried out in a similar manner as at KS. In total, we carried out 67 tracking sessions in KH. In both villages radio-tracking commenced along with trapping (July) and ended in June the following year. In both protocols, any random sightings of both radio-collared as well as unmarked individuals were recorded.

OVERVIEW OF STUDY DESIGN

We manipulated the availability of anthropogenic resources for foxes in two villages, KS and KH, by applying sanitation protocols (see below) to half of each village. At the time of study, KS had 47 active poultry family farms and KH had 62. Each farm raises 2000–5000 hens; most did not practice sound disposal of chicken carcasses, which were discarded in the open. Sanitation was applied 6 months after we began radio-collaring foxes, providing sufficient data on fox movements and survival prior to the manipulation. Specifically, in KS we captured and radio-collared foxes between July and November 2006 and KH during the same months in 2007. Both villages are oriented on a north-south axis, so we divided both latitudinally into two halves: north and south (Fig. 3). We arbitrarily decided to subject the southern parts of both villages to the resource manipulation, whereas the northern parts were left unchanged as controls.

We started the sanitation protocol in KS in January 2007 and in KH in January 2008. In cooperation with the farmers, we distributed in KS sealed trashcans for 21 of the 22 poultry farms in the south and left the remaining 34 poultry farms in the northern part of the village uninterrupted to continue discarding refuse in the open. In KH we distributed 26 trashcans for each poultry farm in the south, leaving the 36 northern poultry farms undisturbed. The farmers in the southern parts of each village agreed to dispose of the dead hens into the provided trashcans, and we, in turn, collected the refuse in both KS and KH in a large 3-m deep container in the northern part of the village, which was not accessible to any animal and was cleared several times a month. By doing so, access to poultry waste in the southern parts of the villages was all but obliterated. In KS, resource manipulation was carried out between 1 December 2006 and the end of March 2007. Over the course of 3·5 months, 1·5 tonnes of refuse (average of 70 kg per poultry farm and 13 kg per day) were collected and disposed of. In

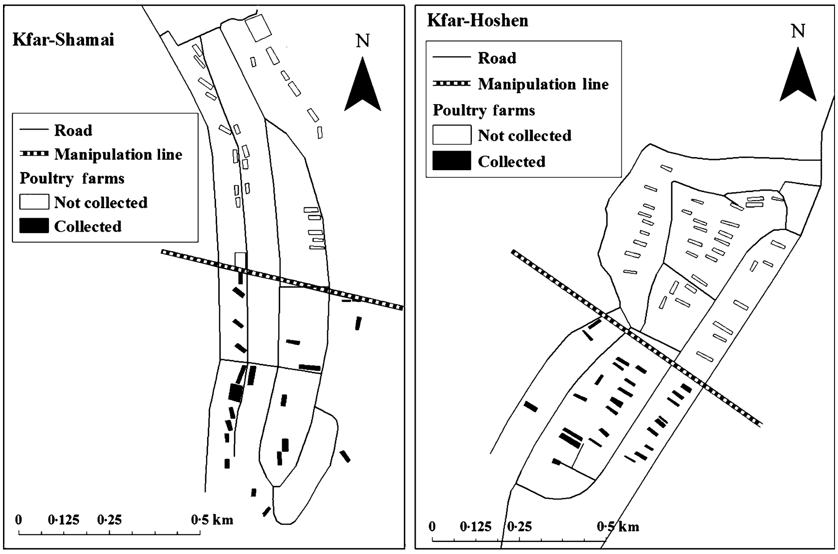

Fig. 3. The two villages, Kfar-Shamai (KS) and Kfar-Hoshen (KH) in which the southern half of each was subjected to sanitation procedures. Lines are the roads, rectangles are the poultry sheds, and the broken line delineates the division between the treated and untreated area.

KH, we began a 4-month resource manipulation the subsequent year, from 1 January 2008 until 30 April. Over the course of 4 months, 2·2 tonnes of refuse (average of 86 kg per poultry farm and 19 kg per day) were collected and disposed of. Towards the end of both manipulation periods we notified the farmers of our intention to stop collecting carcasses and discussed with them the possibility of them continuing the disposal practice. Based on conversations with the farmers and observations, in KS the majority of farmers (i.e. 17 including the bigger poultry farms) and in KH all farmers continued to disposal of carcasses soundly. Even though the sanitation level in KS was somewhat reduced after our manipulation period, we consider the treatment as persisting throughout the remainder of our study period.

Radio-collared animals were defined as having a spatial association to one of the two village segments based on the majority of their recorded locations prior to treatment. In this context, we sought to examine behavioural and survival responses to the manipulation as changes over time for foxes in the manipulated area, with temporal patterns in these parameters for foxes in the unmanipulated area acting as a control. Throughout the study we also trapped and radio-collared foxes in more pristine areas away from the villages and in three similarly untreated villages. These acted as additional controls, providing information on survival and movement patterns in regions where anthropogenic influences are minimal and high, respectively.

SURVIVAL ANALYSIS

Radio transmitters were fitted with activity sensors with a 4-h time delay. Animals emitting a no-activity signal were located to confirm their death. We used an information-theoretic approach (Burnham & Anderson 2002) using the Known-Fates module in program MARK (White & Burnham 1999) to estimate fox survival and the effect of the treatment on it. Within the framework of the known fates module, no assumptions are made regarding animals whose radio signal is lost (i.e. MARK right censors the data). However, we performed periodic aerial surveys to try and locate 'lost' animals within and outside the study area to determine their fate. We considered the following variables as potential predictors of survival: (1) *Time related variables*, including year, season and treatment period (treat). We recognized three seasons according to the biology of the species: April–August (spring) – reproduction and caring for young, September–December (autumn) – dispersal of sub-adults, and January–March (winter) – mating and gestation (Fig. 2). The treatment periods were considered from the time of application to the end of the study. (2) *Group related variables,* including the study sites [consisting of eight groups in total: all pristine areas (p.sites) being one group, the five villages (v.sites), of which the two where the treatment was applied to one half of the village were considered as two groups each (treated and untreated area)], and gender (two groups – males and females) (Fig. 2). All time parameters (including the treatment) were considered as additive (using MARK's design matrix), e.g. the magnitude of the impact of season on the basic survival parameter was additive and similar in all areas. To this end, the treatment effect is a time related parameter applied to two groups (i.e. the treated areas) within KH and KS. The treated and untreated areas in these two villages were parameterized the same before the treatment was applied even when a village effect was modelled. Our occasion unit was 1 month using the standard calendar.

We compared the various potential models (Table 1) with the quasi-Akaike Information Criterion adjusted for small sample size (QAICc; Burnham & Anderson 2002) focussing on the treatment effect by calculating the evidence ratios between similar models with and without the treatment effect. In total, we evaluated 30 models from which we then estimated survival by averaging across all models.

HOME RANGE SIZE

We employed a kernel-based estimate to measure each animal's probability distribution (Worton 1989). The kernel

Table 1. Model results of fox survival using Known-Fates module in program MARK. Potential time predictors included: year, season and treatment period (treat)

#	*Model*	*QAIC*	*Parameters*	*Delta*	*Likelihood*	*Weights*	*Deviance*
1	{t(treat), g(p.sites)}	419·74	7	0·00	1·00	0·47	230·28
2	{t(treat season), g(p.sites)}	419·94	9	0·19	0·82	0·38	226·48
3	{t(treat), g(p.sites gender)}	421·33	8	1·58	0·21	0·10	229·86
4	{t(treat season year), g(.)}	422·96	10	3·22	0·04	0·02	227·50
5	{t(treat season), g(.)}	423·68	4	3·94	0·02	0·01	240·22
6	{t(treat year), g(.)}	423·78	8	4·03	0·02	0·01	232·32
7	{t(treat), g(.)}	423·87	2	4·13	0·02	0·01	244·41
8	{t(treat year), g(p.sites)}	424·77	13	5·03	0·01	0·00	223·31
9	{t(treat season year), g(v.sites)}	424·89	11	5·15	0·01	0·00	227·43
10	{t(treat season), g(v.sites)}	425·54	5	5·80	0·00	0·00	240·08
11	{t(treat year), g(v.sites)}	425·62	9	5·88	0·00	0·00	232·16
12	{t(treat), g(v.sites)}	425·68	3	5·93	0·00	0·00	244·21
13	{t(treat season year), g(p.sites)}	425·84	15	6·10	0·00	0·00	220·38
14	{t(year), g(.)}	432·26	7	12·52	0·00	0·00	242·80
15	{t(season), g(.)}	433·04	3	13·29	0·00	0·00	251·58
16	{t(.), g(.)}	433·05	1	13·30	0·00	0·00	255·59
17	{t(season year), g(.)}	433·16	9	13·41	0·00	0·00	239·70
18	{t(year), g(v.sites)}	434·25	8	14·50	0·00	0·00	242·78
19	{t(season), g(v.sites)}	434·83	4	15·09	0·00	0·00	251·37
20	{t(.), g(v.sites)}	434·92	2	15·17	0·00	0·00	255·46
21	{t(season year), g(v.sites)}	435·09	10	15·34	0·00	0·00	239·63
22	{t(t.KS), g(p.sites)}	435·19	7	15·44	0·00	0·00	245·73
23	{t(t.KS season), g(p.sites)}	435·42	9	15·68	0·00	0·00	241·96
24	{t(.), g(p.sites)}	435·49	6	15·74	0·00	0·00	248·03
25	{t(season), g(p.sites)}	435·68	8	15·94	0·00	0·00	244·22
26	{t(year), g(p.sites)}	436·48	12	16·73	0·00	0·00	237·02
27	{t(t.KH), g(p.sites)}	437·30	7	17·55	0·00	0·00	247·84
28	{t(.), g(p.sites gender)}	437·41	7	17·66	0·00	0·00	247·87
29	{t(t.KH season), g(p.sites)}	437·45	9	17·70	0·00	0·00	243·98
30	{t(season year), g(p.sites)}	437·76	14	18·02	0·00	0·00	234·30

Potential group predictors included eight study sites (pristine – p.sites, five villages - v.sites of which the half of two consisted also were subjected to the sanitation treatment: t.KS and t.KH, and untreated area: KS and KH) and gender.

utilization distribution was used to calculate fox home range size (95% isopleths) and its centre point of activity in the two treated villages. Kernel analysis used MATLAB 7·3 (MathWorks 2006). Bandwidth values were calculated via Least Square Cross Validation (Silverman 1986), which is a sensitive method for identifying tight clumps, including areas of peak use (Gitzen, Millspaugh & Kernohan 2006). The plug-in approach was avoided due to its tendency to over-smooth real peaks in the underlying density (Loader 1999).

Even though the change in availability of resources took place over night, we assumed that foraging animals would require time to learn and respond spatially to the new situation. Because several animals did not survive to the end of the manipulation period, the full effects of the manipulation were not fully manifested in terms of foraging behaviour. In order to ascertain the continuous learning and adaptive process by the animals, a technique we termed 'Moving Window Kernel' (MWK) was employed which is conceptually similar to a running average. This process was achievable only in KS where sampling intensity was high enough. The process is based on estimating the home range kernel for a series of 30 chronologically consecutive locations for each animal (T_1–T_{30}). Following, the first location is subtracted, while a new location is added (T_2–T_{31}), and again the home range kernel is estimated. By doing so, a continuous process of home range shifting is represented. For each animal, all locations prior to the beginning of the manipulation were pooled and home range estimated. The MWK was conducted from day one of the manipulation (29 locations prior to the manipulation + 1 location from the first day of the manipulation) to the end of the study, or to mortality. Using the MWK procedure, a linear regression for each fox was fitted between its home range size and time since manipulation began (days) and the slope extracted. Slopes from each village side (i.e. treated and untreated) were compared using an independent *t*-test.

Identifying changes in home range size in KH, where sampling intensity was lower, was achieved by comparing home range locations before and after the manipulation period began. We employed a permutation procedure to control for variation in sample sizes in the two sampling periods. For each individual, we examined the sample size before and after the manipulation and calculated the animal's home range using all available locations for the time period with the least number of locations (i.e. pre manipulation). We then estimated the animal's home range during the contrasting time period (i.e. post manipulation) using 1000 permutations of unique location combinations using a similar sample size. Distributions of obtained home range sizes were compared to the estimated home range sizes in the contrasting time period and a *P*-value for each individual extracted. We then conducted a Fisher's combined probability test (Fisher 1948) for foxes in both the northern and southern parts of the villages.

SPATIAL DISPLACEMENT

Assuming that the depletion of resources would induce a displacement in home range of foxes within the manipulation area, spatial displacement of home ranges of animals from the control and manipulated areas was investigated using the MWK technique in a similar manner to that used to detect changes in home range size. Specifically, we identified the centroid of each home range and calculated its shortest distance to the manipulated area (represented as a surrounding polygon). Distances received a negative distance when the centre point of activity fell within the manipulated area. Thus, we obtained for each animal a chronological change in the distance of its centre of activity from the manipulation area. For each animal two linear regressions were fitted to the observed changes in distances from the manipulation area: one before and one after the manipulation began. Both slopes obtained from each individual were then grouped according to the animal's pre-manipulation geographic affiliation and a paired t-test was employed to detect any changes between the groups of foxes from the two village areas. Analysis of spatial displacement in KH was conducted by examining changes in the ratio of recorded individual fox locations in the northern, unmanipulated area in comparison to the southern, manipulated area. Fox locations were assigned either as north or south of the manipulation line and the ratio calculated. Ratios for each animal were recorded for each time period (pre and post manipulation) and a paired *t*-test used to test for any significant changes.

Results

In total, we radio-collared 134 foxes (74 females, 60 males). In KS, we radio-collared 17 foxes (10 females, 7 males). In KH we radio-collared 18 foxes (11 females, 7 males). In a previous study (Dolev 2006), we radio-collared: KS – 28 foxes (15 females, 13 males), Shefer – 6 foxes (1 female, 5 males), Parod – 5 foxes (3 females, 2 males), Hazon – 17 foxes (11 females, 6 males) and in the pristine regions – 43 foxes (23 females, 20 males).

SURVIVAL

At the time of the resource manipulation, nine foxes were present in the treated area of KS and six in the untreated area. By the end of 6 months, eight foxes had perished in the treated area (i.e. mortality of 89%). In the untreated area only one was found dead and another's signal was lost. After 12 months, all foxes (100%) had perished in the treated area, contrasting with only three (50%) in the untreated area. In KH, 11 foxes were subjected to the resource manipulation. Only five foxes (55%) survived after 6 months and four (64%) after 12 months. In the untreated area, five adult foxes were present at the onset of the resource manipulation with four (i.e. mortality of 20%) surviving after 6 months and three (40%) after 12 months.

All the leading models using the known-fates module in MARK included the treatment effect (Table 1). Three models had substantial support (QAICc $< 2{\cdot}0$) and included, other than the treatment, a site effect (labelled 'p.sites' in Table 1) with all eight groups, a season effect (one model) and a sex effect (one model). Evidence ratios for these three leading models compared to their counterpart without the treatment effect were $>$ 40,000:1 (model 1 vs. 24), $>$ 38,000:1 (model 2 vs. 25), and 9,000:1 (model 3 vs. 28). Models with all untreated areas grouped together (termed 'v.sites' in Table 1) had lesser support.

Monthly survival estimates per season dropped in the treated area in KS from ~0·97 before treatment to 0·80–0·83 (Table 2) and in KH from 0·98–0·99 to 0·92–0·94. This amounts to an annual decline in survivorship from 0·69 to $<$ 0·01 in KS and from 0·78 to 0·42 in KH. Seasonal survivorship in the natural areas ranged from 0·95 to 0·97. Monthly survival in all villages (including the pre-treatment values for the treatment areas in KS and KH) was as much as 0·99, except in Hazon where it ranged from 0·96 to 0·94.

HOME RANGE SIZE

In KS, 1128 and 605 telemetry locations were recorded in the pre- and post-manipulation periods, respectively. Average telemetry locations per animal were 64 ± 24. Prior to the manipulation, average fox home range size in KS was 0·47 km^2 ± 0·25 (n = 17). The slope of change in home range size from the start of the manipulation using the MWK procedure showed significant differences in the rates at which home range size increased between foxes from the two sides of the village (t = 6·97, df = 9, P < 0·001). Home range size of southern foxes more than doubled to an average of 1·2 km^2 ± 0·35 (n = 3). In KH, 169 and 258 telemetry locations were recorded in the pre- and post-manipulation periods, respectively, with 25 ± 13 locations per animal. Pre-manipulation average fox home range size was 0·56 km^2 ± 0·41 (n = 12). A significant increase in home range size was observed in both sides of the village in the post-manipulation period (North: χ^2 = 17·87, df = 6, P = 0·007, South: χ^2 = 51·84, df = 18, P < 0·001).

SPATIAL DISPLACEMENT

Linear regression slopes obtained through the MWK procedure, showed that the centroid of activity of foxes in the southern part of KS moved away from the manipulation area. Distance from the manipulation area increased for animals foraging in the southern part of the village from 28 m prior to the manipulation to 136 m in the months following (t = −21·23, df = 2, P = 0·002). By contrast, the distance of the centroid of activity of animals foraging in the northern part

Table 2. Estimated monthly survival rates per season (S – spring, A – autumn, and W – winter) for each of the areas, stratified by gender. Treated periods are highlighted in grey.

		Site\Gender															
Year	Season	KS ♀	KS ♂	KS.T ♀	KS.T ♂	KH ♀	KH ♂	KH.T ♀	KH.T ♂	Parod ♀	Parod ♂	Shefer ♀	Shefer ♂	Hazon ♀	Hazon ♂	Pristine ♀	Pristine ♂
2002	S	0·97								0·97			0·99				
2002	A	0·98								0·98			0·99			0·97	
2003	W	0·98								0·98		0·99	0·99			0·97	
2003	S	0·97								0·97	0·97	0·99	0·99			0·97	
2003	A	0·97		0·97						0·98	0·98	0·99	0·99			0·97	
2004	W	0·98	0·98	0·98						0·98	0·98	0·99	0·99			0·97	0·97
2004	S	0·97	0·97	0·97						0·97	0·97		0·98	0·94	0·94	0·96	0·96
2004	A	0·97	0·97	0·97						0·98	0·97		0·99	0·95	0·95	0·97	0·97
2005	W	0·97	0·97	0·97							0·98		0·99	0·95	0·95	0·97	0·97
2005	S	0·97	0·97	0·97									0·99	0·95	0·94	0·97	0·97
2005	A	0·98	0·97	0·98									0·99	0·95	0·95	0·97	
2006	W	0·98	0·98	0·98									0·99	0·96	0·96	0·97	0·97
2006	S	0·96	0·96	0·96	0·96								0·98	0·94	0·94	0·96	0·96
2006	A		0·97	0·97	0·97								0·98	0·95	0·95	0·97	0·97
2007	W	0·97	0·97	0·83	0·83								0·99	0·95		0·97	
2007	S	0·97	0·97	0·80	0·80	0·98	0·98	0·98	0·98				0·98	0·94		0·96	
2007	A		0·97			0·99	0·99	0·99	0·99				0·99			0·97	
2008	W	0·98	0·97			0·99	0·99	0·93	0·93				0·99			0·97	
2008	S	0·97	0·97			0·99	0·99	0·93	0·92				0·99			0·97	
2008	A	0·98	0·97			0·99	0·99	0·94	0·94				0·99			0·97	
2009	W	0·98	0·98			0·99	0·99	0·94	0·94				0·99			0·97	
2009	S	0·97	0·97			0·99	0·99	0·94	0·94				0·99			0·97	

of the village remained unchanged ($t = -1{\cdot}40$, df = 6, $P = 0{\cdot}21$). Recorded location ratios for foxes exposed to the resource manipulation in KH increased significantly towards the northern side of the village in the post-manipulation period in comparison to the pre-manipulation period ($t = -2{\cdot}46$, df = 9, $P = 0{\cdot}036$). No significant changes were observed in fox location ratios in the unmanipulated area ($t = -0{\cdot}99$, df = 2, $P = 0{\cdot}43$). Telemetry surveillance over 7 years prior to the resource manipulation revealed foraging distances of only several hundred metres from original capture sites. Long range forays and dispersal – defined as locations outside average home range size boundaries +20% – (3·6 km) (Dolev 2006) – were rare events (0·5%). All long distance movements were confined to foxes moving from the villages to neighbouring natural habitat. As pristine locations were distant from investigated villages, we recorded no cases of long range movements of foxes into treated villages.

Discussion

Increased food availability from human waste can have a profound effect on the reproductive success (Lewis, Sallee & Golightly 1999; Reichmann & Saltz 2005) and densities of wild canids (Panez & Bresinski 2002; Dolev 2006). Prior to our manipulation, the maximum numbers of collared foxes located within the boundaries of the treated villages in one night were 14 in KS and 18 in KH. Given the size of the villages this would translate to an estimated density of 30 and 36 foxes km^{-2}, respectively, within the village areas. These values are at the extreme of previously reported densities for foxes (Macdonald & Reynolds 2005). In addition, sightings of uncollared animals were frequent and, therefore, the above estimates represent an underestimate of the true numbers of foxes within the villages.

The sanitation procedures we applied in both cases reduced available organic refuse and resulted in rapid demographic and behavioural changes in foxes. Responses were manifested in reduced survival rates, changes in home range size, and spatial shifts in home ranges. A cause-and-effect relationship between the availability of food resources and these patterns was established through comparison with individuals residing in the unmanipulated area combined with a temporal comparison to the pre-manipulation patterns in both the manipulated and unmanipulated areas as well as survival rates in other villages and more pristine areas.

SURVIVAL

Predator populations are expected to respond to changes in prey availability either functionally, i.e. by switching to alternative prey (Angerbjorn, Tannerfeldt & Erlinge 1999), and/or numerically, i.e. via increased mortality (Fuller & Sievert 2001), reduced reproductive success, and reduced immigration and emigration. To date, studies of predators addressing demographic changes in response to declining food availability provide only circumstantial evidence and involve mainly seasonal variation in resources (Pereira *et al*. 2006).

Average annual survival probability of 77 foxes collared in northern Israel was estimated to be 45·5% during an 18-month period (Dolev 2006). Dolev (2006) further suggested that subadult foxes foraging in the vicinity of villages and poultry farms had a slightly higher survival probability compared to that of foxes foraging in natural areas. Our results provide further support for this observation. Thus, the low survival of the animals foraging in the treated sections is notable. The spatial response of the southern foxes to the treatments, either away from the village into the more natural and agricultural areas or to the northern part of the village, suggests these animals might have attempted to establish new foraging grounds and in doing so may have encountered strong intra-specific competition with individuals having a 'home court advantage.' Thus, mortality may have been caused by elevated stress resulting from functioning in a less familiar (and thus unpredictable) environment and frequent aggressive interactions, both leading to higher probability of starvation.

It certain cases animals subjected to the resource manipulation dispersed (as opposed to just shifting foraging grounds) to distant, unknown areas. Dispersal has several associated costs, such as increased energy demands, difficulty in finding prey in unfamiliar areas and lack of suitable cover (Woollard & Harris 1990; Koopman, Cypher & Scrivner 2000). Several studies of the red fox have shown that philopatric juveniles generally have higher survival than dispersing juveniles (Harris & Trewhella 1988; Lindstrom 1989; Woollard & Harris 1990). In the case of animals in the manipulated areas, both home range size and the foraging locations changed as a result of the resource manipulation. However, even if the daytime resting site locations remained unchanged (i.e. animals did not disperse), the energy expenditure involved in shifting foraging grounds away from these areas could be excessive.

SPATIAL RESPONSES

According to the Resource Dispersion Hypothesis (RDH) (Macdonald 1983), when resources are clumped in space and/or in time, the economics of exploiting these patches enables several individuals to share resources over a common area, satisfying their resource needs without imposing large costs on each other (Johnson *et al*. 2002), but see Revilla (2003) and Johnson *et al*. (2003). Although several studies support the RDH (Johnson *et al*. 2002), the strongest test for the RDH would be through controlled experiments. Surprisingly, we found no designed studies investigating alterations in food availability and its effect on behavioural responses of carnivores (Johnson *et al*. 2002). The literature examining carnivore responses addresses this issue only by finding predicted correlations between the relevant variables (Baker 2000; Gilchrist & Otali 2002; Johnson *et al*. 2002; Pereira *et al*. 2006). The results of this study corroborate the RDH predictions regarding both home range size and density (suggested by the sharp decrease in survival) as a function of the spatial and temporal dispersion of resources (Macdonald 1983; Johnson *et al*. 2002). The pre-manipulation home range sizes and implied densities were comparable to documented low and high-end values, respectively (Macdonald & Reynolds 2005). This is in line with the high spatial concentration of food patches along with high patch richness and predictability in the study area. Prior to the manipulation, animals' energetic requirements were met within a small territory. Moreover, the high overlap in fox home ranges, while foraging within the village, suggests a reduced pressure on territoriality by animals and the sharing of foraging grounds. According to the RDH, the spatial distribution of resources may explain both positive and negative deviations by social canids from the home range predicted by their metabolic requirements (McNab 1963; Macdonald & Sillero-Zubiri 2004). Average adult fox weights in KS and KH [4·9 and 4·1 kg for males ($n = 18$) and females ($n = 18$), respectively] were relatively low for foxes (Macdonald & Reynolds 2005). Along with small home range sizes (and high fox density), our results provide positive affirmation to the allometric relationship (McNab 1963).

As noted in previous studies (Doncaster & Macdonald 1991), the flexible spatial organization of the red fox allows individuals to adapt their home range in light of variation in resource availability. When faced with declining resources in the southern parts of KS and KH, foxes as central place foragers would have two alternatives if they were to maintain their den/day-time shelter while upholding needed energy requirements: forage more in the natural and agricultural landscapes, thus dictating larger dispersion and heterogeneity of patch resources, or forage at longer distances from the den/day-time shelter by venturing into the northern part of the villages (Meia & Weber 1993; Lucherini, Lovari & Crema 1995). In both cases home range is expected to increase and/or shift, as supported herein.

CONSERVATION IMPLICATIONS

Our results demonstrate that improved sanitation is highly effective in controlling overabundant canids, with rapid changes in their dynamics manifested mostly by reduced survival rather than successful dispersal into adjacent pristine areas. The conflict of overabundant carnivores with humans due to agricultural (Sillero-Zubiri & Switzer 2004; Holmern, Nyahongo & Roskaft 2007), epidemiological (Anderson *et al.* 1981; Yakobson 2007), and environmental concerns (Dickman 1996; Saltz *et al.* 2002; Clark *et al.* 2005) necessitates management (Mendelssohn 1972; Yom-Tov, Ashkenazi & Viner 1995; Nemtzov & King 2002). Carnivore control has been practiced for centuries (Reynolds & Tapper 1996). Nevertheless, active reduction of overabundant predators by poisoning or shooting, although still widely practiced (Saunders *et al.* 1995; Treves & Karanyh 2003), is subject to public and professional debate. On the one hand, while labour-intensive shooting is species-specific, it is often ineffective (Baker & Harris 2006). On the other hand, cost-effective poisoning can cause indiscriminate eradication of non-target species (Sillero-Zubiri & Switzer 2004). Reducing available anthropogenic resources through improved sanitation, recognized as a solution tackling the problem at its source, has been considered a long-term process with delayed results, i.e. numerical responses might be lagged and can be preceded by overexploitation of the surrounding resources (Fuller & Sievert 2001). However, our findings suggest that improved sanitation is highly effective in controlling overabundant foxes, with rapid changes in their dynamics manifested more by reduced survival than by successful dispersal into adjacent pristine areas. Moreover, reduction of anthropogenic resources had little consequence for lower trophic levels of fauna (Ben-Zvi 2010). Our results support the use of sanitation as a key protocol for managing problematic predator populations (Fedriani *et al.* 2001; Nyhus & Tilson 2004; Swarner 2004; Peirce & Van Daele 2006). The application of this study to invasive species may be more complex if the increasing abundance of a carnivore species is not attributed solely to human subsidies or livestock depredation. Nonetheless, eliminating access of invasive animals to open landfills and improved husbandry protection and sanitation will inevitably have an adverse effect on their populations. Finally, although not addressed specifically in this study, the changes in abundance of canids in and around the treated villages were noticed by farmers themselves and have encouraged them to maintain a higher level of sanitation after the study was terminated.

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References

Adkins, C.A. & Scott, P. (1998) Home range movements and habitat association of red foxes *Vulpes vulpes* in suburban Toronto, Ontario, Canada. *Journal of Zoology (London.)*, **244**, 335–346.

Anderson, R.M., Jackson, H.C., May, R.M. & Smith, A.M. (1981) Population-dynamics of fox rabies in Europe. *Nature*, **289**, 765–771.

Angerbjorn, A.M., Tannerfeldt, M. & Erlinge, S. (1999) Predator–prey relationship, arctic foxes and lemmings. *Journal of Animal Ecology*, **68**, 34–49.

Asheim, L.J. & Mysterud, I. (2004) Economic impact of protected large carnivores on sheep farming in Norway. *Sheep and Goat Research Journal*, **19**, 89–96.

Baker, P.J. (2000) Flexible spatial organization of urban foxes, *Vulpes vulpes*, before and during an outbreak of sarcoptic mange. *Animal Behaviour*, **59**, 127–146.

Baker, P.J. & Harris, S. (2006) Does culling reduce fox (*Vulpes vulpes*) density in commercial forests in Wales, UK? *European Journal of Wildlife Research*, **52**, 99–108.

Ben-Zvi, A. (2010) *Anthropogenic Impacts in Rural Environment – The Effect of Resource and Predator Overabundance in Agricultural Villages on Small Mammals in the Natural Surroundings*. MSc Thesis, Ben-Gurion University of the Negev.

Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York.

Cavallini, P. (1996) Variation in the social system of the red fox. *Ethology Ecology & Evolution*, **8**, 323–342.

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 non-native red foxes. *Western North American Naturalist*, **65**, 153–163.
Daszak, P., Cunningham, A.A. & Hyatt, A.D. (2000) Emerging infectious diseases of wildlife–threats to biodiversity and human health. *Science*, **287**, 443–449.
Dickman, C.R. (1996) Impact of exotic generalist predators on the native fauna of Australia. *Wildlife Biology*, **2**, 185–195.
Dolev, A. (2006) *Modelling the Spatial Dynamics of Rabies in Canid Vectors Using a Realistic Landscape: A Tool for Optimizing the Spatial Scattering of Oral Rabies Vaccination*. PhD Thesis, Ben-Gurion University of the Negev.
Dolev, A., Saltz, D., King, R. & Hankin, Z. (2004) *Optimization of the Spatial Distribution of Rabies Oral Vaccination in the Galilee, Final Report (in Hebrew)*. The Ministry of Science and Technology, Jerusalem, Israel.
Doncaster, C.P. & Macdonald, D.W. (1991) Drifting territoriality in the red fox *Vulpes vulpes*. *Journal of Animal Ecology*, **60**, 423–439.
Fedriani, J.M., Fuller, T.K. & Sauvajot, R.M. (2001) Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California *Ecography*, **24**, 325–331.
Fisher, R.A. (1948) Combining independent tests of significance. *American Statistician*, **2**, 30.
Fuller, T.K. & Sievert, P.R. (2001) Carnivore demography and the consequences of changes in prey availability. *Carnivore Conservation* (eds J.L. Gittleman, S.M. Funk, D. MacDonald & R.K. Wayne), pp. 163–178. Cambridge University Press, Cambridge.
Gilchrist, J.S. & Otali, E. (2002) The effects of refuse-feeding on home-range use, group size, and intergroup encounters in the banded mongoose. *Canadian Journal of Zoology*, **80**, 1795–1802.
Gitzen, R.A., Millspaugh, J.J. & Kernohan, B.J. (2006) Bandwidth selection for fixed-kernel analysis of animal utilization distributions. *Journal of Wildlife Management*, **70**, 1334–1344.
Harris, S. & Trewhella, W.J. (1988) An analysis of some of the factors affecting dispersal in an urban fox (*Vulpes vulpes*) population. *Journal of Applied Ecology*, **25**, 409–422.
Holmern, T., Nyahongo, J. & Roskaft, E. (2007) Livestock loss caused by predators outside the Serengeti National Park, Tanzania. *Biological Conservation*, **135**, 518–526.
Johnson, D.D.P., Kays, R., Blackwell, P.G. & Macdonald, D.W. (2002) Does the resource dispersion hypothesis explain group living? *Trends in Ecology and Evolution*, **17**, 563–570.
Johnson, D., MacDonald, D., Kays, R. & Blackwell, P.G. (2003) Response to Revilla, and buckley and Ruxton: the resource dispersion hypothesis. *Trends in Ecology and Evolution*, **18**, 381.
Koopman, M.E., Cypher, B.L. & Scrivner, J.H. (2000) Dispersal patterns of San Joaquin kit foxes (*Vulpes macrotis mutica*). *Journal of Mammalogy*, **81**, 213–222.
Lewis, J.C., Sallee, K.L. & Golightly, R.T. (1999) Introduction and range expansion of nonnative red foxes (*Vulpes vulpes*) in California. *American Midland Naturalist*, **142**, 372–381.
Lindstrom, E. (1989) Food limitation and social regulation in a red fox population. *Ecography*, **12**, 70–79.
Loader, C.R. (1999) *Local Regression and Likelihood*. Springer-Verlag, New York.
Lucherini, M., Lovari, S. & Crema, G. (1995) Habitat use and ranging behaviour of the red fox (*Vulpes vulpes*) in a Mediterranean rural area: is shelter availability a key factor? *Journal of Zoology*, **237**, 577–591.
Macdonald, D.W. (1983) The ecology of carnivore social behaviour. *Nature*, **301**, 379–384.
Macdonald, D.W. & Reynolds, J. (2005) Red fox (*Vulpes vulpes*). *Canids: Foxes, Wolves, Jackals and Dogs* (eds C. Sillero-Zubiri, M. Hoffmann & D.W. Macdonald). IUCN, Gland Switzerland and Cambridge, UK.
Macdonald, D.W. & Sillero-Zubiri, C. (2004) *The Biology and Conservation of Wild Canids*. Oxford University Press, Oxford.
MathWorks (2006) MATLAB: The Language of Technical Computing. The Mathworks Inc., Natick, MA.
McNab, B.K. (1963) Bioenergetics and determination of home range size. *American Naturalist*, **97**, 133–139.
Meffe, G.K. & Carroll, C.R. (1997) *Principles of Conservation Biology*. Sinauer Associates, Sunderland, MA.
Meia, J.-S. & Weber, J.-M. (1993) Choice of resting sites by female foxes *Vulpes vulpes* in mountainous habitat. *Acta Theriologica*, **38**, 81–91.
Mendelssohn, H. (1972) Ecological effect of chemical control of rodents and jackals in Israel. *The Careless Technology: Ecology and International Development* (eds T.M. Farvar & J.P. Milton), pp. 527–544. Natural History Press, New-York.
Michalski, F., Boulhosa, R.L.P., Faria, A. & Peres, C.A. (2006) Human-wildlife conflicts in a fragmented Amazonian forest landscape: determinants of large felid depredation on livestock. *Animal Conservation*, **9**, 179–188.
Nemtzov, S.C. & King, R. (2002) Management of wild canids (fox, jackal and wolf) in Israel, with respect to their damage to agriculture and to the spread of rabies. *Advances in Vertebrate Pest Management II* (eds H.J. Petz, D.P. Cowan & C.J. Feare), pp. 219–230. Filander Verlag, Furth, Germany.
Newton, I. (1998) *Population Limitation in Birds*. Academic Press, San Diego.
Nyhus, P.J. & Tilson, R. (2004) Characterizing human-tiger conflict in Sumatra, Indonesia: implications for conservation. *Oryx*, **38**, 68–74.
Panez, M. & Bresinski, W. (2002) Red fox (*Vulpes vulpes*) density and habitat use in a rural area of western Poland in the end of 1990s, compared with the turn of 1970s. *Acta Theriologica*, **47**, 433–442.
Peirce, K.N. & Van Daele, L.J. (2006) Use of a garbage dump by brown bears in Dillingham, Alaska. *Ursus*, **17**, 165–177.
Pereira, J.A., Fracassi, N.G. & Uhart, M.M. (2006) Numerical and spatial responses of geoffroy's cat (*Oncifelis geoffroyi*) to prey decline in Argentina. *Journal of Mammalogy*, **87**, 1132–1139.
Reichmann, A. & Saltz, D. (2005) The Golan wolves: the behavioral ecology and dynamics of an endangered pest. *Israel Journal of Zoology*, **51**, 87–133.
Revilla, E. (2003) Moving beyond the resource dispersion hypothesis. *Trends in Ecology and Evolution*, **18**, 380.
Reynolds, J.C. & Tapper, S.C. (1996) Control of mammalian predators in game management and conservation. *Mammal Review*, **26**, 127–155.
Saltz, D. (1994) Reporting error measures in radio location by triangulation - a review. *Journal of Wildlife Management*, **58**, 181–184.
Saltz, D., Kaplan, D., Loten, R. & Dgani, G. (2002) *Building a Predator/Pray Model for Establishing an Interface Policy for the Prevention of Further Decline and Rehabilitation as well as Insuring the Viability Over Time of the Gazelle Population in the Golan Heights (in Hebrew)*. The Ministry of Science and Technology, Jerusalem, Israel.
Saunders, G., Coman, B., Kinnear, J. & Braysher, M. (1995) *Managing Vertebrate Pests: Foxes*. Australian Government Publishing Service, Canberra, Australia.
Sillero-Zubiri, C. & Switzer, D. (2004) Management of wild canids in human-dominated landscapes. *Canids: Foxes, Wolves, Jackals and Dogs* (eds C. Sillero-Zubiri, M. Hoffmann & D.W. Macdonald), pp. 257–266. Information Press Oxford, UK.
Silverman, B.W. (1986) *Density Estimation for Statistics and Data Analysis*. Chapman and Hall, London.
Swarner, M. (2004) *Human-Carnivore Conflict over Livestock: The African Wild Dog in Central Botswana*. Breslauer Symposium on Natural Resource Issues in Africa, Center for African Studies, UC Berkeley.
Treves, A. & Karanyh, K.U. (2003) Human-carnivore conflict and perspective on carnivore management worldwide. *Conservation Biology*, **17**, 1491–1499.
White, G.C. & Burnham, K.P. (1999) Program MARK: survial estimation from populations of marked animals. *Bird Study*, **46**, S120–S138.
Woollard, T. & Harris, S. (1990) A behavioural comparison of dispersing and non-dispersing foxes (*Vulpes vulpes*) and an evaluation of some dispersal hypothesis. *Journal of Animal Ecology*, **59**, 709–722.
Worton, B.J. (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, **70**, 164–168.
Yakobson, A.B. (2007) *Current Situation of Rabies in Israel*. (In Hebrew) http://agri3.huji.ac.il/~yakobson/rabheb/ [accessed on 10/09/10]. Kimron Veterinary Institute, Israel.
Yom-Tov, Y., Ashkenazi, S. & Viner, O. (1995) Cattle Predation by the Golden Jackal Canis aureus in the Golan-Heights, Israel. *Biological Conservation*, **73**, 19–22.
Yom-Tov, Y. & Mendelssohn, H. (1988) The zoogeography of Israel: changes in distribution and abundance of vertebrates in Israel during the 20th century. *The Distribution and Abundance at a Zoogeographical Crossroad* (eds Y. Yom-Tov & E. Tchernov), pp. 515–547. Dr. W. Junk Publishers, Dordrecht, the Netherlands.

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