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Cascading Effects of Anthropogenic Excess Food for Predators on a Peri-Urban Population of an Endangered Ungulate

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ABSTRACT

A major side effect of urbanization is the increased availability of food for wildlife in peri-urban areas. Most research has focused on highly adaptive exploiter species that thrive under such conditions, overlooking avoider species, which are often preyed upon by exploiters. Moreover, peri-urban areas are often grazed by livestock, mainly to reduce the frequency and intensity of fires, a practice that can also adversely affect vulnerable wildlife species. We examined the long-term effects of excess food provided to discourage exploiter species, namely golden jackal (*Canis aureus*) and wild boar (*Sus scrofa*), from foraging on farmland and in human residencies. Both species prey on endangered mountain gazelles (*Gazella gazella*) in our peri-urban study area, which is nested within a mosaic of settlements and agricultural lands in Mediterranean Israel. Because the park is routinely subjected to seasonal cattle ranching, we included cattle stocking rate (mean \pm SD: 51.77 \pm 18.21 cow grazing days/ha) as an alternative factor, into our analysis. We used Generalized Linear Mixed Models to analyze an extensive dataset, comprising 724 surveys conducted over 17 years, and modeled gazelle encounter rates in response to excess food and cattle ranching, while controlling for environmental factors. Our results suggest that anthropogenic excess food through diversionary feeding led to decreasing gazelle densities, probably through increased predation by exploiter species. When diversionary feeding ceased after 12 years, gazelle encounter rates increased. We argue that this increase corresponds to population recovery, although it could be consistent with alternative mechanisms such as altered space-use and movement patterns. To conserve vulnerable and endangered wildlife species in urban and peri-urban areas, managers should reduce the availability of anthropogenic food for predators and scavengers. Furthermore, moderate cattle ranching (i.e., seasonal with low stocking rates) could mitigate potential adverse impacts of cattle ranching on mountain gazelle populations.

1 | Introduction

Since the neolithic revolution, the human footprint has become larger and deeper across ecosystems. Habitat loss and alteration caused by rapid urbanization is one of the leading

reasons for species decline and extinction (Esbah, Cook, and Ewan 2009; Aronson et al. 2014). Additionally, sprawling cities and settlements increasingly fragment the landscape, leading to decreased connectivity among remnant patches of original habitat (Esbah, Cook, and Ewan 2009). Human settlements

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usually come along with a surplus of predictable anthropogenic food sources, which are typically exploited by generalist wildlife species (Oro et al. 2013). Such urban *exploiters* (*sensu* McKinney 2006), adapted to the presence of humans, benefit from various anthropogenic sources of excess food, and thus thrive in urbanized areas (Kark et al. 2007; Angert et al. 2011). Most work conducted on wildlife in urban and peri-urban areas focused on human–wildlife conflicts, particularly on over-abundant exploiter species such as predators or scavengers (Murray et al. 2015; König et al. 2020). In North America, for example, coyotes (*Canis latrans*) evoke negative attitudes among urban residents (Henger et al. 2022; Hunold and Lloro 2022), while in Eurasia, the presence of wild boars (*Sus scrofa*) has become a prominent issue in recent years (Toger et al. 2018; Conejero et al. 2019). In contrast, neighboring populations of *avoider* species (i.e., wildlife that tends to avoid urban or developed areas; *sensu* McKinney 2006) face various stressors including limited mobility (Sawyer et al. 2013), human disturbance (Polfus and Krausman 2012), and competition with livestock (Berdoucou 1986; Mysterud 2000; Mussa et al. 2003; La Morgia and Bassano 2009). Moreover, they often experience a decline of genetic diversity, and thus an increased risk of local extinction, due to the fragmentation and isolation of their natural habitat (Magle et al. 2010). An increase in exploiter abundance may also increase the predation pressure on their prey species (Maeda et al. 2019; Moore et al. 2023), corresponding to the concept of hyperpredation (Courchamp, Langlais, and Sugihara 2000; Roemer et al. 2001; Roemer, Donlan, and Courchamp 2002; Tablado et al. 2010; Maeda et al. 2019), in which, a predator population increases due to the abundance of primary prey (or an anthropogenic food source, such as in our study), and intensifies its hunting pressure on a secondary prey species.

In Israel, 94% of the human population (current population size: 9.4 million) resides in urban areas, and 10%–18% of the land is urbanized. Israel's human population growth (currently 1.63% per annum; Desa 2024) is among the highest in the world, and an ever-growing part of natural habitat is transformed into urban or peri-urban areas (Ben-Moshe and Renan 2022). Among the medium-sized mammals in Israel, two exploiter species essentially benefit from urbanization and excess food, namely golden jackal (*Canis aureus*) and the wild boar (Mendelssohn and Yom-Tov 1999; Yom-Tov et al. 2020). The most prevalent avoider species is the threatened mountain gazelle (*Gazella gazella*). Once widely distributed across the Mediterranean rangelands of the Levante, the IUCN categorizes the mountain gazelle as endangered, with nearly all populations occurring in Israel (IUCN SSC Antelope Specialist Group 2017). Outside Israel, there is one population in Turkey (ca. 1000 individuals; Kirac 2021) and possibly one in Jordan (presumably extinct; Eid, Abu Baker, and Amr 2020). The gazelle population in Israel is estimated at ± 5000 individuals, distributed in relatively isolated, local populations (Yom-Tov et al. 2020).

One of these small, isolated gazelle populations persists in Ramat Hanadiv Nature Park (RHNP), a privately owned conservation area in central Israel. Surrounded by urban areas and farmland, RHNP is representative of many other peri-urban areas in Israel with similar climate, landscape, ecology, and degree of human

disturbance. In 2000, the management of RHNP implemented diversionary feeding of jackals and wild boar to encourage them to stay within the park's boundary, and thus mitigate human–wildlife conflicts with adjacent farmers and urban residents. Diversionary feeding is commonly used to deter wildlife from unwanted activities such as predation of one species on another (Redpath, Thirgood, and Leckie 2001; Finne et al. 2019), crop raiding (Witmer, Nolte, and Stewart 2000; Ziegler 2008), or direct threats to human safety (Kaplan et al. 2011; Rogers 2011; Garshelis et al. 2017). However, if conducted year-round, and/or over extended periods, diversionary feeding has been reported to increase predator abundance, which may adversely affect the abundance of their prey (Kubasiwicz et al. 2016; Finne et al. 2019).

Another threat potentially affecting gazelle populations in peri-urban areas is free-ranging livestock. Along with meat production, cattle in Israel (as in other parts of the world, especially the Mediterranean), is often herded into areas of natural vegetation to reduce the frequency and intensity of wildfires, and prevent the spread of fire into adjacent residential areas, by removing fuel (Depietri and Orenstein 2020; Ornai, Ne'eman, and Keasar 2020). Other positive effects of cattle ranching include the restriction of shrub encroachment (Henkin 2021), which promotes biological diversity (Perevolotsky 2005). However, there are also concerns about negative effects of cattle ranching on wild ungulate populations due to scramble competition for space and food (Berdoucou 1986; Mysterud 2000; Mussa et al. 2003; La Morgia and Bassano 2009), altered movement patterns and changes in habitat use (Mattiello et al. 2002; Young, Palmer, and Gadd 2005), or the attraction of predators (Graham, Beckerman, and Thirgood 2005; Treves et al. 2006). In RHNP, Shamon, Dayan, and Saltz (2017) reported that cattle presence was positively correlated with the presence of golden jackals and wild boar, but negatively with that of female gazelles, and proposed that predators were attracted to cattle in search of newborn calves and their afterbirth.

In our study, we took advantage of the rare opportunity to investigate the effects of increased food availability due to long-term diversionary feeding of urban exploiters (jackal and wild boar), and cattle ranching on an endangered avoider species (mountain gazelle) in the isolated, peri-urban environment of RHNP. We asked whether these two factors had an impact on the growth of the gazelle population, by modeling the gazelle encounter rate, in response to excess food and the presence of cattle over a period of 17 years, accounting for temporal autocorrelation and several key environmental factors. We hypothesized that excess food and cattle ranching could have negative impacts on gazelle abundance and may thus jeopardize the continued persistence of the species in Israel.

2 | Materials and Methods

2.1 | Study Location

RHNP is at the southern edge of Mt. Carmel in central Israel (32°30' N; 34°57' E) and covers an area of about 5.0 km² at an altitude of 120 m above sea level (Figure 1a). The park is

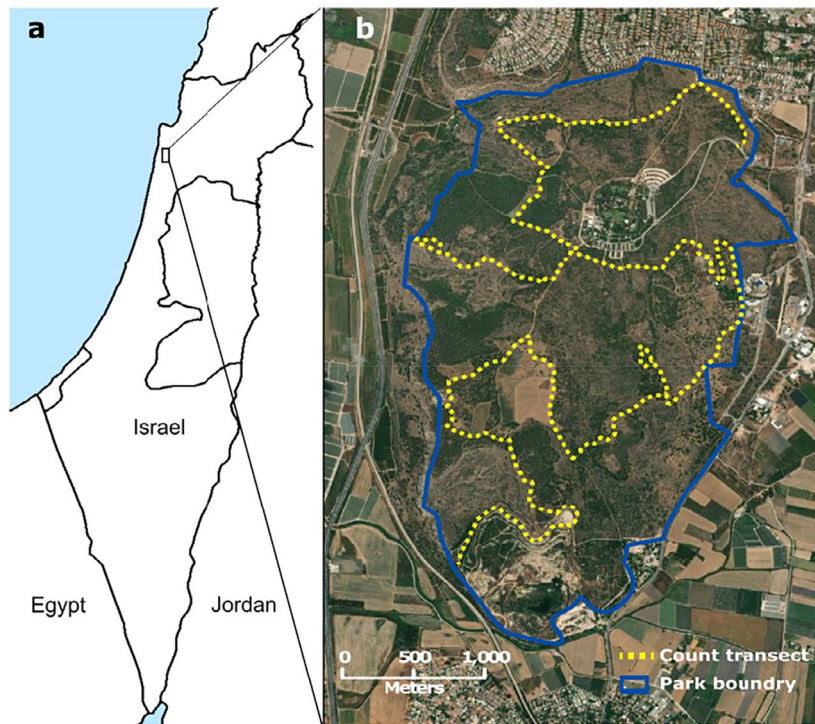


FIGURE 1 | Ramat Hanadiv Nature Park in northern Israel (a). The park's boundary (blue) and survey route (yellow), plotted on an aerial image of the study area (b).

surrounded by a mosaic of settlements and agricultural land, with little connectivity to other mountain gazelle populations, and is not only managed for public benefits such as recreation and leisure activities, but also to preserve the historical and cultural Mediterranean landscape with its flora and fauna (specifically the mountain gazelle population). The climate is Mediterranean, with cool, wet winters (mean monthly temperature in January: 11.9°C) and hot, dry summers (mean monthly temperature in August: 24.9°C). The mean annual precipitation is 500–600 mm, primarily occurring between November and March. The vegetation comprises mostly dense, evergreen *garrigue*, a mixture of high and low shrubs, interspaced by open areas with annual and perennial herbaceous plants.

2.2 | Study Species

Mountain gazelles live in small groups of related females and their offspring, often accompanied by a territorial male. Non-territorial males are solitary or organized in small, loose bachelor groups. Male territories measure about 50 ha (Grau and Walther 1976), encompassing the home range of two or three female groups (average female home range size (mean \pm SD): 16.5 \pm 0.51 ha; Geffen et al. 1999). Both sexes show a strong site fidelity (Geffen et al. 1999), marking their home range with fecal and glandular deposits, often placed at scent-mark stations (Walther, Mungall, and Grau 1983). After a gestation of 6 months, females give birth to a single fawn. Parturition occurs throughout the year, with a strong peak in spring and a smaller one in autumn (Geffen 1995; Mendelsohn, Yom-Tov, and Groves 1995). Mountain gazelles are a staple prey species for jackals (Borkowski, Zalewski, and Manor 2011; Yom-Tov

et al. 2020). Wild boar were not reported to prey on gazelles, but they might prey on gazelle fawns, since they were reported to occasionally prey on roe deer (*Capreolus capreolus*) and blackbuck (*Antilope cervicapra*) fawns (Ballari and Barrios-García 2014; Jabaraj Frank, Gopi, and Sankar 2015).

2.3 | Gazelle Surveys

Gazelle surveys were conducted along a 12.2 km route (Figure 1b), corresponding to a sampling intensity of 2.4 km per 1.0 km². Driving speed was about 6 km/h along pre-established, unpaved roads traversing most parts of the park. Surveys were repeated four times a month, starting twice at sunrise (dawn surveys), and twice 2 hours before sunset (dusk surveys). During surveys, the observer scanned along both sides of the route, occasionally using binoculars to search for gazelles at elevated points with a good overview. For each gazelle encounter, the sex/age class was identified as either male or female/subadult, because separating adult females from subadult gazelles was difficult, due to similar body size and the absence of horns in many adult females, making them look like subadults (Geffen et al. 1999; Wronski et al. 2010; Figure 2). Additionally, females and subadults usually move together (Yom-Tov 2016). The approximate location of each observation was recorded using GPS.

From November 2003 to December 2011, surveys were accomplished by one observer, either on horseback or by driving a vehicle. From January 2012 onward, a different observer completed the surveys by vehicle only. Due to logistical constraints, such as harsh weather or observer illness, 92 surveys (11% of the surveys planned) were not conducted, resulting in a total of 724 surveys.

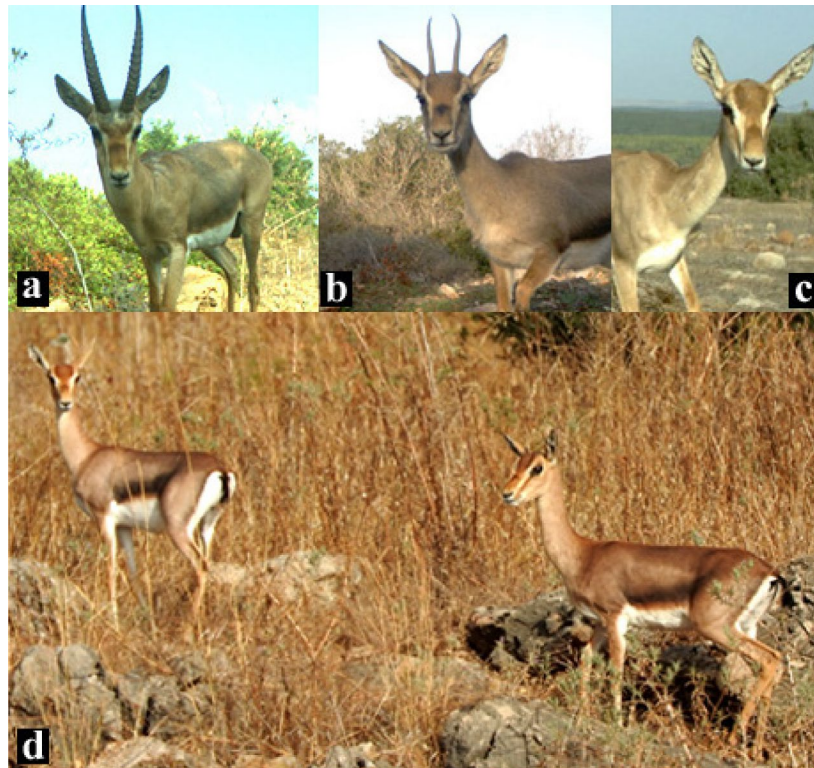


FIGURE 2 | Mountain gazelles (*Gazella gazella*) of different age/sex class in Ramat Hanadiv Nature Park: (a) adult male; (b) horned adult female; (c) hornless adult female; (d) adult female with very short horns (in the foreground), and a subadult (in the background).

2.4 | Gazelle Encounter Rate (Response Variable)

We used the gazelle encounter rate, that is, the total number of gazelles observed during each survey, as our response variable. The encounter rate is determined by both the true gazelle density, and by gazelle detectability (Buckland et al. 2005) which is strongly affected by behavioral responses of gazelles to environmental conditions and by the ability of the observer to detect them (Berthiaume, Bélisle, and Savard 2009; Kubečka, Terhune, and Martin 2021). For example, the time of day, temperature, and wind speed may affect whether a gazelle is active or resting, and an active gazelle is more likely to be seen. To control for the influence of environmental conditions on detectability, we included several seasonal, temporal, and environmental factors as covariates, using a stratified modeling approach (see below).

2.5 | Diversionary Feeding and Cattle Ranching

Diversionary feeding of jackals and wild boar started in 2000 at a permanent feeding station inside the park and included an almost daily supply of fruits, vegetables, and livestock carcasses. However, over the years, there were concerns that diversionary feeding might have increased the densities of these species in the park, and their predation on gazelles. Consequently, diversionary feeding in the park ceased in 2012. We included diversionary feeding in our models as a binary variable, that is, absent versus present (Table 1).

Cattle ranching in RHNP was strictly seasonal with a herd of approximately 200 individuals typically entering the park by

late winter (February) and leaving in early summer (June). We calculated the annual stocking rate of cattle as the entering herd size multiplied by the number of days inside the park and divided by the area available to the herd in that year (Stuth and Heitschmidt 1991). A missing record for 2011 was imputed as the mean stocking rate of the previous and the subsequent year. The mean (\pm SD) cattle stocking rate was established as 51.77 ± 18.21 cow grazing days/ha. To test for the lagged impact of cattle on gazelles, we included the stocking rate of the current year and that of the previous year as explanatory variables in our models (Table 1).

2.6 | Intrinsic and Environmental Covariates

We included sex/age class as a binary covariate in our models (Table 1). When the sex/age class could not be determined, the observation was excluded from our analysis (1.2% of all observations).

To account for circadian effects on the gazelle encounter rate, we included the time of day (i.e., dawn or dusk) and the degree of moonlight the night before the survey (percentage full moon, Ignatavičius et al. 2021, obtained with the AstroExcel (2021) tool as explanatory variables in our models (Table 1). We included mean temperature, mean wind speed, and cumulative rainfall 1 h prior to the survey as covariates to account for short-term local weather; these measures were obtained from the RHNP meteorological station. Since animals respond to meteorological conditions at different time scales (Gilbert et al. 2022), we also tested these conditions at 10 min, and at 2, and 24 h prior to the count.

TABLE 1 | Type of data, range and categorical level of various factors, as well as seasonal, temporal, and environmental covariates used as explanatory variables of mountain gazelle (*Gazella gazella*) encounter rates in Ramat Hanadiv Nature Park, in a set of generalized linear mixed models.

Variables	Type	Range (mean \pm SD)	Categorical levels	Included in final models
Diversionsary feeding	Binary	—	Yes, no	Yes
Cattle stocking rate (cow grazing days/ha) ^a	Continuous	27.82–93.55 (51.77 \pm 18.21)		Yes
Sex/age class	Binary		Males, females/subadults	Yes
Time of day	Binary		Dawn, dusk	Yes
Temperature ($^{\circ}$ C) ^{b,c}	Continuous	2.8–33.5 (20.3 \pm 5.8)		Yes
Wind speed (m/s) ^c	Continuous	0.4–9.3 (3.0 \pm 1.6)		No
Rain (mm/h) ^c	Continuous	0.0–6.0 (0.0 \pm 0.3)		Yes
Moon percent	Continuous	0.11–99.88 (49.72 \pm 24.80)		No
Hydrological year	Continuous	2004–2020 (2012.17 \pm 5.04)		Yes
Hydrological month	Trigonometric	1–12 (6.55 \pm 3.42)		Yes

^aIncluded separately for the current, and the previous years.

^bLinear and quadratic terms were tested.

^cValues presented are averaged (temperature and wind speed) or accumulated (rain), over 1 h prior to the count. These covariates were also tested at a resolution of 10 min, 2, or 24 h prior to the count.

When accounting for temporal trends, we followed the natural annual climate cycle by using “hydrological years,” starting on October 1 and ending on September 30 of the subsequent calendar year (Likens 2013). Month was included in our models as a combination of sine and cosine terms (the sine and cosine functions of $2\pi \times \text{month}/12$) to account for potential cyclical seasonal variation throughout a year (Stolwijk, Straatman, and Zielhuis 1999).

2.7 | Statistical Analyses

We built generalized linear mixed models (GLMMs) of encounter rates using the *glmmTMB* package in *R* (version 4.0.2.; Brooks et al. 2017). The models assumed a Poisson distribution for the residuals because there was no evidence for overdispersion of the residuals (Hartig 2024) and using a negative binomial distribution increased the AIC. Since consecutive surveys could not be assumed to be independent and were not evenly distributed over time, we accounted for temporal autocorrelation using the continuous Ornstein–Uhlenbeck temporal correlation term (Uhlenbeck and Ornstein 1930). Our *basic model* of encounter rate included only the sex/age class, time of day, month, year, and the environmental covariates. We used a spline of the “hydrological year” with two turning points because this was the configuration with the lowest AIC among models without year; models with a linear effect of year or splines with one, or three turning points did not perform

as well. Subsequently, we separately added each of the three meteorological variables over 1 h prior to the survey; if a variable’s addition did not reduce the AIC by ≥ 2.0 , we omitted the variable to avoid overfitting. Similarly, we tested whether adding a quadratic term for temperature, or using time resolutions of 10 min, 2, or 24 h prior to the survey to our initial model, would improve model fit. As a result of these preliminary steps, the completed *basic model* (Table 1) included sex/age class, time of day, temperature, rain, sine and cosine of the month, a spline on the year with two turning points, and the Ornstein–Uhlenbeck temporal correlation term. Finally, we built three additional models considering management practice as a predictor: one model with diversionsary feeding (as a proxy for excess food in the environment), one with the current year’s, and one with the previous year’s cattle stocking rate. These management practice models also included interaction terms of management practice with (i) sex/age class, to test for differential responses of these classes to the presence of cattle (Shamoon, Dayan, and Saltz 2017) and to predation (e.g., Morris 1956); and (ii) the time of the day, to account for activity shifts between dawn and dusk, since *G. gazella* is crepuscular (Yom-Tov 2016). We used the AIC to compare our final models, and the Incident Rate Ratio (IRR) to look at the effects of the different factors on gazelle encounter rates. The IRR is a measure of relative difference used to compare the incidence rates of events occurring in an exposed group (in our case diversionsary feeding or cattle stocking rate) with those in the nonexposed group (Cummings 2009).

2.8 | Effect of Group Size on Gazelle Encounter Rates

When surveying gregarious animals, the positive impact of group size on individual detectability should be considered (Buckland 2001). To evaluate whether such a bias affected our results, we grouped gazelle sightings obtained within 5 min and ≤ 50 m from each other into one group, characterized by the age/sex class of its members. A mixed group was recorded as both a male group and a female/subadult group. We then multiplied the number of groups observed during each count, by the mean group size for that age/sex class in the corresponding year (Buckland 2001; Rosenblatt et al. 2019), and used the resulting encounter rates as the response variable in a separate set of models with the two management practices and the explanatory variables, following the same workflow as for individual-based models.

3 | Results

During the 17-year study, 2020 gazelle group observations were recorded, including 3942 individuals, of which 23.4% were males and 76.6% were females/subadults. During 7.6% of surveys, no gazelles were observed. The mean encounter rate (\pm SE) for the entire study period was 5.44 (± 0.20) gazelles per survey. Qualitatively, the study period appears to have been composed of four phases (Figure 3): (i) low or declining encounter rates between 2004 and 2011–2012, (ii) a slow increase between 2013

and 2015, (iii) stable generally higher encounter rates between 2015 and 2018, and (iv) declining rates between 2018 and 2020. There was a slight, although statistically nonsignificant, increase in cattle stocking rate by 3% after diversionary feeding ceased ($\bar{X} \pm$ SE: 44.42 \pm 2.97 cow grazing days per hectare before vs. 56.7 \pm 7.67 after; two-tailed t -test: $t(10.04) = -1.51$, $p = 0.16$).

3.1 | Effects of Excess Food (Diversionary Feeding) and Cattle Ranching on Gazelle Encounter Rates

The AIC best model included diversionary feeding and had an Akaike weight of 0.96 (Table 2). Excess food, in form of diversionary feeding, had a negative effect on gazelle encounter rate, and encounter rates were 44% lower when it was practiced (IRR = 0.56, $z = -3.09$, $p < 0.01$; Table 3A). Moreover, there was an interaction between diversionary feeding and sex/age class (IRR = 1.28, $z = 2.35$, $p < 0.05$; Table 3A), indicating that the negative effect of diversionary feeding was 28% stronger on males than on females/subadults. There was also an interaction between diversionary feeding and time of day (IRR = 1.22, $z = 2.57$, $p < 0.05$; Table 3A), suggesting a more pronounced negative effect of diversionary feeding on encounter rate in the morning. The second-best model (Δ AIC = 6.87, Akaike weight = 0.03; Table 2) included cattle ranching as a management practice (Basic + cattle ranching current year) with a positive—however insignificant—effect of cattle ranching during the current year (IRR = 1.11, $z = 1.94$, $p = 0.051$; Table 3A). The total Akaike weights of all other models were approximately 0.00 (Table 2).

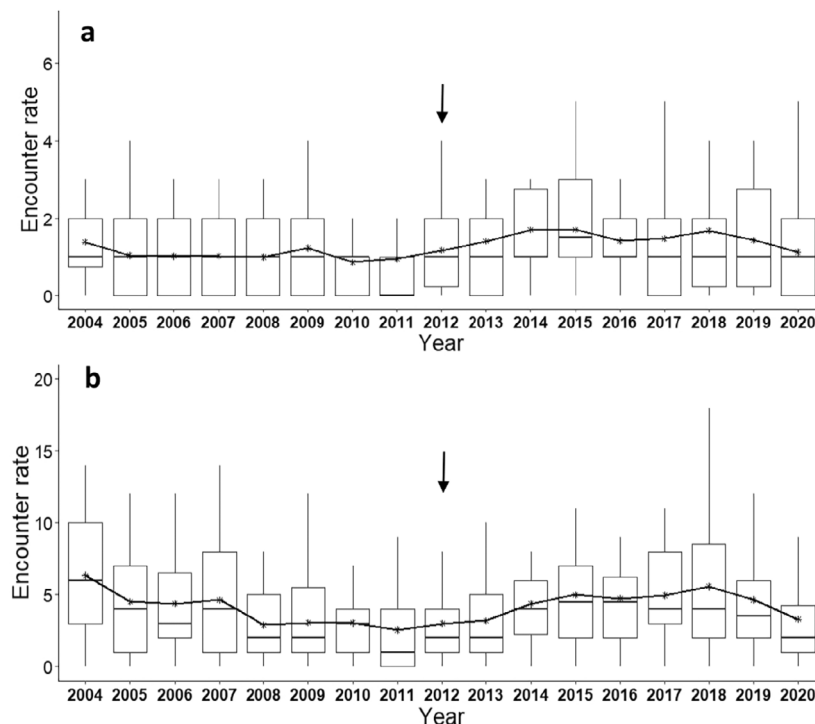


FIGURE 3 | Encounter rates (number of gazelles observed during a survey) of (a) male and (b) female/subadult mountain gazelles (*Gazella gazella*) in Ramat Hanadiv Nature Park from 2004 to 2020. Horizontal lines depict medians. Boxes indicate the 25% and 75% interquartile ranges, and whiskers represent percentiles. Asterisks show the global annual means, connected by the bold line, illustrating the dynamics across the study period. Vertical arrow points at the year when diversionary feeding was ceased (February 2012). Note, the scale of the y-axes differs between (a) and (b) to facilitate the comparison of trends.

TABLE 2 | Performance of five generalized linear mixed models examining the effect of excess food through diversionary feeding (DF), and cattle stocking rate in the current year (C(Y)), and the previous year (C(Y-1)) on the encounter rate (ER) of individual mountain gazelles (*Gazella gazella*) in Ramat Hanadiv Nature Park. The basic model included the sex/age class (males vs. females/subadults), time of day (dawn vs. dusk), average temperature (Temp), the sum of rain 1 h prior to the count (Rain), sine and cosine of the month (Month), a spline on the year with two turning points (Year), and an Ornstein–Uhlenbeck continuous term for temporal correlation (OU). The null model included only year and a temporal autocorrelation term.

Model name	Model specification	K	AIC	ΔAIC	Akaike wt
Basic + DF	ER ~ DF × (Sex/age class + Time of Day) + Temp + Rain + Month + Year + OU	16	5381.68	0.00	0.96
Basic + C(Y)	ER ~ C(Y) × (Sex/age class + Time of Day) + Temp + Rain + Month + Year + OU	16	5388.55	6.87	0.03
Basic	ER ~ Sex/age class + Time of Day + Temp + Rain + Month + Year + OU	13	5391.39	9.71	0.00
Basic + C(Y-1)	ER ~ C(Y-1) × (Sex/age class + Time of Day) + Temp + Rain + Month + Year + OU	16	5393.83	12.15	0.00
Null—intercept only	ER ~ Year + OU	3	6809.56	1427.88	0.00

TABLE 3 | Results of the best generalized linear mixed models examining the effect of diversionary feeding and other variables on the encounter rate (ER) of individual mountain gazelle (A) and of mountain gazelle groups (B) in Ramat Hanadiv Nature Park.

Variables	A. Individuals			B. Groups		
	IRR	95% CI	z	IRR	95% CI	z
(Intercept)	2.36***	(1.63, 3.43)	4.52	2.79***	(1.99, 3.91)	5.93
Diversionary feeding (DF)	0.56**	(0.39, 0.81)	−3.09	0.52***	(0.37, 0.73)	−3.78
Sex/age class (Females/subadults)	3.00***	(2.72, 3.31)	22.3	3.25***	(2.95, 3.58)	23.84
Time of day (Dusk)	0.67***	(0.56, 0.8)	−4.27	0.73***	(0.62, 0.86)	−3.70
DF × Class	1.28*	(1.06, 1.56)	2.35	1.21*	(1.04, 1.41)	−3.22
DF × Time of day	1.22*	(1.04, 1.43)	2.57	1.19.	(0.98, 1.43)	3.27
Temp	0.80***	(0.71, 0.9)	−3.78	0.84**	(0.76, 0.94)	2.34
Rain	1.07**	(1.03, 1.12)	3.08	1.07**	(1.03, 1.11)	3.56
Cosine (Hydro month)	1.14*	(1.01, 1.28)	2.19	1.14*	(1.02, 1.26)	−6.85
Sine (Hydro month)	1.28***	(1.14, 1.44)	4.27	1.20***	(1.09, 1.33)	−0.19
Hydro year, $df=1$	0.38***	(0.27, 0.54)	−5.46	0.33***	(0.24, 0.46)	−5.24
Hydro year, $df=2$	1.20 ns	(0.75, 1.92)	0.72	0.96 ns	(0.63, 1.47)	−2.96
Hydro year, $df=3$	0.38***	(0.23, 0.62)	−3.89	0.31 ns	(0.20, 0.48)	2.50
Hydro year, $df=4$	0.61*	(0.4, 0.94)	−2.24	0.55**	(0.37, 0.82)	1.78

Note: Model parameters: Incidence rate ratio (IRR), 95% confidence intervals (95% CI), and z-statistic (z).

Abbreviation: ns, not significant.

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.001$.

3.2 | Effect of Intrinsic and Environmental Covariates on Encounter Rates

The encounter rate of females and subadults was three times higher than that of males (IRR = 3.00, $z = 22.3$, $p < 0.001$; Table 3A), and dusk counts yielded 33% lower encounter rates than dawn counts (IRR = 0.67, $z = -4.27$, $p < 0.001$; Table 3A).

Encounter rates were lower when temperatures were higher (IRR = 0.80, $z = -3.78$, $p < 0.001$; Table 3A) and higher when there was more rain in the hour preceding the count (IRR = 1.07, $z = 3.08$, $p < 0.01$; Table 3A). The effects of cosine (IRR = 1.14, $z = 2.19$, $p < 0.05$; Table 3A) and sine (IRR = 1.28, $z = 4.27$, $p < 0.001$; Table 3A) of the hydrological month indicated a seasonal change in gazelle encounter rates. The effect

TABLE 4 | Performance of five generalized linear mixed models examining the effect of excess food through diversionary feeding (DF), and cattle stocking rate in the current year (C(Y)), and the previous year (C(Y-1)), on the encounter rate (ER) of mountain gazelle (*Gazella gazella*) groups in Ramat Hanadiv Nature Park.

Model name	Model specification	K	AIC	ΔAIC	Akaike wt
Basic + DF	ER ~ DF × (Sex/age class + Time of Day) + Temp + Rain + Month + Year + OU	16	5402.56	0.00	0.99
Basic + C(Y)	ER ~ C(Y) × (Sex/age class + Time of Day) + Temp + Rain + Month + Year + OU	16	5413.51	10.95	0.01
Basic	ER ~ Sex/age class + Time of Day + Temp + Rain + Month + Year + OU	13	5413.56	11.00	0.00
Basic + C(Y-1)	ER ~ C(Y-1) × (Sex/age class + Time of Day) + Temp + Rain + Month + Year + OU	16	5418.17	15.61	0.00
Null—intercept only	ER ~ Year + OU	3	6981.74	1579.18	0.00

Note: The basic model included the sex/age class (males vs. females/subadults), time of day (dawn vs. dusk), average temperature (Temp), and the sum of rain 1 h prior to the count (Rain), sine and cosine of the month (Month), a spline on the year with two turning points (Year), and an Ornstein–Uhlenbeck continuous term for temporal correlation (OU). The null model included only year and a temporal autocorrelation term.

size and direction of sex/age class, time of day, month, temperature, and rain on the encounter rate were similar across all models, irrespective of the management practice (results not shown). Wind speed, percentage moonlight, and squared temperature were omitted from all models because including them did not decrease model AIC by ≥ 2.0 . Similarly, we kept the meteorological data obtained during the hour preceding the survey because replacing them with other time resolutions, that is, 10 min, 2, or 24 h prior to the count, did not decrease model AIC by ≥ 2.0 .

3.3 | Effect of Group Size on Encounter Rates

Results obtained when encounter rates were corrected for group size were remarkably similar to those from individual encounter rates. The best model incorporated diversionary feeding, with a high Akaike weight of 0.99 (Table 4). Moreover, the ranking of the other models was identical (compare Tables 2 and 4). The IRR estimates for seasonal, temporal, and environmental covariates in the best group model (Table 3B) were also consistent with those obtained from the individual encounter rate model (Table 3A).

4 | Discussion

In this study, we followed the dynamics of an isolated gazelle population in a peri-urban nature park. We used an extensive dataset to compare alternative GLMMs with gazelle encounter rate as the response variable, and diversionary feeding (as a proxy for excess food) and cattle stocking rate as the main factors, along with several covariates and a temporal autocorrelation term. The model including diversionary feeding had a substantially lower AIC score than the other models and a high AIC weight, which implies that when food for predators was abundant, gazelle encounter rates were lower than at times when no excess food was provided. We did not find a relationship between cattle stocking rates and gazelle encounter rates.

4.1 | Excess Food Through Diversionary Feeding

Diversionary feeding was instigated to prevent golden jackals and wild boars from leaving RHNP. We do not know the degree to which it has reduced human–wildlife conflicts in the neighboring areas of RHNP, but the results from both the individual count and the group-based models (likely to be more conservative), suggest that the introduction of excess food into the system has led to a decline in gazelle encounter rates. Although low encounter rates might be due to increased emigration, rather than to decreased numbers, the isolated nature of the reserve—RHNP is almost completely surrounded by settlements, highways and industrial estates—makes the emigration of gazelles from the reserve highly unlikely. Moreover, decreased encounter rates might be also due to behavioral changes (e.g., increased shyness), or more nocturnal activity (see below). Assuming diversionary feeding to be accountable for decreased population size is in line with other studies worldwide (e.g., Sullivan and Klenner 1993; Kubasiewicz et al. 2016), which showed that unintentional effects of excess food through diversionary feeding (e.g., enhanced reproduction and population growth of the target species) occur more frequently than anticipated effects (e.g., mitigated human–wildlife conflict), and are more likely with increasing duration of the feeding program (e.g., Milner et al. 2014).

Given this, we propose that increased predation on gazelles may be attributed to higher reproduction rates in golden jackals and wild boar following diversionary feeding (e.g., Massei, Genov, and Staines 1996; Mendelssohn and Yom-Tov 1999), similar to what was reported from feral pigs triggering an increase in golden eagle (*Aquila chrysaetos*) abundance, and thus hyperpredation on the native island fox (*Urocyon littoralis*; Roemer et al. 2001; Roemer, Donlan, and Courchamp 2002). An intriguing scenario in this context is that diversionary feeding in RHNP may have increased jackal density through elevated predation on wild boar (Lange, Lelieveld, and De Knecht 2021), which in turn, has resulted in hyperpredation of jackals on gazelles. This scenario would be similar to what

was reported from British Columbia (Canada), where the expansion of moose (*Alces alces*) was followed by a decline of the endangered woodland caribou (*Rangifer tarandus caribou*) due to predation by wolf (*Canis lupus*)—their common predator (Serrouya et al. 2015).

The increased predation could also be attributed to changes in predator space-use and movement patterns; for example, Rotem et al. (2011) found that jackals near settlements with abundant and predictable anthropogenic food had smaller home ranges compared to jackals in natural areas of the same region. A similar effect was reported from bearded vultures in the Spanish Pyrenees, where supplementary feeding caused a decrease in dispersal distances and home range size (Margalida et al. 2013). In RHNP, this could imply an increase in predation pressure on gazelles by those jackals residing in the park. Once feeding stopped, the fast recovery of gazelles (Figure 3) suggests that predator densities decreased quite rapidly. Such quick responses were also reported from protected areas in Israel, where the reduction of anthropogenic food was shortly followed by a rapid dispersion and decreased survival rates of golden jackals and red foxes (Kapota 2014), or from northern Spain, where a rapid decline of yellow-legged gulls followed the closure of landfill sites (Delgado et al. 2023).

Patterns of gazelle encounter rates throughout the study period seem to indicate a lagged response to the introduction of diversionary feeding in 2000 (Figure 3). Gazelle encounter rates reached their minimum several years after diversionary feeding was introduced, suggesting a continuous population decline. Later, that is, about 1 year after the cessation of diversionary feeding, gazelle encounter rates started increasing again, which corresponds to the age of first parturition in females (Mendelssohn, Yom-Tov, and Groves 1995). The lagged recovery, together with the populations' isolation, support the interpretation that increased encounter rates represent an actual increase in the gazelle abundance, rather than gazelles immigrating into the park, or a shift in their activity patterns. Otherwise, the lag would have been less pronounced. Nevertheless, there are numerous examples reporting that a change in predator numbers has not only a direct impact on the size of the prey population, but also on its behavior manifested by a change in activity patterns and the active avoidance of potential predators (e.g., Martínez-Abraín et al. 2023). Our study indeed found a change in gazelle activity patterns in response to predation, with a stronger negative effect of diversionary feeding on the dawn encounter rate (Table 3). This is in line with a previous study (Shamoon et al. 2018), in which gazelles were reported to increase nocturnality in response to increased human and predator presence (Gaynor et al. 2018; Zukerman, Sigal, and Berger-Tal 2021). Once diversionary feeding stopped and predation decreased, gazelles likely shifted some of their activity back to preferable morning hours.

Males seem to have been more affected by diversionary feeding than females and subadults. Male ungulates are generally exposed to higher predation risks than females or subadults since some sexually selected traits can increase their predation risk. Sexual selection includes both mate choice and male–male competition, of which the latter factor can substantially increase

male predation risk (Owen-Smith 1993; Ginsberg and Milner-Gulland 1994; Mysterud, Coulson, and Stenseth 2002).

4.2 | Cattle Ranching

Following the global increase in the frequency and intensity of wildfires over recent years, grazing by large herbivores is increasingly promoted as a fire mitigation tool, especially in Mediterranean areas (Moreira et al. 2020). In Israel, recent wildfires have encouraged government legislation and incentives for livestock grazing in natural and peri-urban areas to reduce the frequency of wildfires and to create fuel breaks near park boundaries (Ornai, Ne'eman, and Keasar 2020). Indeed, approximately half of Israel's Mediterranean nature parks and forests, where most mountain gazelles occur, are subjected to cattle ranching (Seligman et al. 2016), so negative effects of cattle could have devastating implications for the global population of mountain gazelles. Most studies found negative effects of livestock ranching on wild ungulate populations, including competition (Madhusudan 2004; Chirichella, Apollonio, and Putman 2014), disease transmission (East, Bassano, and Ytreus 2010; Serrano et al. 2011; Hatam-Nahavandi et al. 2019), or the attraction of predators and scavengers (Treves et al. 2004; Antonelli et al. 2016; Mahajan et al. 2022), though few studies reported on positive effects (Odadi et al. 2011; Schieltz and Rubenstein 2016). For RHNP, Shamoon, Dayan, and Saltz (2017) suggested that the increased presence of predators in the vicinity of cattle may prompt female gazelles to avoid these areas, which might lead to a disruption of maternal care and thus to decreased fawn survival. Spatial or temporal avoidance of patches regularly visited by predators is a common prey response to increased predation risks (Lima 1998; Kronfeld-Schor and Dayan 2003; Blumstein 2006; Thaker et al. 2011). However, in stark contrast to the strong effect of excess food on the gazelle population, we did not detect a demographic response of gazelles to cattle ranching, which could have important ramifications for the conservation of mountain gazelles. The time of gazelle population recovery is consistent with this: if cattle were responsible for the decline in gazelle densities, we would not expect a quick recovery as observed after the cessation of diversionary feeding in 2012.

The cattle stocking rate in RHNP is relatively low compared to typical Israeli rangeland management practices (Henkin et al. 2005). One might argue that higher stocking rates or year-round cattle ranching may yield more pronounced direct (or indirect) effects on gazelles. However, since cattle ranching in RHNP coincides with the peak of gazelle's birth season (Geffen 1995; Mendelssohn, Yom-Tov, and Groves 1995), the effect of cattle on fawn survival would have been most pronounced at this time.

Furthermore, recent DNA metabarcoding analysis in RHNP revealed minimal dietary overlap between gazelles and cattle (Pianka's overlap index < 10%; Arnon et al. 2022), suggesting that competition for food is of minor importance and that the impact of seasonal cattle ranching on mountain gazelles is negligible. This does not only apply to our study area but also across all mountain gazelle habitats in the Mediterranean, and we thus

recommend seasonal cattle ranching to be applied throughout the species' range.

4.3 | Environmental Factors

Our analyses also documented relationships with intrinsic and environmental factors that provide insight into sex/age-related, seasonal, or temporal factors impacting ungulates in Mediterranean climates. Temperature, for example, was negatively related, and rainfall was positively related to gazelle encounter rates (Table 3). The effect of these short-term, seasonal conditions may be attributed to fewer visitors (pedestrians and mountain bikers) entering the park when weather conditions are less favorable, causing less disturbance to gazelle activity. However, we believe that these short-term changes do not challenge the interpretation of the long-term patterns unraveled by our study.

Seasonal differences in encounter rates could also reflect changes in demography due to the semiannual breeding cycle of gazelles (Mendelssohn, Yom-Tov, and Groves 1995). However, if this were the case, we would expect the highest encounter rates in the summer following the largest seasonal breeding event, usually starting in early spring. Instead, encounter rates peaked in December and January for both sex/age classes (results not shown). This is likely due to gazelles grazing on herbaceous vegetation in more open areas during the cooler seasons (Baharav 1975), while predominantly browsing on woody vegetation in dense habitats during the dry seasons (Mendelssohn, Yom-Tov, and Groves 1995), suggesting that the impact of month on the encounter rate reflected a behavioral rather than a demographic response.

4.4 | Potential Observer Bias

Since the first observer recorded data from 2003 to 2011, a period coinciding with diversionary feeding, and the second observer recorded data after 2011, that is, a period without diversionary feeding, it may be argued that the observed encounter rate is due to an observer bias. Both observers were employed by RHNP as wildlife managers, and the second observer was trained by the first one during a period of overlap. Furthermore, if observer bias was the primary driver of the observed changes, an abrupt change in encounter rates would be expected following the personnel transition. Instead, our data demonstrate a gradual change (increase) over time suggesting that observer bias is rather unlikely.

5 | Conclusions

While we found no significant impact of cattle ranching on gazelles, our results showed that the provision of excess food for jackals and wild boar had substantial knock-on effects on the gazelle encounter rate. Through cascading effects, excess food can thus negatively impact avoider populations, and may eventually lead to a decline in species richness (Oro et al. 2013), which further highlights the complexity of conservation and management in peri-urban areas (Shafer 1995). Our study provided the rare

opportunity to follow such a cascading process. Although the case presented here raises concerns for the future of endangered avoider species in peri-urban habitats, it also gives reason for hope. Given a potentially high reproductive rate, as that of mountain gazelles (Baharav 1983), reducing the availability of excess food can reverse the demographic trend. Based on our previous assumptions (see above), we propose that the fast recovery of gazelles in RHNP after the cessation of diversionary feeding demonstrates such resilience, similar to that observed in the border region between Turkey and Syria (Kirac 2021), where overhunted gazelle populations quickly recovered due to the presence of military personnel during a period of political unrest.

Author Contributions

Amir Arnon: conceptualization, methodology, data analysis, writing – original draft, and funding acquisition. **Torsten Wronski:** conceptualization, methodology, writing – original draft, and supervision. **Dan Malkinson:** conceptualization, methodology, writing – original draft, and supervision. **Ido Izhaki:** conceptualization, methodology, writing – original draft, and supervision. **Miranda Davis:** conceptualization, methodology, data analysis, and writing – original draft.

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Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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