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Poor health is associated with use of anthropogenic resources in an urban carnivore

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Rates of encounters between humans and wildlife are increasing in cities around the world, especially when wildlife overlap with people in time, space and resources. Coyotes (*Canis latrans*) can make use of anthropogenic resources and reported rates of conflict have increased in cities across North America. This increase may be linked to individual differences in the use of human food and developed areas. We compared the relationships between coyote age, sex or health and the use of anthropogenic resources, which we defined as using developed areas over large home ranges, being active during the day, and consuming anthropogenic food. To do so, we applied GPS collars to 19 coyotes and sampled hair for stable isotope analysis. Eleven coyotes appeared to be healthy and eight were visibly infested with sarcoptic mange (*Sarcoptes scabiei*), a mite that causes hair loss. Diseased coyotes used more developed areas, had larger monthly home ranges, were more active during the day, and assimilated less protein than coyotes that appeared to be healthy. We speculate that anthropogenic food provides a low-quality but easily accessible food source for diseased coyotes, which in turn may increase reliance on it and other anthropogenic resources to promote encounters with people.

1. Introduction

There is mounting global pressure to minimize negative interactions between people and wildlife while maintaining wildlife populations and functional ecosystems, emphasizing the need to understand the causes of human–wildlife conflict [1]. Urban areas are the fastest-growing ecosystems on the Earth [2] and have some of the highest rates of human–wildlife conflict because they have high densities of people, anthropogenic attractants and urban-adapted wildlife [3]. Conflicts can arise when wildlife are attracted to anthropogenic resources that provide food, shelter and breeding sites, including damage to property, transmission of zoonotic disease and depredation on pets or livestock (reviewed in [4]). For example, raccoons (*Procyon lotor*) that den in houses can damage buildings and spread raccoon roundworm (*Baylisascaris procyonis*) to humans [5]. Carnivores may attack pets, e.g. red foxes (*Vulpes vulpes*) in Europe [6], and even people, e.g. tigers (*Panthera tigris*) in Russia [7]. These actions are often preceded by behavioural cues that reveal habituation to people, such as frequenting human-dominated areas [8], being active during daylight hours [9], and eating anthropogenic food [10]. These behaviours create potential for food conditioning, wherein wildlife associate humans with food either through intentional or unintentional feeding, which often results in human–wildlife conflict, particularly when it involves carnivores [11,12].

Over the past 20 years, reports of encounters between humans and coyotes (*Canis latrans*) have been increasing in cities across North America [13]. This trend follows decades of increase in the range of coyotes [14], but the reasons for rising conflict are unclear [15] and coyotes appear to vary in their reliance on anthropogenic resources. Many urban coyotes seldom leave natural areas [15–17] where they feed mainly on small mammals and berries [15], but some are known to frequent developed areas where they are more likely to

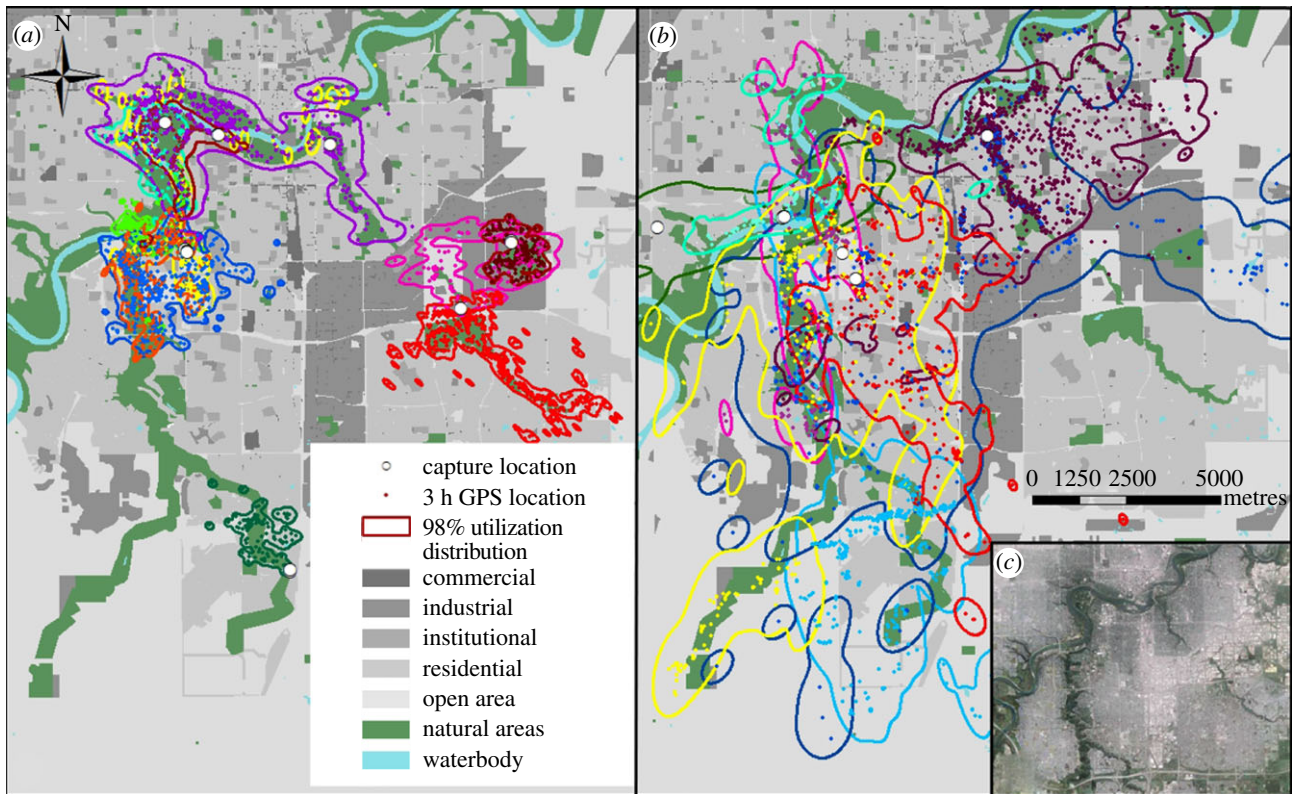


Figure 1. Map of study area showing the capture locations (white circles), 3 h GPS locations (points) and 95% utilization distribution home ranges (polygons) for GPS-collared coyotes that were apparently healthy ($n = 11$; *a*) or were visibly diseased ($n = 8$; *b*). Colours distinguish individual coyotes and land use types, either developed (grey) or urban natural areas (green). (*c*) Aerial photo of map section of Edmonton from Google Earth.

elicit nuisance wildlife reports [13] and where anthropogenic food can comprise up to 30% of their diets [15]. A better understanding of this variation in resource use could identify the contexts, locations and individuals that are most likely to elicit human–coyote conflict.

The use of anthropogenic resources by coyotes could vary for many reasons, including sex, age and health. For example, breeding male coyotes appear to be more prone to killing domestic sheep (*Ovis aries*) [18], perhaps to support their larger body size, which produces similar sex-biased conflict in several other carnivore species [19]. By contrast, dispersing subadult [19] or transient coyotes [17] may be more likely to seek out human-occupied areas because they are relegated to lower-quality habitat with fewer hunting opportunities [20]. Any age or sex class may be infected by disease, which can make animals less afraid of people (e.g. rabies virus [21]), more reliant on easily accessible food [7,22] and less able to tolerate cold temperatures [23], all of which could promote interactions with humans. Rates of disease in urban-adapted species are sometimes higher than in rural areas because of higher densities of animals supported by anthropogenic resources [24], altered community structure that can increase contact between parasites and hosts [25], or from chronic stressors that increase disease susceptibility [26].

Few studies have examined multiple hypotheses for increasing conflict behaviour in coyotes, or any urban carnivore, and examining the effects of disease is especially difficult in wild, free-living animals. This opportunity exists in northwestern North America, where there is a high prevalence of sarcoptic mange [27], which is highly visible because of associated hair loss, skin thickening and lesions [28]. This form of mange is caused by the mite *Sarcoptes scabiei* that causes infected animals to bite and chew at the affected

areas, in turn providing entry routes for secondary infections and other parasites [23,28], reducing thermoregulatory and foraging abilities [23], and can ultimately lead to emaciation and death [28].

In this study, we examined the relationships between three explanatory variables—age, sex and health status—and four measures of anthropogenic resource use: using developed areas both more frequently and over larger home ranges, being active during the day, and consuming anthropogenic food. We assumed that coyotes which made more extensive use of anthropogenic resources or increased spatial and temporal overlap with people would be more likely to elicit conflict reports, which has been linked to habituation and food conditioning [9,11]. Based on the associations reported in the literature, we predicted that coyotes which were young, male or sick would use more developed areas, have larger home ranges, be more active during the day and consume more anthropogenic food.

2. Material and methods

(a) Study area

Our study took place within the city of Edmonton, Alberta, Canada, a northern city (53.5472° N, 113.5006° W) large in both area (684.4 km^2) and population (812 201 in 2011 census) and characterized by warm summers (average temp: 17.5°C), and cold winters (-11.7°C). Edmonton also has a large network of contiguous parkland connected to a central river valley (figure 1) which provides habitat for coyotes, white-tailed deer (*Odocoileus virginianus*), white-tailed jackrabbits (*Lepus townsendii*), snow-shoe hares (*Lepus americanus*), beaver (*Castor canadensis*), and various small mammals. The frequency of human–coyote interactions has increased in

Edmonton over the past several years to generate multiple reports per day throughout the year (A. Murray 2014, unpublished data).

(b) Sample collection

We captured coyotes using four-coil padded foot-hold traps (no. 3 Victor Soft Catch Coilspring; Animal Trap Co., Lilitz, Pennsylvania, PA, USA) and physically restrained captured coyotes using catch poles. We selected capture sites where coyote sightings had been reported to city officials and dogs were prohibited to minimize their accidental capture. Our capture sites ranged in their proximity to human development and included several urban natural areas, the natural area bordering a zoo, and an agricultural research facility surrounded by residential areas (figure 1) but were all within city limits (6.2 ± 3.1 km s.d. of city centre). Captured coyotes were aged as either sub-adult (less than 1 year old) or adult (greater than or equal to 1 year old) by tooth wear [29], sexed, weighed, ear tagged, fitted with a global positioning system (GPS) collar and a hair sample was collected for stable isotope analysis. Coyotes were fitted with collars that acquired locations every 3 h that were either stored and downloaded after collars were recovered (Lotek 3300S), downloaded remotely (Lotek 4400S) or communicated via the cell phone network (Wildcell GSM collar; Lotek Wireless Inc., Newmarket, Ontario, Canada). Most coyotes were collared in the dispersal season (September–December) and wore their collars for an average of four months (range: 1–10 months, electronic supplementary material, table S1). To account for different durations of monitoring, we weighted the spatial data from each coyote by the number of months the coyote was collared or used monthly averages to compare individuals. We assessed disease status (i.e. mange) by the presence of hair loss, skin thickening and lesions on the hind legs and tail at time of capture. We used an ordinal body condition score as follows: 1 = $\leq 10\%$ of body affected, usually the back of hind legs; 2 = 10–25% of body affected, usually back of hind legs and tail; 3 = 25–50%; 4 = 50–75%; 5 = 75–100% (figure 2, electronic supplementary material, table S1). We also radio-tracked coyotes periodically to monitor body condition and recorded any visible changes in mange severity. The coyotes we classified as appearing healthy were not screened for other ailments, but they all exhibited good coat quality, some body fat and no apparent health problems.

(c) Space use

We calculated three metrics of space use to test whether male, sub-adult or parasitized coyotes were more likely to overlap with people in space and time. To compare habitat use, we condensed six land cover classes into two habitat types based on the presence of human activity and infrastructure: developed (residential, commercial, industrial, institutional, and open areas that were undesignated and typically composed of mown grass; 93% of available habitat) and undeveloped (urban ravines and parks; 7% of available habitat; figure 1). We measured differences in habitat selection within our study area (second order habitat selection; [30]) by comparing the habitat type at each used GPS location to one available location generated randomly within a minimum convex polygon around all coyote locations using GEOSPATIAL MODELLING ENVIRONMENT [31]. We then used logistic regression to model the probability of a location being used or available as a function of the habitat type at the location (i.e. developed or undeveloped) and the age, sex and health status of the associated coyote. Landcover data provided by the City of Edmonton (2010) had a spatial resolution of 10 m. For those locations that occurred on an ecotone we used the land cover class covering the majority of a 10 m buffer around the location to account for collar error [32]. We also estimated monthly home range sizes for individual coyotes using 95% kernel density utilization

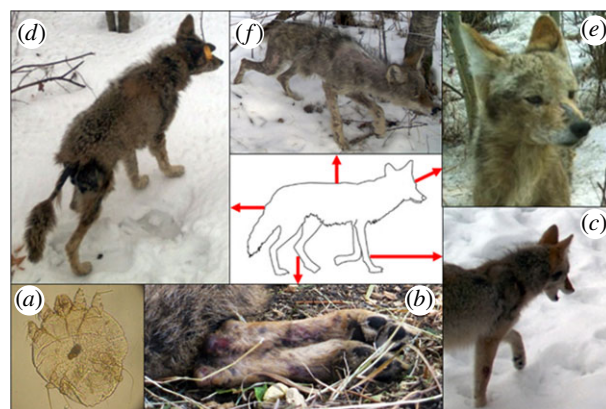


Figure 2. Signs of sarcoptic mange *Sarcoptes scabiei* (a) used to visually assess coyote health status at time of capture. Coyotes we classified as exhibiting mange at time of capture had lesions on (b) hind legs and (c) forelegs which could progress to the tail (d), the face (e) and in severe cases, over the whole body (f). Photo credit (a) Wikimedia, all others from authors.

distributions generated using a plug-in bandwidth estimator in GEOSPATIAL MODELLING ENVIRONMENT [33].

To determine whether individual coyotes were similarly active at different times of day, we measured step lengths, which we defined as the distance travelled between successive 3 h locations. We then modelled step length as a function of coyote age, sex, health and time period. We defined time periods as during the day (from 1 h after sunrise to 1 h before sundown), crepuscular (± 1 h from sunrise or sundown) and night (1 h after sundown to 1 h before sunrise) with adjustment to reflect seasonal changes in day length.

(d) Diet

We examined differences in the diets of individual coyotes by analysing hair samples collected at capture using stable isotope analysis. Guard hairs were collected from the nape of the neck and prepared for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope analysis following the methods of Hilderbrand *et al.* [34]. We expected stable isotope analysis to provide a measure for assimilation of anthropogenic food into body tissue because corn, as a C4 plant, has a conspicuously high $\delta^{13}\text{C}$ signature and is ubiquitous in processed food in the form of corn syrup and starch [35]. Stable isotope analysis can also provide an estimate of trophic level because $\delta^{15}\text{N}$ correlates with protein ingestion [36]. We used the results of previous studies of coyote diet based on scat contents [37,38] to identify several food sources for inclusion in our analysis as reference samples. For each of 18 dietary items, we sampled at least three sources for their stable isotopic signatures, which we categorized *a priori* into three groups based on the similarity of their ^{13}C and ^{15}N values. We grouped mammals and insects known to be consumed by coyotes as prey: white-tailed deer, beaver, muskrat (*Ondatra zibethicus*), cricetid rodents, sciurids, lagomorphs and insects. We also grouped several species of fruit that are common in Edmonton: crabapples (*Malus* spp.), Saskatoon berries (*Amelanchier alnifolia*), blueberries (*Vaccinium* spp.) and raspberries (*Rubus idaeus*). Lastly, we grouped several sources of anthropogenic food that are at least partly derived from corn products: human hair (which provided an estimate of human diet), domestic cats (*Felis catus*) and dogs (*Canis lupus familiaris*), pet food, food waste from compost piles, and published isotopic values for chicken and beef [39], which provided estimates of scavenged meat.

To determine whether coyotes consumed relatively more prey, fruit or anthropogenic food, we built three-source mixing models using the program SIAR [40]. Such models provide a framework for testing hypotheses about diet because they provide a

Table 1. Summary of candidate model outputs for coyote habitat selection, home range size, activity patterns, and diet. (We used model weights, calculated using corrected Akaike information criterion (AICc) scores, to calculate weighted-average parameter estimates. Entries in bold indicate the largest model-averaged parameter estimate for each response variable.)

behavioural metric (response variable)	model terms	ΔAICc	w_i	D^2	model-averaged $\beta \pm \text{s.e. (term)}$
habitat selection (used or available)	global (all terms)	0	1.00	0.24	
	health + health \times habitat type	110	0.00	0.21	1.34 \pm 0.28 (health \times habitat type)
	age + age \times habitat type	491	0.00	0.07	0.504 \pm 0.23 (age \times habitat type)
	sex + sex \times habitat type	637	0.00	0.07	0.076 \pm 0.032 (sex \times habitat type)
	null model (intercept)	2922	0.00	0.00	
home range size (km ²)	health	0.00	0.66	0.22	1.75 \pm 0.12 (health)
	global (all terms)	2.53	0.19	0.27	
	sex	4.40	0.073	0.09	0.30 \pm 0.024 (sex)
	null model (Intercept)	4.90	0.057	0.00	
	age	7.00	0.020	0.02	-0.052 \pm 0.003 (age)
activity patterns (m)	global (all terms)	0.00	1.00	0.26	
	health + health \times time period	269	0.00	0.21	1.04 \pm 0.13 (health \times time period)
	age + age \times time period	7255	0.00	0.17	-0.324 \pm 0.078 (age \times time period)
	sex + sex \times time period	7320	0.00	0.15	-0.0193 \pm 0.021 (sex \times time period)
	null model (intercept)	9421	0.00	0.00	
changes in diet ($\delta^{13}\text{C}$)	age	0.00	0.30	0.10	-0.23 \pm 0.11 (age)
	global model (all terms)	0.53	0.23	0.23	
	null model (intercept)	0.63	0.22	0.00	
	health	1.44	0.14	0.05	0.10 \pm 0.031 (health)
	sex	1.92	0.11	0.02	-0.082 \pm 0.027 (sex)
changes in diet ($\delta^{15}\text{N}$)	health	0	0.49	0.19	-0.57 \pm 0.34 (health)
	null model (intercept)	2.16	0.17	0.00	
	global model (all terms)	2.36	0.15	0.22	
	age	2.94	0.11	0.03	-0.037 \pm 0.061 (age)
	sex	3.57	0.082	0.01	0.033 \pm 0.022 (sex)

deterministic solution for estimating the probability that each food item accounts for a given proportion of the consumer's diet [41]. We assumed that fractionation rates were isotope-specific across dietary sources and accounted for digestibility following the methods of Newsome *et al.* [42].

We measured the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope signatures of individual coyotes and diet sources using an elemental analyser (EuroEA Elemental Analyzer, EuroVector) and a continuous-flow isotope ratio mass spectrometer (Isoprime Mass Spectrometer, GV Instruments) at the Biogeochemical Analytical Service Laboratory (Department of Biological Sciences, University of Alberta, Edmonton, Canada). These instruments had a measurement standard deviation of ± 0.1 and $\pm 0.3\%$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements, respectively.

(e) Model building and selection

We evaluated our hypotheses that one or more of coyote age, sex and health status best explained variation in coyote habitat selection, home range size, activity patterns and diet by ranking candidate models (*sensu* [43]). For each of our four response variables, we built five candidate models: a null model, a model for each of age, sex and health (and their interactions with habitat type for habitat selection and time period for activity patterns), and a global model that included all terms (table 1). We then

ranked these candidate models based on their Akaike information criterion scores (corrected for small sample size; AICc) and corresponding model weights. From all models in which each covariate appeared, we calculated an average parameter estimate after adjusting the contribution of each model by its weight [43,44]. We used mixed effects models of three types depending on the best-fitting distribution of the dependent variables; generalized linear mixed model (GLMM) with a logistic link for habitat selection, a linear mixed effects model for home range size and assimilated diet, and a GLMM with a Poisson distribution for diel patterns of activity via step lengths. We partitioned the effect of individual by including animal identification as a random effect and accounted for temporal non-independence of successive GPS fixes by including an autocorrelation function (function AR1 in R with a lag of one 3 h step [45]) in our analysis of habitat selection and activity patterns. We assessed the fit of each candidate model using the proportion of explained deviance (D^2) because it can be used across different model types [46].

3. Results

Between 2009 and 2012, we captured and sampled 21 coyotes of which 19 wore functional GPS collars and were included in

our spatial analyses. Eleven of the 21 sampled coyotes had good coat quality and appeared to be healthy (hereafter 'healthy') and 10 coyotes exhibited signs of mange (hereafter 'diseased'), but only eight of these had sufficient data for inclusion in our spatial analyses. The healthy coyotes we collared included five adult females, two subadult females, two adult males and two subadult males; and the diseased coyotes we collared included four adult females, one subadult female, two adult males and one subadult male. Sex and age classes were balanced across healthy and diseased coyotes in the 19 collared coyotes ($G_{\text{Age} \times \text{Mange}} = 0.12$, d.f. = 1, $p = 0.74$; $G_{\text{Sex} \times \text{Mange}} = 0.28$, d.f. = 1, $p = 0.60$). Coyotes that exhibited signs of mange at their times of capture typically had mild or moderate infestations and became more severely affected over time, no coyotes with mange appeared to have recovered and no coyotes we considered to be healthy when captured exhibited signs of mange while they were monitored (electronic supplementary material, table S1). Over the study period, six of the 10 diseased study coyotes died; four from exposure (i.e. were found dead in sleeping positions in -20°C temperatures) and two were euthanized following reports of conflict by the public. Of these, three coyotes were necropsied at the University of Calgary where the presence of *S. scabiei* mites and/or alopecia consistent with sarcoptic mange infestation was confirmed (A. Massolo University of Calgary 2010 and 2012, personal communication). Of the 11 healthy coyotes, four were killed by collisions with vehicles.

Comparing the model-averaged parameter estimates revealed which of age, sex or health status best explained variation in each of habitat selection, home range size, activity patterns and diet. Health status was the most important variable for each of habitat selection, home range size, activity patterns and $\delta^{15}\text{N}$ (protein) assimilation (table 1). Coyote age had the most support for $\delta^{13}\text{C}$ (processed food) assimilation (table 1).

The monthly home ranges of diseased coyotes were an average of 3.9 times larger than those of healthy coyotes ($U_{10,7} = 88$, $p < 0.001$; figures 1 and 3a). The home ranges of diseased coyotes also overlapped in space and time with at least one other coyote, whereas those of healthy coyotes did not overlap in both space and time. Diseased coyotes also had 5.5 times more GPS fixes in developed areas than did healthy coyotes ($\beta_{\text{Intercept}} = 0.62 \pm 0.05$ s.e., $\beta_{\text{Mange}} = -0.32 \pm 0.08$, $\beta_{\text{Developed}} = -2.10 \pm 0.05$, $\beta_{\text{Mange} \times \text{Developed}} = 1.38 \pm 0.06$, $p < 0.001$; figure 3b). Diseased and healthy coyotes were similarly active overall (diseased = $618.42 \text{ m/step} \pm 925.88$ s.d.; healthy = 591.91 ± 876.09 ; $p = 0.624$). Healthy coyotes were more active at night than during the day, whereas diseased coyotes were similarly active during all three time periods and 2.2 times more active during the day than healthy coyotes ($\beta_{\text{Intercept}} = -0.10 \pm 0.08$, $\beta_{\text{Mange}} = -0.01 \pm 0.13$, $\beta_{\text{Time}} = -0.72 \pm 0.02$, $\beta_{\text{Mange} \times \text{Time}} = 1.52 \pm 0.03$, $p < 0.001$; figure 3c).

Diseased coyotes assimilated only 60% as much dietary nitrogen as healthy coyotes, a difference of approximately one trophic level [36] ($U_{11,10} = 27$, $p = 0.009$; figure 4a). Based on the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of our reference samples, the SIAR mixing model estimated that diseased coyotes assimilated 32.8% more anthropogenic food and 87.2% less prey than healthy coyotes (figure 4b). Coyote age had the most model support for differences in the assimilation of $\delta^{13}\text{C}$ (processed anthropogenic food), however, the difference in model support for age, sex and health was small; all models had AICc scores \leq

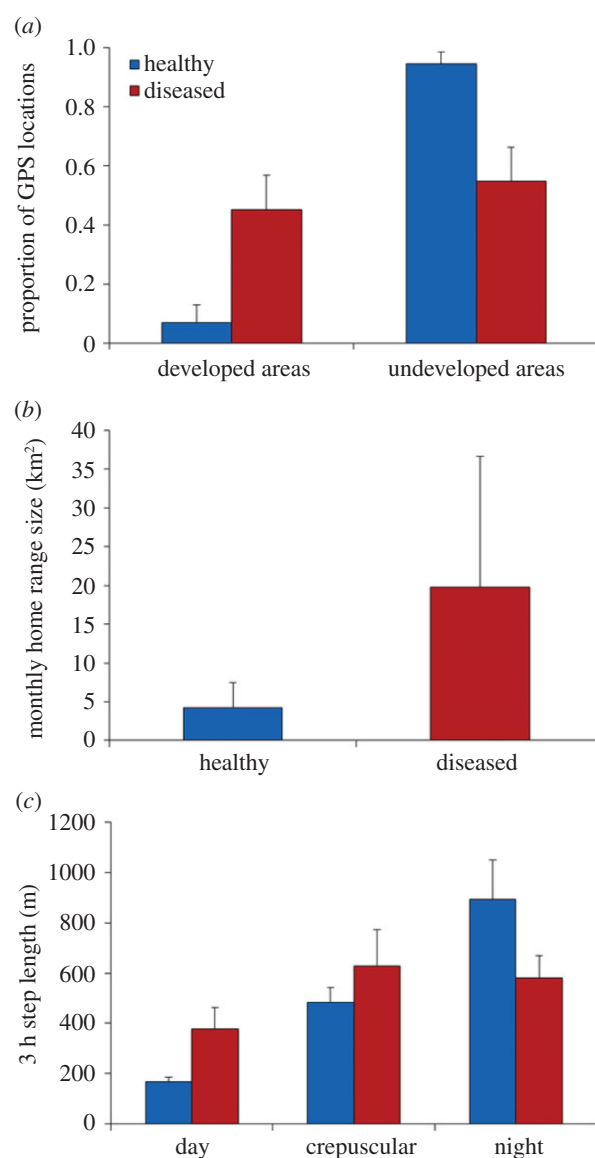


Figure 3. Differences in space use between apparently healthy ($n = 11$; blue) and coyotes with visible ectoparasite infestations ($n = 8$; red), including (a) habitat selection, (b) home range size and (c) activity patterns. Columns show averages across individuals and bars show standard deviations.

2 points from each other (table 1). Adult coyotes assimilated only 5% more $\delta^{13}\text{C}$ than did subadults ($\delta^{13}\text{C}_{\text{Adults}} = -22.33 \pm 0.82$, $\delta^{13}\text{C}_{\text{Subadults}} = -21.24 \pm 1.67$; $U_{10,9} = 113$, $p = 0.09$).

4. Discussion

Although rates of conflict with coyotes appear to have increased throughout North America [13], there is no general explanation for the mechanism. We evaluated three existing hypotheses for higher rates of conflict in other carnivores—sex, age and health status—and related these variables to four measures of using anthropogenic resources that we considered to be precursors of conflict with people. Health status was most associated with all four of these behaviours; coyotes with hair loss and lesions consistent with mange infestation made more use of developed areas, had larger home ranges, were more active during daylight hours, assimilated less protein and consumed more anthropogenic food (as estimated by our mixing model) than coyotes that appeared to be healthy at their times of capture.

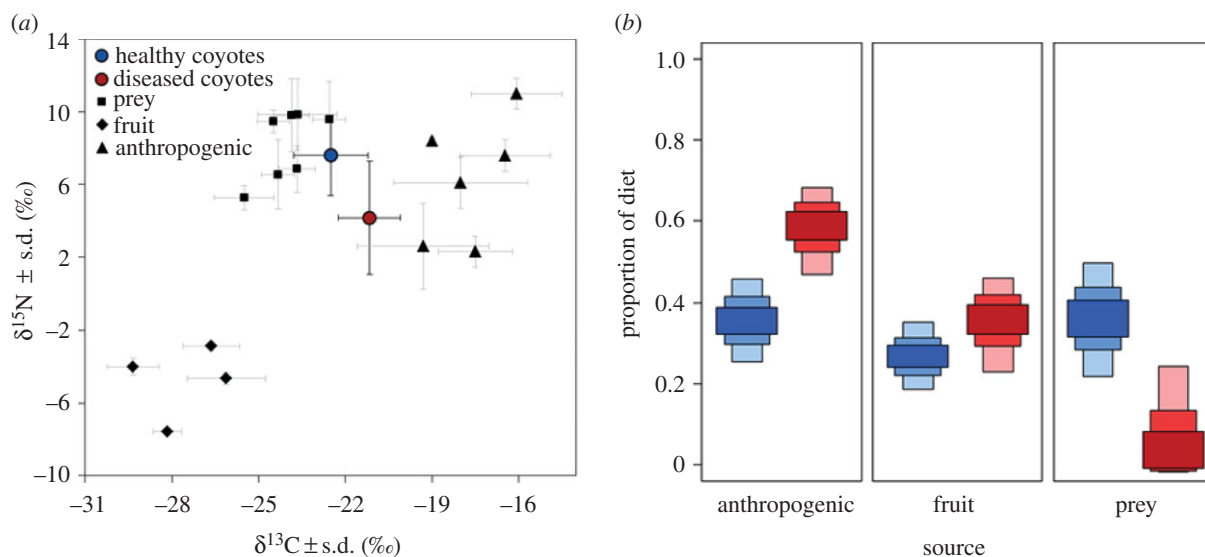


Figure 4. Assimilated diets of urban coyotes. (a) Isotopic $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures for visibly diseased ($n = 11$, red) and healthy ($n = 12$, blue), and food sources we grouped as prey (squares), fruit (diamonds) and anthropogenic food (triangles). Bars show standard deviations. (b) Proportional contribution of anthropogenic food, fruit and prey to the diet of healthy and diseased coyotes as modelled by a three-source mixing model (SIAR). Bars show the 50, 75 and 95% CIs, respectively, with lighter shades.

Diseased coyotes used developed areas more frequently than did healthy coyotes, and this suggests that they had a greater tolerance of human development and human presence, both of which are indicators of habituation and precursors of conflict in many contexts, including injured tigers [7] and nutritionally stressed polar bears (*Ursus maritimus*; [22]). Diseased coyotes also ranged over much larger areas than other coyotes and their home ranges were less exclusive, suggesting that diseased coyotes had similar home ranges as transient individuals that do not maintain territories [17,20]. Such transient behaviour often characterizes young individuals [47], but we found no difference in age between healthy and diseased coyotes. In other areas, transient coyotes may be more likely to be in poor condition [48] because they typically use less suitable habitat on the fringes of resident coyote home ranges [20], which may manifest as developed areas in the urban landscape [17]. In this way, differences in health between individual coyotes may be related to their social status and habitat use. For example, healthy individuals that range widely as transients might be more likely to encounter unrelated coyotes, thereby potentially increasing their exposure to infected individuals [49]. Conversely, animals that are already sick or otherwise subordinate may be less capable of defending territories [48], more reliant on easily accessible food, and more likely to range widely to find it. Despite having much larger home ranges, diseased coyotes were not significantly more active. We suspect that residential and commercial areas may contain relatively more unsuitable habitat such as buildings and other impervious surfaces relative to urban natural areas and thus animals may range more widely but use proportionately less of their home range [17].

Diurnal activity may be an especially important precursor to human–coyote conflict because temporal avoidance of humans by carnivores is widespread and may be important for coexistence between wildlife and humans in developed areas. For example, bobcats (*Lynx rufus*) [50], wolves (*Canis lupus*; [51]) and tigers [52] all exhibit lower activity levels during the day where they overlap spatially with humans. The lack of nocturnal behaviour exhibited by diseased coyotes in our study corroborates anecdotes that diseased coyotes are

more likely to encounter people and approach houses during the day [17,23] and could have resulted from compromised thermoregulatory ability, in turn caused by hair loss [23]. Sub-zero temperatures in the winter months could encourage the use of developed areas in our northern study area by offering shelter under buildings. The costs of compromised thermoregulation may be considerable as several diseased coyotes died of exposure during the study period.

The greater importance of anthropogenic food in the diet mixing model of diseased coyotes is an important precursor of potential conflict because it increases the likelihood an individual will become food conditioned [11]. Urban coyotes tend to consume mainly small rodents and berries, however, the extent to which they are reliant on human food varies across cities [15] and, as demonstrated in our study, among individuals. In general, conflicts between humans and wildlife are more likely to arise when animals are reliant on human food, rather than simply tolerant to human disturbance [12,11]. In our study area, coyotes are often seen in alleys where there is accessible waste, and composting is a common but unmanaged practice (City of Edmonton, personal communication). Food waste in compost piles is probably one important food source for the diseased coyotes we sampled as it has conspicuously low protein content and is common in residential areas.

As with health status and habitat use, the relatively protein-poor diets exhibited by diseased coyotes could be both a cause and consequence of the lower-quality diet that anthropogenic waste provides. In general, animals eating a low-protein diet, along with low fat reserves or with high parasite loads, can suffer from immunosuppression and increased energy requirements [53,54]. Sarcoptic mange infestation appears to compromise hunting ability in red foxes because infested individuals have reduced fat reserves and evidence of malnutrition [55]. Further, bobcats and cougars (*Puma concolor*) that use more developed areas are more likely to be exposed to rodenticides, which in turn are linked to mange infestation [56] and have been detected in urban coyotes [57]. Once established, either of disease, poor nutrition or poor hunting ability could be exacerbated by

the other, creating a 'vicious circle' of low-quality diet, poor body condition and disease susceptibility [58] that has been documented in several other species [59,60] including humans [61].

The larger home ranges in developed urban areas, increased diurnal activity and reliance on anthropogenic food by diseased coyotes are likely to increase the rate at which they encounter people, pets and other coyotes. By increasing encounter rates, these behaviours in turn may be contributing to the rise in well-publicized reports of coyote encounters in many North American cities and the corresponding steady increase in public demand for more active coyote management [13]. If cities promote the survival of otherwise moribund animals by providing easily accessible food, or promote the transmission of parasites at communal feeding sites [26], the relationships we have observed between health and conflict behaviour may become more prevalent. This may also partly explain why the majority of urban coyotes do not appear to exhibit conflict behaviour [15] despite more frequent reports of human–coyote conflict [62].

Our results suggest that disease may be an underappreciated aspect of human–coyote conflict with two important implications for urban residents and wildlife managers. First, if wildlife disease can promote behaviours that may lead to conflict, wildlife managers should aim to reduce disease prevalence and avoid passive reliance on disease to regulate wildlife populations (e.g. [63]) in urban areas, particularly for diseases that can be transmitted to people (e.g. [64]). Second, although disease prevalence and spread could potentially be reduced by selectively removing highly diseased animals, reliance on lethal management may be reduced by identifying and securing hyper-abundant but low-quality

anthropogenic food waste. Reducing coyote access to neighbourhood compost, fallen fruit, birdseed, rubbish and other waste food could be achieved with a combination of education and by-law creation. Both of these management implications may generalize to other species, locations and contexts of human–wildlife conflict to promote positive experiences for urbanites with coyotes and other urban-adapted wildlife around the world.

Ethics statement. All animal handling was in accordance with the guidelines of the University of Alberta Animal Care and Use Committee and Canadian Council on Animal Care.

Data accessibility. The GPS location dataset used in this manuscript is stored in Dryad doi:10.5061/dryad.9mt2v.

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References

- Treves A, Karanth KU. 2003 Human-carnivore conflict and perspectives on carnivore management worldwide. *Conserv. Biol.* **17**, 1491–1499. (doi:10.1111/j.1523-1739.2003.00059.x)
- Angel S, Parent J, Civco DL, Blei AM. 2011 *Making room for a planet of cities*. Cambridge, MA: Lincoln Institute of Land Policy.
- Ditchkoff SS, Saalfeld ST, Gibson CJ. 2006 Animal behavior in urban ecosystems: modifications due to human-induced stress. *Urban Ecosyst.* **9**, 5–12. (doi:10.1007/s11252-006-3262-3)
- Sillero-Zubiri C, Sukumar R, Treves A. 2006 Living with wildlife: the roots of conflict and the solutions. In *Key topics in conservation biology* (eds D MacDonald, K Service), pp. 255–272. New York, NY: Wiley-Blackwell.
- Page LK, Gehrt SD, Robinson NP. 2008 Land-use effects on prevalence of raccoon roundworm (*Baylisascaris procyonis*). *J. Wildl. Dis.* **44**, 594–599. (doi:10.7589/0090-3558-44.3.594)
- Contesse P, Hegglin D, Gloor S, Bontadina F, Deplazes P. 2004 The diet of urban foxes (*Vulpes vulpes*) and the availability of anthropogenic food in the city of Zurich, Switzerland. *Mamm. Biol.* **69**, 81–95. (doi:10.1078/1616-5047-00123)
- Goodrich JM, Seryodkin I, Miquelle DG, Berezuk SL. 2011 Conflicts between Amur (Siberian) tigers and humans in the Russian Far East. *Biol. Conserv.* **144**, 584–592. (doi:10.1016/j.biocon.2010.10.016)
- Prange S, Gehrt SD, Wiggers EP. 2004 Influences of anthropogenic resources on raccoon (*Procyon lotor*) movement and spatial distribution. *J. Mammal.* **85**, 483–490. (doi:10.1644/B05-121)
- Schmidt RH, Timm RM. 2007 Bad dogs: why do coyotes and other canids become unruly? In *Proc. 12th Wildlife Damage Management Conference*, pp. 287–302. Lincoln, NE: University of Nebraska.
- McCarthy TM, Seavoy RJ. 1994 Reducing non-sport losses attributable to food conditioning: human and bear behavior. *Bears: Biol. Manag.* **9**, 75–84.
- Herrero S. 1985 *Bear attacks: their causes and avoidance*. Piscataway, NJ: Winchester Press.
- Hopkins JB, Koch PL, Schwartz CC, Ferguson JM, Greenleaf SS, Kalinowski ST. 2012 Stable isotopes to detect food-conditioned bears and to evaluate human-bear management. *J. Wildl. Manage.* **76**, 703–713. (doi:10.1002/jwmg.318)
- White LA, Gehrt SD. 2009 Coyote attacks on humans in the United States and Canada. *Hum. Dimens. Wildl.* **14**, 419–432. (doi:10.1080/10871200903055326)
- Gompper ME. 2002 Top carnivores in the suburbs? Ecological and conservation issues raised by colonization of North-Eastern North America by coyotes. *Bioscience* **52**, 185–190. (doi:10.1641/0006-3568(2002)052[0185:TCITSE]2.0.CO;2)
- Gehrt SD, Riley SPD. 2010 Coyotes (*Canis latrans*). In *Urban carnivores: ecology, conflict, and conservation* (eds SD Gehrt, SPD Riley, BL Cypher), pp. 79–95. Baltimore, MD: The Johns Hopkins University Press.
- Grinder MI, Krausman PR. 2001 Home range, habitat use, and nocturnal activity of coyotes in an urban environment. *J. Wildl. Manage.* **65**, 887–898. (doi:10.2307/3803038)
- Gehrt SD, Anchor C, White LA. 2009 Home range and landscape use of coyotes in a metropolitan landscape: conflict or coexistence? *J. Mammal.* **90**, 1045–1057. (doi:10.1644/08-MAMM-A-277.1)
- Blejwas KM, Williams CL, Shin GT, McCullough DR, Jaeger MM. 2006 Salivary DNA evidence convicts breeding male coyotes of killing sheep. *J. Wildl. Manage.* **70**, 1087–1093. (doi:10.2193/0022-541X(2006)70[1087:SDECBM]2.0.CO;2)
- Linnell JDC, Odden J, Smith M, Aanes R, Swenson JE. 1999 Large carnivores that kill livestock: do 'problem individuals' really exist? *Wildl. Soc. Bull.* **27**, 698–705.

20. Kamler JF, Gipson PS. 2000 Space and habitat use by resident and transient coyotes. *Can. J. Zool.* **78**, 2106–2111. (doi:10.1139/z00-153)
21. Randall DA *et al.* 2004 Rabies in endangered Ethiopian wolves. *Emerg. Infect. Dis.* **10**, 2214–2217. (doi:10.3201/eid1012.040080)
22. Towns L, Derocher AE, Stirling I, Lunn NJ, Hedman D. 2009 Spatial and temporal patterns of problem polar bears in Churchill, Manitoba. *Polar Biol.* **32**, 1529–1537. (doi:10.1007/s00300-009-0653-y)
23. Samuel W, Pybus MJ, Kocan AA. 2001 *Parasitic diseases of wild mammals*, 2nd edn. Ames, IA: Iowa State University Press.
24. Wright AN, Gompper ME. 2005 Altered parasite assemblages in raccoons in response to manipulated resource availability. *Oecologia* **144**, 148–156. (doi:10.1007/s00442-005-0018-3)
25. Deplazes P, Hegglin D, Gloor S, Romig T. 2004 Wilderness in the city: the urbanization of *Echinococcus multilocularis*. *Trends Parasitol.* **20**, 77–84. (doi:10.1016/j.pt.2003.11.011)
26. Bradley CA, Altizer S. 2007 Urbanization and the ecology of wildlife diseases. *Trends Ecol. Evol.* **22**, 95–102. (doi:10.1016/j.tree.2006.11.001)
27. Todd AW, Gunson JR, Samuel WM. 1981 Sarcopic mange, an important disease of coyotes and wolves of Alberta, Canada. In *Worldwide Furbearer Conference Proceedings* (eds JA Chapman, D Pursley), pp. 706–729, Frostburg, MD.
28. Pence DB, Windberg LA, Pence BC, Sprowls R. 1983 The epizootiology and pathology of sarcoptic mange in coyotes, *Canis latrans*, from South Texas. *J. Parasitol.* **69**, 1100–1115. (doi:10.2307/3280873)
29. Bowen WD. 1982 Determining age of coyotes, *Canis latrans*, by tooth sections and tooth-wear patterns. *Can. Field Nat.* **96**, 339–341.
30. Johnson DH. 1980 The comparison of usage and availability measurements for evaluating resource preference. *Ecology* **6**, 65–71. (doi:10.2307/1937156)
31. Beyer HL. 2012 Geospatial modelling environment (version 0.7.2.0) (software). See <http://www.spatial ecology.com/gme/>.
32. Rettie WJ, McLoughlin PD. 1999 Overcoming radiotelemetry bias in habitat-selection studies. *Can. J. Zool.* **1184**, 1175–1184. (doi:10.1139/z99-079)
33. Gitzen RA, Millspaugh JJ, Kernohan BJ. 2006 Bandwidth selection for fixed-kernel analysis of animal utilization distributions. *J. Wildl. Manag.* **70**, 1334–1344. (doi:10.2193/0022-541X(2006)70[1334:BSFFA0]2.0.CO;2)
34. Hilderbrand GV, Farley SD, Robbins CT, Hanley TA, Titus K, Servheen C. 1996 Use of stable isotopes to determine diets of living and extinct bears. *Can. J. Zool.* **74**, 2080–2088. (doi:10.1139/z96-236)
35. Newsome SD, Ralls K, Job CVH, Fogel ML, Cypher BL. 2010 Stable isotopes evaluate exploitation of anthropogenic foods by the endangered San Joaquin kit fox (*Vulpes macrotis mutica*). *J. Mammal.* **91**, 1313–1321. (doi:10.1644/09-MAMM-A-362.1)
36. DeNiro MJ, Epstein S. 1981 Influence of diet on the distribution of nitrogen isotopes in animals. *Geochemica Cosmochim. Acta* **45**, 341–351. (doi:10.1016/0016-7037(81)90244-1)
37. Pruss SD. 2002 Ecology of coyotes (*Canis latrans*) in Elk Island National Park, Alberta, Canada. Thesis, University of Alberta, Edmonton, Alberta, Canada.
38. Morey PS, Gese EM, Gehrt S. 2007 Spatial and temporal variation in the diet of coyotes in the Chicago Metropolitan Area. *Am. Midland Nat.* **158**, 147–161. (doi:10.1674/0003-0031(2007)158[147:SATVIT]2.0.CO;2)
39. Jahren AH, Kraft RA. 2008 Carbon and nitrogen stable isotopes in fast food: signatures of corn and confinement. *Proc. Natl Acad. Sci. USA* **105**, 17 855–17 860. (doi:10.1073/pnas.0809870105)
40. Parnell AC, Inger R, Bearhop S, Jackson AL. 2010 Source partitioning using stable isotopes: coping with too much variation. *PLoS ONE* **5**, e9672. (doi:10.1371/journal.pone.0009672)
41. Moore JW, Semmens BX. 2008 Incorporating uncertainty and prior information into stable isotope mixing models. *Ecol. Lett.* **11**, 470–480. (doi:10.1111/j.1461-0248.2008.01163.x)
42. Newsome SD, Phillips DL, Culleton BJ, Guilderson TP, Koch PL. 2004 Dietary reconstruction of an early to middle Holocene human population from the central California coast: insights from advanced stable isotope mixing models. *J. Archaeol. Sci.* **31**, 1101–1115. (doi:10.1016/j.jas.2004.02.001)
43. Burnham KP, Anderson DR. 2002 *Model selection and inference: a practical information-theoretic approach*. New York, NY: Springer.
44. Hegyi G, Garamszegi LZ. 2010 Using information theory as a substitute for stepwise regression in ecology and behavior. *Behav. Ecol. Sociobiol.* **65**, 69–76. (doi:10.1007/s00265-010-1036-7)
45. Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team. 2012 nlme: linear and nonlinear mixed effects models. R package version 3.1-120. See <http://CRAN.R-project.org/package=nlme>.
46. Midgley GF, Hannah L, Millar D, Thuiller W, Booth A. 2003 Developing regional and species-level assessments of climate change impacts on biodiversity in the Cape Floristic Region. *Biol. Conserv.* **112**, 87–97. (doi:10.1016/S0006-3207(02)00414-7)
47. Windberg LA, Knowlton FF. 1988 Management implications of coyote spacing patterns in southern Texas. *J. Wildl. Manag.* **52**, 632–640. (doi:10.2307/3800922)
48. Pence DB, Windberg LA. 1994 Impact of a sarcoptic mange epizootic on a coyote population. *J. Wildl. Manag.* **58**, 624–633. (doi:10.2307/3809675)
49. Altizer S *et al.* 2003 Social organization and parasite risk in mammals: integrating theory and empirical studies. *Annu. Rev. Ecol. Syst.* **34**, 517–547. (doi:10.1146/annurev.ecolsys.34.030102.151725)
50. Riley SPD, Sauvajot RM, Fuller TK, York EC, Kamradt DA, Bromley C, Wayne RK. 2003 Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. *Conserv. Biol.* **17**, 566–576. (doi:10.1046/j.1523-1739.2003.01458.x)
51. Ciucci P, Boitani L, Francisci F, Andreoli G. 1997 Home range, activity and movements of a wolf pack in central Italy. *J. Zool.* **243**, 803–819. (doi:10.1111/j.1469-7998.1997.tb01977.x)
52. Carter NH, Shrestha BK, Karki JB, Man N, Pradhan B, Liu J. 2012 Coexistence between wildlife and humans at fine spatial scales. *Proc. Natl Acad. Sci.* **109**, 15 360–15 365. (doi:10.1073/pnas.1210490109)
53. Alzaga V, Vicente J, Villanua D, Acevedo P. 2008 Body condition and parasite intensity correlates with escape capacity in Iberian hares (*Lepus granatensis*). *Behav. Ecol. Sociobiol.* **62**, 769–775. (doi:10.1007/s00265-007-0502-3)
54. Taylor AK, Cao W, Vora KP, De La Cruz J, Shieh W-J, Zaki SR, Katz JM, Sambhara S, Gangappa S. 2013 Protein energy malnutrition decreases immunity and increases susceptibility to influenza infection in mice. *J. Infect. Dis.* **207**, 501–510. (doi:10.1093/infdis/jis527)
55. Newman TJ, Baker PJ, Harris S. 2002 Nutritional condition and survival of red foxes with sarcoptic mange. *Can. J. Zool.* **80**, 154–161. (doi:10.1139/Z01-216)
56. Riley SPD, Bromley C, Poppenga RH, Uzal FA, Whited L, Sauvajot RM. 2007 Anticoagulant exposure and notoedric mange in bobcats and mountain lions in urban southern California. *J. Wildl. Manag.* **71**, 1874–1884. (doi:10.2193/2005-615)
57. Poessel SA, Breck SW, Fox KA, Gese EM. 2014 Anticoagulant rodenticide exposure and toxicosis in coyotes in the Denver Metropolitan Area. *J. Wildl. Dis.* **51**, 116. (doi:10.7589/2014-04-116)
58. Beldomenico PM, Begon M. 2010 Disease spread, susceptibility and infection intensity: vicious circles? *Trends Ecol. Evol.* **25**, 21–27. (doi:10.1016/j.tree.2009.06.015)
59. Ezenwa VO. 2004 Interactions among host diet, nutritional status and gastrointestinal parasite infection in wild bovines. *Int. J. Parasitol.* **34**, 535–542. (doi:10.1016/j.ijpara.2003.11.012)
60. Blanchet S, Méjean L, Bourque J-F, Lek S, Thomas F, Marcogliese DJ, Dodson JJ, Loot G. 2009 Why do parasitized hosts look different? Resolving the ‘chicken-egg’ dilemma. *Oecologia* **160**, 37–47. (doi:10.1007/s00442-008-1272-y)
61. Ezzati M, Riboli E. 2012 Can noncommunicable diseases be prevented? Lessons from studies of populations and individuals. *Science* **337**, 1482–1487. (doi:10.1126/science.1227001)
62. Garthwaite J. 2012 *Learning to live with urban coyotes*. New York Times, 24 October 2012.
63. Bellows TS. 2001 Restoring population balance through natural enemy introductions. *Biol. Control* **21**, 199–205. (doi:10.1006/bcon.2001.0936)
64. Liccioli S, Kutz SJ, Ruckstuhl KE, Massolo A. 2014 Spatial heterogeneity and temporal variations in *Echinococcus multilocularis* infections in wild hosts in a North American urban setting. *Int. J. Parasitol.* **44**, 457–465. (doi:10.1016/j.ijpara.2014.03.007)