

Utilization of harvester ant nest sites by Persian goitered gazelle in steppes of central Iran

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Abstract

Ants are among the most important elements in many ecosystems and known as famous ecosystem engineers. By changing physical and chemical properties of soil, ants may provide suitable habitats for other species. Based on previous observations, we hypothesized that Persian goitered gazelles (*Gazella subgutturosa subgutturosa*) exhibit a preference for utilizing sites close to seed harvester ant (*Messor* spp.) nests. We tested our hypothesis by (1) mapping the occurrence of harvester ant nests and aggregated gazelle pellet groups along 31 strip transects, (2) monitoring pellet group accumulation bimonthly at 56 pairs of permanent plots established on ant nests and at adjacent control sites for a complete year, and (3) comparing vegetation and soil parameters between ant nest sites used by gazelles and paired control plots without ant nests. Although the area of *Messor* spp. nest sites covered only about 0.29% of the sampled transects, 84% of the gazelle pellet group aggregation sites were positioned upon ant nests, suggesting that gazelles actively selected *Messor* spp. nest sites. Pair-wise comparisons between ant nest plots and paired control plots also confirmed higher use of ant nest sites by gazelles compared to sites without ant nests in all time periods. Percent soil organic matter, percent cover of gravel, and annual herb vegetation significantly differed between ant nest and paired control plots in all the vegetation communities. We suggest that the alterations brought about by harvester ants on soil and vegetation make these sites attractive to gazelles. Gazelle territoriality behaviour and use of ant nests as bedding sites may be the reasons for selection of ant nest sites by gazelles.

Zusammenfassung

Ameisen gehören zu den wichtigsten Elementen in vielen Ökosystemen und sind als Ökosystemingenieure bekannt. Indem sie die physikalischen und chemischen Eigenschaften des Bodens verändern, können Ameisen geeignete Habitate für andere Arten bereiten. Basierend auf früheren Beobachtungen stellten wir die Hypothese auf, dass die Persische Kropfgazelle (*Gazella subgutturosa subgutturosa*) eine Präferenz für die nähere Umgebung von Nestern der Ernteameisen (*Messor* spp.) zeigt. Wir überprüften diese Hypothese, indem wir (1) die Ameisennester und aggregierte Dungpillengruppen der Gazelle entlang von 31 Streifen transekten kartierten, (2) über ein Jahr zweimonatlich die Akkumulation von Dungpillengruppen auf 56 Paaren von Dauerflächen mit bzw. ohne Ameisennester überwachten und (3) die Vegetations- und Bodenparameter verglichen für von Gazellen genutzten Ameisennestplätzen und Kontrollflächen ohne Ameisennester. Obwohl die Gesamtfläche der *Messor*-Nestplätze nur etwa 0.29% der untersuchten Transekte einnahm, befanden sich hier 84% der aggregierten Kotpillengruppen, was nahelegt, dass die Gazellen aktiv *Messor*-Nestplätze auswählten. Paarweise Vergleiche zwischen Ameisennestplätzen

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und gepaarten Kontrollflächen bestätigten ebenfalls eine höhere Nutzung von Nestplätzen durch die Gazellen für alle Untersuchungsperioden. Der prozentuale Anteil von organischer Substanz im Boden, die relative Bedeckung mit Kies und der Bewuchs mit einjährigen Kräutern unterschieden sich in allen untersuchten Pflanzengemeinschaften signifikant zwischen Ameisennestplätzen und gepaarten Kontrollflächen. Wir schlagen vor, dass die von den Ernteameisen verursachten Veränderungen des Bodens und der Vegetation diese Stellen für die Gazellen attraktiv machen. Territorialverhalten und die Nutzung von Ameisennestern als Schlafstellen könnten die Gründe für die Präferenz der Gazellen für Ameisennestplätze sein.

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Introduction

The interaction between different organisms in an ecosystem is a fundamental process in ecological communities (Krebs 1985; Begon, Harper, & Townsend 1990). Some relationships between organisms are not directly trophic or competitive; instead, interactions may include alteration and modification of habitats by ecosystem engineer species making them suitable for other species of the community (Jones, Lawton, & Shachak 1994).

Ants are among the most important elements of an ecosystem and known as famous ecosystem engineers owing to their significant impacts on ecosystem structures (Jones et al. 1994). By changing physical and chemical properties of soil (Cammeraat, Willott, Compton, & Incoll 2002; Wagner et al. 2004; Whitford, Barness, & Steinberger 2008) and vegetation patterns (Whitford & Dimarco 1995; Folgarait, Perelman, Gorosito, Pizzio, & Fernandez 2002; Schutz, Kretz, Dekoninck, Irvani, & Risch 2008) ants may alter habitats of other species (Jones et al. 1994; Folgarait 1998). For instance, Schutz et al. (2008) showed that ants may alter vegetation patterns, which in turn affects spatial use of the habitat by red deer (*Cervus elaphus*) in Alpine grasslands. Beaver and Herrick (2006) reported a negative correlation between ant mound density and the density of feral horse (*Equus caballus*) dung in Nevada, USA. Impacts of large herbivores on ants have also been investigated in a number of other studies (e.g. deer: Nash et al. 2001, 2004; Bugalho et al., 2011).

Patterns of dung deposition have been used to infer habitat associations of different ungulates since 1940s (Neff 1968). The quality and distribution of habitat elements required by the species influence the spatial pattern of a species' pellet groups (Apio, Plath, & Wronski 2006; Attum et al. 2006), and the distribution of pellet groups reflects patterns of the species' habitat use (Hemami et al. 2005). Apart from random distribution, aggregated pattern of pellet groups has been reported for different antelope species (e.g. dik dik, *Madoqua kirki*, Hendrichs & Hendrichs 1971; Garnt's gazelle, *Gazella granti*, Estes 1991; Thomson's gazelle, *Gazella thomsoni*, Walther 1978; bushbuck, *Tragelaphus scriptus*, Apio et al. 2006; Mountain gazelle, *Gazella gazella*, Wronski & Plath 2010). Some studies linked the aggregated pattern of pellet groups to different behaviour of the studied animal (e.g. territoriality: Walther, Mungall, & Grau 1983, Estes 1991;

avoiding parasites: Ezenwa 2004; Apio et al. 2006; communication signals: Johnson 1973; Wronski, Apio, & Plath 2006). Nevertheless, with the exception of allelomimetic behaviour (being elicited to defecate at the same spot on which another antelope species has previously defecated; Leuthold 1977), aggregation of ungulates' faecal pellets associated with the activities of other animal species has not been reported. In the present paper we report on a relationship between ants and Persian goitered gazelles (*Gazella subgutturosa subgutturosa*), which may influence spatial patterns of resource use in both gazelles and ants.

Gazelles are among the main ruminants occupying the desert steppes of Asia (Martin 2000). Persian goitered gazelles prefer steppe areas, especially plains and adjacent foothills covered by plant species such as *Artemisia* spp. and *Salsola* spp. (Hemami & Groves 2001). Goitered gazelles (*G. subgutturosa*) have been declining in abundance and distribution over recent decades and have been categorized as vulnerable (VU) since 2006 (Mallon 2008). Several studies have been conducted on habitat use of Goitered gazelles at the local scale (e.g. Nowzari, Behrouzi Rad, & Hemami 2007; Akbari et al. 2008; Chu et al. 2009; Hazeri, Hemami, & Khajedin 2009; Xu et al. 2010), but the ecological associations of this or other antelope species with invertebrates (ants) has hitherto not been studied.

The overall aim of this study was to investigate the relationship between Persian goitered gazelle and sites modified by the ants' nest-building activities. We had previously noted that gazelle dung piles predominately occur close to ant nests and therefore hypothesized that (i) ant nests are disproportionately important sites for gazelles, (ii) the mean rate of faeces deposition on ant nest sites differs between vegetation communities and/or (iii) bimonthly survey periods. As selection of ant nest sites by gazelles could be a consequence of ant activities, we also hypothesized that (iv) ants alter ground vegetation and physicochemical properties of the soil.

Materials and methods

Study area

The study was conducted in Kolah-Qazi National Park (32° 15'–32° 28' N, 51° 41'–52° 8' E), with a 48,000 ha area located in steppes of the central Iranian plateau (Fig. 1).

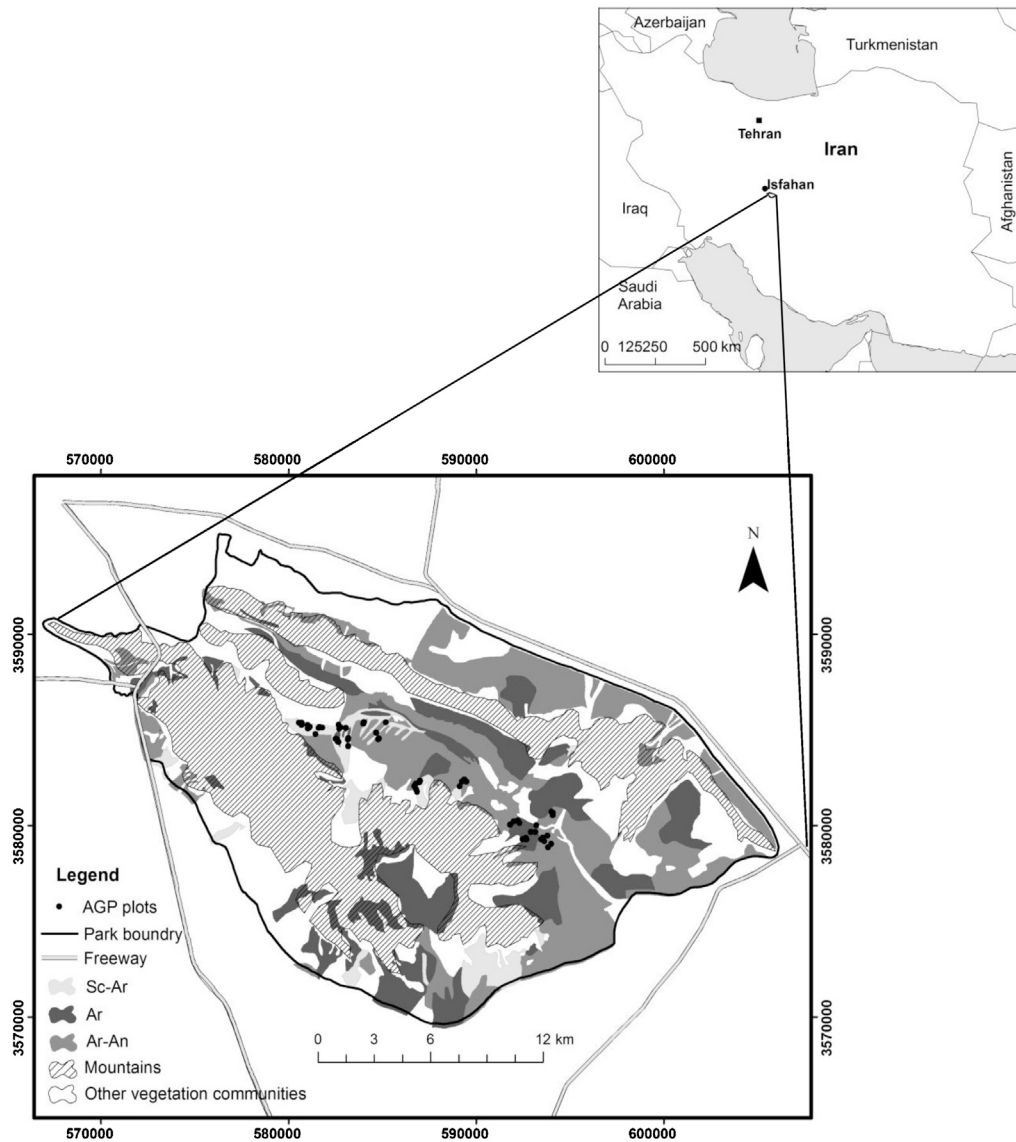


Fig. 1. Location and map of Kolah-Qazi National Park. The study was conducted in the central plain of the park surrounded by two parallel mountain chains. Roads, vegetation communities (modified from [Irvani 2002](#)), and AGP (ant nests with gazelle pellet groups) plots are shown on the map. Vegetation communities: Sc–Ar, *Scariola–Artemisia*; Ar, *Artemisia*; Ar–An, *Artemisia–Anabasis*.

Historically protected as a royal hunting preserve, the region was officially selected as protected area in 1963 and promoted to National Park status in 1996. The average elevation is 1720 m a.s.l. Average annual temperature is 15.6 °C, with mean high and low temperature of 23.5 °C and 7.75 °C respectively. The warmest month with mean 27.9 °C is July, and January with mean 3.4 °C is the coldest. The climate is dry with mean annual precipitation of 144.6 mm, of which most occurs in winter (59.3%).

The plains are dominated by *Artemisia sieberi*, *Anabasis aphylla* and *Scariola orientalis* which form three main vegetation communities ([Irvani 2002](#)) 1 – *Scariola orientalis–Artemisia sieberi* (Sc–Ar), 2 – *Artemisia sieberi* (Ar), 3 – *Artemisia sieberi–Anabasis aphylla* (Ar–An). Total vegetation cover ranges from 0.7% to 5% with a mean of

3.4% ([Irvani 2002](#)). There are no villages, main roads or livestock inside the park.

The Persian goitered gazelle is the sole ungulate occurring in the plain habitat of the area with numbers estimated at 1000–1300 in autumn 2010 ([Isfahan Department of Environment 2010](#)) The study was carried out in the central plains of the park with an area of c. 8200 ha where the highest density of gazelles occurs.

We found two main types of ant nests scattered throughout the area: (1) colonies of *Messor* ants with modified soil, seed litter and annual herbs forming distinct flat discs and (2) small pebble mounds of *Cataglyphis* ants with no sign of modified soil or distinct vegetation around the openings. We only considered *Messor* spp. nests in our study. Throughout the study area, there were sites where gazelle pellet groups

were aggregated. Aggregated pellet groups occurred both on *Messor* spp. ant nest discs and in sites where ant nests were absent. Other signs of gazelles including body imprints and scraped soil were present on the majority of ant nest discs. Apart from these sites, large pellet aggregation sites, presumably used as latrines were observable especially near water troughs. Latrine sites were substantially larger in size and had higher densities of pellet groups; hence they were easily discernible from smaller pellet groups aggregated at ant nests.

Data collection

Use of ant nest sites by gazelles

To assess the proportion of ant nest sites used by gazelles, the number of ant nests and pellet group aggregation sites were quantified within the study area. Gazelles may use the vegetation communities unevenly (e.g. Nowzari et al. 2007; Hazeri et al. 2009), and such a pattern could affect the use of ant nests by gazelles. On the other hand, nest site selection of ants could be different between the vegetation communities. We therefore quantified the density of ant nest sites used by gazelles in each of the three dominant vegetation communities. The number of large independent patches of each vegetation community was limited to two in our study area, which were selected as experimental replicates. Strip transects with 20-m width and 800-m lengths were randomly established within each of the two replicates of each vegetation community. Stratified random sampling was used to establish transects relative to the area of the vegetation communities (total number of transects in each vegetation community: Sc–Ar: $n=6$; Ar: $n=9$; Ar–An: $n=16$). We mapped the occurrence of ant nest sites with pellet groups (AGP), ant nests with no pellet groups around, and aggregations of gazelle pellet groups (no ant nest), within the transects. As the study area was flat and had a low density of vegetation, ant nest discs or gazelle pellet group aggregation sites were easily detected across the width of the transects.

Intensity, spatial and temporal pattern of ant nest site use by gazelles

To assess the intensity of use of ant nest sites by gazelles, we compared pellet group density in plots centred on ant nest sites and adjacent ‘paired control plots’ where ant nests were absent. We also located a number of independent ‘random plots’ ($n=62$) across the study area to compare gazelle pellet group density in ant nest sites with the mean of gazelle pellet group density in the study area. We were also interested to see whether the intensity of use of ant nest sites by gazelles was similar between vegetation communities, and or bimonthly time periods. Within each of the two patches of each vegetation community (replicates), three points were randomly selected and at each point a temporary 500 m × 500 m square plot was established. Within each of these larger plots, 3 or 4 AGP sites were opportunistically selected to be

monitored year around. To meet the independence assumption of observations, ant nests were selected at least 100 m apart. For each AGP site, a permanent 5 m × 5 m square plot, which was large enough to cover the ant nest disc, was centred on the ant nest (AGP plot). The four corners of the plots were marked with painted stones, and the geographic coordinates of the plots were recorded by GPS. A paired control plot, with no sign of ant nests or dung piles, was placed c. 100 m away from each AGP plot by walking in a random direction. Overall, 56 pairs of plots in the three vegetation types were established (total pairs of plots in each vegetation community: Sc–Ar: $n=16$; Ar: $n=20$; Ar–An: $n=20$). To estimate the initial mean pellet group density (standing crop) for the first sampling period (September 2009), we established independent 5 m × 5 m plots ($n=62$) in the studied vegetation communities. All existing pellet groups, defined as faecal pellet clusters with the same shape and colour, were counted in AGP, paired control and independent random plots. Immediately after the standing crop count, pellet groups were cleared from AGP and paired control plots in preparation for the pellet group accumulation count (see Putman 1984; Mayle et al. 1999). The accumulated pellet groups were thereafter counted and cleared from the plots every two months over a complete year. Although the decomposition rate of pellet groups was expected to be similar for all plots and intervals, we roughly assessed pellet group disappearance by marking at least 6 relatively fresh pellet groups in each vegetation type. None of the marked pellet groups disappeared entirely between two consecutive visits or over the whole study period.

To calculate the proportion area of oval-shaped ant nest discs in relation to the whole study area, the shortest and longest diameters of selected ant nest discs were measured.

Vegetation density and composition

To assess the impact of ant activities on ground vegetation, we compared shrubs and annual herbs percent cover, shrub species richness and diversity between AGP and paired control plots. To quantify percent cover of shrubs within both AGP and paired control plots we used a 20 cm × 20 cm frame and estimated the number of frames needed to cover the shrub’s canopy. We subsequently calculated the total area covered by vegetation in each plot. The mean height of shrub species was measured using a graduated rule. All shrubs within each plot were counted and identified and the diversity of shrub species was estimated using Simpson’s diversity index (Simpson 1949). Percent cover of annual herbs was visually estimated in April when the vegetation cover was fully grown.

Soil physicochemical properties

To determine the impact of ant nest building activities on soil physicochemical properties, the percent of stone and gravel covering the surface of plots was estimated. For soil physical and chemical analysis, soil blocks (20 cm long, 10 cm wide and 20 cm deep) were collected from the centre

of the AGP ($n = 56$) and in paired control plots ($n = 56$). Soil samples were air-dried and sieved through 2-mm mesh prior to analysis. Soil texture (hydrometer method, Klute 1986), organic matter (Walkley and Black Method 1934, Weaver, Angle, & Bottomely 1994) and electrical conductivity (using a conductivity metre JENWAY model: 4310) were measured for each sample. For measuring available phosphorus (mg/kg) and total nitrogen (%), using Olsen and Kjeldahl method, respectively (Weaver et al. 1994), only 20 pairs of plots (out of the total of 56 pairs of AGP and control plots) were selected.

Statistical analysis

To compare the density of ant nests, pellet aggregated sites, and AGP sites between the vegetation communities, either one-way ANOVA or Kruskal–Wallis H -test was used. The non-parametric Mann–Whitney U -test was used to compare gazelle pellet group standing crop density between AGP and randomly selected independent plots across the study area. As with the spatial pattern of ant nest site use by gazelles, faecal deposition rates in both AGP and paired control plots did not differ significantly between the vegetation communities in any bimonthly time period; pellet group accumulation data were therefore pooled across vegetation communities and compared between AGP and paired control plots by Wilcoxon paired-sample test in each bimonthly time period. Paired-sample t -test was used to compare vegetation and soil variables between AGP and paired control plots in each vegetation community.

To control for the effect of gazelle faecal deposition on nutrient elements of the soil, general linear models (GLM) were used with total Nitrogen and or available Phosphorus as dependant variable, presence/absence of ant nests as fixed factor, and accumulated pellet groups on AGP and paired control plots from the beginning of the study to the time of soil sampling, as covariate.

To achieve normality and homogeneity of variances as the assumptions of statistical parametric tests, data were $\log + 1$ transformed wherever appropriate. Non-parametric tests were used where the assumptions were not met even after transformations. All statistical analyses were performed using SPSS (v.16).

Results

Use of ant nest sites by gazelles

Mean area of *Messor* ant nest discs was 4.76 m^2 ($SD = 0.48$) covering only 0.29% (95% CI: 0.0026–0.0032) of the strip transects area. Of the 333 counted *Messor* spp. ant nest sites, gazelle pellet groups were detected on 298 sites (89%). On the other hand, of the total 355 pellet group aggregation sites, 298 were located on ant nests (84%).

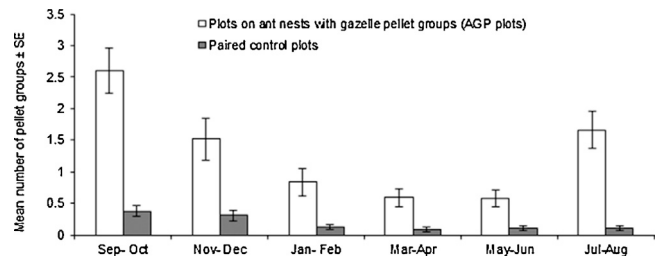


Fig. 2. Mean number of Persian goitered gazelle pellet groups \pm SE accumulated in 25 m^2 AGP (ant nests with gazelle pellet groups) and paired control plots in each two-month period from September 2009 to September 2010.

The density of ant nests, pellet aggregated sites, and AGP sites, did not differ significantly among the three vegetation communities (one-way ANOVA, $P \geq 0.12$).

Intensity, spatial and temporal pattern of ant nest site use by gazelles

Standing crop counts at the beginning of the study showed a highly significant difference in pellet group density between AGP ($18.41 \pm 3.34SE$, $n = 56$) and paired control plots ($1.69 \pm 0.23SE$, $n = 56$) (Paired sample t -test: $t = 14.69$, $df = 55$, $P \leq 0.001$), and between AGP and independent random plots ($0.42 \pm 0.13SE$, $n = 62$) (Mann–Whitney U -test: $Z = -9.641$, $P \leq 0.001$).

No significant difference was detected between the vegetation communities with respect to pellet group accumulation in AGP and paired control plots in each bimonthly sampling period (Kruskal–Wallis H -test, all $df = 2$, $P \geq 0.08$). However, gazelles used AGP plots significantly more than the paired control plots in all sampling periods (Wilcoxon paired-sample test: Sep–Oct: $Z = -5.27$, $P \leq 0.001$; Nov–Dec: $Z = -4.21$, $P \leq 0.001$; Jan–Feb: $Z = -4.43$, $P \leq 0.001$; Mar–Apr: $Z = -3.57$, $P \leq 0.001$; May–Jun: $Z = -3.19$, $P \leq 0.001$; Jul–Aug: $Z = -4.78$, $P \leq 0.001$) (Fig. 2).

Vegetation density and composition

There was a higher percentage of annual herbs in AGP plots compared to paired control plots, but we did not find any significant difference in percent cover, richness, and diversity of shrub species between AGP and control plots (Table 1).

Soil physicochemical properties

The percentage of soil organic matter was significantly higher in AGP plots, while percent cover of gravel was higher in paired control plots (Table 1). Significant differences were detected in the soil particles between AGP and paired control plots, in the *Artemisia* and *Artemisia–Anabasis* communities, but not in the *Scariola–Artemisia* community (Table 1).

Table 1. Results of paired-sample *t*-test comparing soil and vegetation variables between ant nests with gazelle pellet groups (AGP plots) and paired control plots in the three vegetation communities.

	<i>Scariola–Artemisia</i> (<i>n</i> = 16)				<i>Artemisia</i> (<i>n</i> = 20)				<i>Artemisia–Anabasis</i> (<i>n</i> = 20)			
	Mean±SE		<i>t</i>	<i>P</i>	Mean±SE		<i>t</i>	<i>P</i>	Mean±SE		<i>t</i>	<i>P</i>
	AGP plot	Paired control plot			AGP plot	Paired control plot			AGP plot	Paired control plot		
Shrub species richness	4.50 ± 0.34	4.06 ± 0.25	1.13	0.28	3.20 ± 0.31	3.20 ± 0.34	0.0	1	2.40 ± 0.17	2.20 ± 0.25	0.68	0.51
Shrub species diversity	0.63 ± 0.05	0.64 ± 0.03	−0.09	0.92	0.45 ± 0.05	0.41 ± 0.06	0.47	0.64	0.41 ± 0.04	0.34 ± 0.05	0.80	0.43
Shrubs height (cm)	31.25 ± 2.88	33.12 ± 2.99	−0.46	0.65	31.50 ± 2.54	31.00 ± 2.28	0.21	0.83	35.5 ± 3.44	35.5 ± 2.56	0.0	1.00
Shrub canopy cover (%)	3.83 ± 0.64	3.63 ± 0.55	0.24	0.81	3.15 ± 0.39	3.99 ± 0.44	−1.76	0.09	3.81 ± 0.66	3.14 ± 0.54	0.73	0.48
Annual herbs (%)	75.31 ± 4.14	8.56 ± 1.89	16.53	≤ 0.001	50.50 ± 4.67	2.30 ± 0.82	9.89	≤ 0.001	36.75 ± 3.45	0.95 ± 0.40	10.72	≤ 0.001
<i>Artemisia</i> (%)	0.72 ± 0.19	1.16 ± 0.30	−1.79	0.07	1.72 ± 0.32	2.88 ± 0.34	−2.45	0.02	2.29 ± 0.49	1.45 ± 0.38	1.48	0.15
<i>Scariola</i> cover (%)	0.45 ± 0.16	1.05 ± 0.44	−1.55	0.13								
<i>Anabasis</i> cover (%)									0.79 ± 0.16	1.37 ± 0.3	−1.83	0.08
Gravel (%)	64.06 ± 4.60	91.25 ± 2.52	−4.45	≤ 0.001	58.00 ± 4.51	74.25 ± 5.09	−3.24	0.004	69.50 ± 2.23	94.25 ± 1.59	−8.56	≤ 0.001
Soil Organic matter (%)	1.22 ± 0.13	0.59 ± 0.08	4.86	≤ 0.001	0.95 ± 0.10	0.48 ± 0.06	3.64	0.002	0.93 ± 0.11	0.48 ± 0.06	3.53	0.002
EC ^a (log transformed)	0.48 ± 0.06	0.24 ± 0.04	3.27	0.05	0.40 ± 0.04	0.22 ± 0.03	3.69	0.002	0.41 ± 0.04	0.40 ± 0.08	1.69	0.109
Sand (%)	50.48 ± 2.94	49.08 ± 4.10	0.37	0.71	62.86 ± 1.54	54.47 ± 2.42	3.01	0.007	64.17 ± 1.97	50.54 ± 2.38	5.86	≤ 0.001
Silt (%)	37.64 ± 2.32	37.43 ± 3.61	0.09	0.93	26.69 ± 1.36	32.21 ± 1.86	−2.28	0.03	24.22 ± 1.92	33.17 ± 2.40	−3.75	0.001
Clay (%)	11.83 ± 1.04	13.49 ± 0.92	−1.18	0.26	10.45 ± 0.73	13.32 ± 1.23	−2.40	0.03	11.61 ± 0.76	16.29 ± 1.40	−3.45	0.003

^aEC, electrical conductivity.

Table 2. GLMs obtained by relating total N and P to the two sets of plots (AGP: ant nests with gazelle pellet groups, and paired control plots), and number of gazelle pellet groups accumulated within the 25 m² plots from the beginning of the study to the time of soil sampling.

	Total N			Available P		
	F(d.f.)	B ± SE	P	F(d.f.)	B ± SE	P
Model	4.11 (2,36)		0.02	24.18 (2,34)		≤0.001
AGP plot	7.08 (1,36)	0.02 ± 0.009	0.01	12.99 (1,34)	0.115 ± 0.032	≤0.001
Paired plot		0			0	
Number of pellet groups	6.08 (1,36)	−0.003 ± 0.001	0.02	6.30 (1,34)	0.013 ± 0.005	0.02
R ²		0.19			0.59	

Parameters for AGP plots show their effect relative to the mean for paired control plots (assigned reference value of zero), while controlling for accumulated pellet groups.

Available P was significantly higher in AGP (mean ± SE: 0.26 ± 0.04 mg/kg) compared to paired control plots (mean ± SE: 0.06 ± 0.01 mg/kg) (Paired sample *t*-test: *t* = 4.64, *df* = 19, *P* ≤ 0.001), but total N was not significantly different between the two sets of plots (mean ± SE: AGP plots: 0.05 ± 0.01%, control plots: 0.03 ± 0.01%; paired sample *t*-test: *t* = 1.53, *df* = 19, *P* = 0.14). Controlling for pellet group density (to control for extra N and P entering the sites through gazelle dung), the differences in both total N and available P between AGP and paired control plots became significant with significant effect of pellet groups (Table 2).

Discussion

Use of ant nest sites by gazelles

Messor nest sites covered about 0.29% of the sampled transects. However, 84% of the gazelle pellet group aggregation sites were positioned upon this type of ant nests, suggesting that gazelles have actively selected *Messor* spp. ant nest sites. The general pattern of ant nest occupation by gazelles was similar between the vegetation communities. Ant nest sites located in different vegetation communities were similar in terms of vegetation and soil physicochemical properties, as they have been affected by harvester ant activities and gazelle droppings (including nutrients and annual plants seeds) added to the sites later on. This may be a reason why use of ant nest sites by gazelles did not differ between the vegetation communities.

Vegetation and soil properties

At the micro scale, comparison between physicochemical and vegetation properties in AGP and paired control plots revealed that ant activity altered top soil composition. Other studies obtained similar results (e.g. Cammeraat et al. 2002; Folgarait et al. 2002; Cammeraat & Risch 2008; Whitford et al. 2008). Our study showed that ant's nest-building activities increase soil organic matter and electrical conductivity (EC). Soil from AGP plots contained more organic matter than paired control plots in all three vegetation communities. The biological activities of ants (Whitford & Dimarco 1995;

Frouz et al. 2003; Cammeraat and Risch 2008; Ginzburg et al. 2008), in addition to litter accumulation from seed debris and annual herbs are the main sources of organic matter in ant nest sites. Higher soil organic matter provides a more suitable substrate for growing annuals. In addition, faecal pellets deposited on ant nest sites import herbal seeds to the soil seed bank (Schutz et al. 2008) and act as fertilizer facilitating the growth of annual herbs (Apio et al. 2006).

Proportion of mineral components (sand, silt, clay) may be a less important factor affecting ant nest site selection by gazelles compared to percentage gravel of top soil, as we did not detect significant differences in percentage particles between AGP and paired control plots in one of the three vegetation communities (*Scariola–Artemisia*). Gazelles had however used ant nest sites in the *Scariola–Artemisia* community as intense as other vegetation communities. In all vegetation communities, however, the percent gravel was significantly lower in AGP plots compared to the paired control plots, which could be related to nest site selection by ants. In addition, ants bring up soft soil from deeper layers of the soil covering gravel on the ground.

Intensity, spatial and temporal patterns of ant nest site use by gazelles

Use of ant nest sites by gazelles was not limited to a certain time period (Fig. 1) or vegetation community (Table 1). Different hypotheses may be formulated to speculate about the reason of gazelle pellet group aggregation on ant nest sites:

- (1) Pellet group aggregation on ant nest sites may be the result of gazelle territoriality behaviour during the rut. Aggregation of gazelle pellet groups on small areas has been related to territorial behaviour of males (Walther et al. 1983; Estes 1991). Gazelles usually use natural landmarks for demarcating their territories (Walther et al. 1983; Attum & Mahmoud 2012). As most of Persian goitered gazelle habitats in our study area lack conspicuous features that could be used for marking territories, ant nest sites could be potentially used as landmarks by the gazelles. In Kolah-Qazi N.P., rutting period of Persian goitered gazelle occurs only in December.

However, accumulation of pellet groups at AGP plots showed continued and selective use of ant nests by gazelles throughout the year, suggesting that this is not an indication of the territorial breeding behaviour of this species. Although, marking behaviour is most intense during the rut, male goitered gazelles continue marking their territories throughout the year (Blank 1992). Therefore, territoriality remains a possible reason for aggregation of gazelle pellet groups on ant nest sites, albeit there may be additional reasons for use of ant nest sites by gazelles.

- (2) Gazelles may use ant nest sites for grazing on annual herbs. Building activities of ants have impacts on soil characteristics including an increase in soil nutrients (Lavelle et al. 1997, 2001; Barros et al. 2001, this study). This along with seed harvesting behaviour of ants results in increased coverage of annual herbs on ant nest discs (Table 1). Persian goitered gazelle prefer fresh annual plants when available (Jamsheed 1976). Increased availability of annual herbs on ant nests (Table 1) may attract gazelles to these sites. We did not quantify the density of annual herbs in the bimonthly sampling periods except April. However, it was obvious that annual herbs were not heavily grazed as their fresh or dried biomass could be observed throughout the year on ant nest sites. Furthermore, it is documented that mammalian herbivores (e.g. dik–dik *Madoqua kirkii*, Grant's gazelle *Gazella granti* and impala *Aepyceros melampus*) avoid feeding in areas where faecal pellets are accumulated to lower the risk of infection by gastro-intestinal tract parasites (Ezenwa 2004). Therefore, such an accumulation of pellet groups cannot solely be related to feeding behaviour of Persian goitered gazelle.
- (3) Gazelles may use ant nest discs as bedding sites. As goitered gazelles devote considerable proportion of their time to resting (Xia et al. 2011), finding suitable places to bed upon is inevitably important. The alterations in the physical characteristics of the soil by ants, particularly reduction in the percentage of gravel and an increase in percentage of sand may provide a smoother environment for gazelle bedding. The fine soil and litter of annual plants in combination with dry faecal material, added later to the substrate, may form an insulation layer. Such a layer may keep the deeper soil cooler or warmer depending on the season, and reducing energy loss through conduction when gazelles are bedding. Many animals including gazelles defecate after a long rest and even lie on their faecal pellets (e.g. *Antilope cervicapra* Walther et al. 1983). The accumulation of pellet groups on ant nest sites can therefore be an artefact of bed site selection by gazelles. Walther et al. (1983) and Walther (1978) also pointed out that within territories established by Thompson gazelle *Gazella thomsoni*, dung piles are located in the vicinity of the gazelle bedding sites.

Ungulate faeces contain odoriferous substances that may be used for social communication (Wronski et al. 2006). Whether gazelles use AGP sites for demarcating their territories or use them as bedding sites, the olfactory importance of their accumulated faecal pellets at AGP sites should not be neglected. Scent transmission through excreta may assist in information exchange between group members and repelling intruders (Wronski et al. 2006; Wronski & Plath 2010).

The existing literature on direct interaction of invertebrates and large vertebrates has mainly scrutinized their parasitic relationship, but very few studies have been undertaken to examine facilitative interactions that positively affect vertebrates. For instance, termite and ant activities provide sodium-rich soil for many primate (e.g. Chimpanzee, *Pan troglodytes* and Bonnet macaque, *Macaca radiata* consume termite mound soil; Masked titi monkey, *Callicebus personatus melanochir* and Moustached tamarin, *Saguinus mystax* eat soil of leaf-cutting ant mounds; see Krishnamani & Mahaney 2000) and ungulate species (e.g. sable antelope, *Hippotragus niger variani* eats termite mound soil; Baptista et al. 2012); ants remove external parasites from the nest of birds (Clayton & Vernon 1993; Hart 1997); and assist in eliminating egg predators of the lizard *Mabuya longicaudata* (Huang 2008).

The direct interaction between harvester ants and Persian goitered gazelle demonstrated in this study highlights the importance of considering partnered species' impacts on patterns of resource use by the target species in studies of habitat use. Such interactions may have important consequences to community structure, diversity, productivity and dynamics (Bertness & Callaway 1994). Further studies should be conducted to clarify if the use of ant nest sites by gazelles is individual-, gender-, or family-specific and what is the circadian rhythm of the use. Also, the reason why ant nest sites are extensively used by gazelles, the importance of seed harvester ants on the ecology of gazelle species, and whether or not the interaction between gazelles and ants is mutualistic, deserve more attention.

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