Behavioural Processes 167 (2019) 103922

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

Does intraspecific competition among Allenby's gerbils lead to an Ideal Free Distribution across foraging patches?

Douglas F. Makin*, Burt P. Kotler

Mitrani Department of Desert Ecology, Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Midreshet Ben-Gurion, 8499000, Israel

ARTICLE INFO

Keywords:
Competition
Distribution
Foraging
GUDs
Harvest rates
IFD
Resources

ABSTRACT

Employing the Ideal Free Distribution (IFD) principle as a tool, we investigated how Allenby's gerbils (*Gerbillus andersoni allenbyi*) utilized food patches within and moved between connected quadrants (i.e., 'habitats') in a large outdoor semi-natural enclosure. These habitats differed in initial forager densities, but provided equal numbers of standardized food patches that provided equal rewards (i.e. food) and costs (i.e. predation risk, metabolic, and missed opportunity). We quantified the gerbils' giving-up-densities (GUDs) within foraging patches and recorded their daily distribution between habitats. Individual gerbils were tagged with unique barcoded numbers to compare their locations within and across habitats. The mean number of gerbil foragers (9.1 and 8.9 individuals, respectively) and GUDs evened out across habitats over time. Despite this, the distribution of gerbils did not remain static within foraging patches; instead, gerbils altered their use of patches across and within habitats on a nightly basis. This may be due to a combination of factors including, high levels of interference competition between foragers at patches, a lag effect before the gerbils perceived changes in competition intensity with the arrival and departure of individuals, and gerbils having imperfect knowledge of their environment. Furthermore, the pattern of microhabitat (open vs bush patches) use by gerbils differed over time, indicating that despite the distribution of gerbils and their GUDs evening out between habitats, they still preferred foraging from safer bush patches over riskier open patches. This study provides insights into how under low predation risk, strong levels of intraspecific competition can shape the distribution of foragers across and within habitats.

1. Introduction

Animals consider a number of factors when deciding where to forage, including, competition (Brown, 1988; Kotler and Brown, 1990), resource availability (Hochman and Kotler, 2007; Sih, 1998), landscape features (Lynch et al., 2014; Valeix et al., 2010), and perceived predation risk (Brown, 1999; Creel et al., 2014; Lima and Bednekoff, 1999). In the absence of predators or in areas with low predation risk, competition for resources has been observed to be a major driver of habitat and patch selection, which becomes amplified with increased forager densities (Morris, 1987; Rosenzweig, 1981; Rosenzweig and Abramsky, 1985). Competition can take the form of aggressive interactions between individuals contesting limited resources, passive interference through chemicals released by conspecifics (i.e. interference competition), or exploitation of resources through their foraging performance (Berger-Tal et al., 2015; Dolman, 1995; Kotler and Brown, 1990; Valeix et al., 2007).

Density-dependent competition has been studied for several different desert rodents (Berger-Tal et al., 2015; Hughes et al., 1994; Kotler and Brown, 1988,1990; Lima et al., 2008). For example, dune hairy-footed gerbils (*Gerbillurus tytonis*) in the Namib desert responded to high intraspecific competition by reducing their individual rates of activity in preferred bush microhabitats, leading to lower foraging rates at food patches (Hughes et al., 1994). With a reduction of intraspecific competition through competitor removal, gerbils were able to increase their activity in preferred bush microhabitats and reduce the missed opportunity costs associated with high interference competition (Hughes et al., 1994). Mitchell et al. (1990) recorded a strong negative intraspecific effect between foraging time and increased competitor densities in Allenby's gerbil in the Negev Desert. Berger-Tal et al. (2015) found that competing Allenby's gerbils had reduced foraging rates in patches and increased vigilance levels in the presence of competitors. In contrast, China et al. (2008) found that both Allenby's and greater Egyptian (*Gerbillus pyramidum*) gerbils foraged in a density dependent manner and had higher individual foraging rates as the activity density of foragers increased.

* Corresponding author.
E-mail addresses: doug.makin4@gmail.com (D.F. Makin), kotler@bgu.ac.il (B.P. Kotler).

https://doi.org/10.1016/j.beproc.2019.103922
Received 3 September 2018; Received in revised form 25 June 2019; Accepted 31 July 2019
Available online 01 August 2019

At higher population densities, there are fewer resources available per capita, and foragers should value energy more (Brown, 1988), leading competitors to exploit resource patches more thoroughly (i.e., increase foraging effort) as they place greater value on acquiring energy. Consequently, patch use should be negatively density dependent (Kotler and Brown, 1990; Shrader et al., 2008). At the same time, competition among foragers may reduce the marginal benefits of foraging more than the marginal costs, giving rise to a reduction in per capita foraging effort (i.e. amount of food harvested) with increased competition (Mitchell et al., 1990). This may be due to lower initial food abundance in the patches, lower harvest rates due to lower encounter rates with less common food resources, higher energetic costs associated with competition (i.e. fighting), or increased social monitoring (i.e. vigilance) in the presence of multiple foragers (Berger-Tal et al., 2015).

The Ideal Free Distribution (IFD) model developed by Fretwell and Lucas (1969), assumes that individuals choose the habitat that offers the highest fitness. As more individuals occupy that habitat, the overall level of competition increases, and the quality and attractiveness of the habitat decreases. As this occurs, other habitats should become relatively more attractive, resulting in other foragers settling or moving there. Consequently, the distribution of foragers across habitats at the IFD reflects the foragers' inability to increase their energetic payoff by unilaterally shifting from one patch to another as fitness equilibrates across habitats (Fretwell and Lucas, 1969).

To explore whether patterns of patch use selection reflect an IFD over time in the face of intraspecific competition, we studied the density-dependent habitat selection patterns of Allenby's desert gerbil across two adjacent habitats. These habitats differed in initial forager densities, but were identical in the number of resource patches, microhabitats (bush and open patches), level of predation risk, and the amount of food in each patch. Using the IFD as a predictive tool, we observed how foragers distributed themselves across foraging patches each night and how thoroughly they depleted patches within each habitat.

We present three alternative hypotheses. Firstly, in regards to the distribution of individuals, gerbils will respond to greater forager densities by shifting their use of resource patches to areas with fewer competitors, thus achieving a stable and equal distribution of individuals across habitats over time in accordance with the assumptions of the IFD model. Alternatively, foragers may not distribute themselves evenly, but rather vary their temporal and spatial use of habitats over time to equalize food harvested and activity densities (population density and individual activity) as individuals move back and forth between and within habitats. Secondly, in regards to patch use, gerbil' giving-up-densities (GUDs; the amount of food left in a patch after an animal has quit feeding) will equilibrate across habitats over time as the distribution and activity density of gerbils evens out across foraging patches. Alternatively, if gerbils do not distribute themselves evenly across habitats over time in regard to numbers, GUDs will be lower in the habitat with the highest starting forager densities as increased density-dependent competition for food increases individual gerbil foraging efforts within patches. Lastly, in regards to microhabitat use, if gerbil foraging behavior is influenced primarily through predation risk, as shown in previous studies (Embar et al., 2011; Kotler et al., 1994, 2010), then gerbils should preferentially feed from and achieve lower GUDs in bush microhabitat patches where they perceive a lower risk of predation. Alternatively, if density dependent competition costs of foraging are higher than the costs of predation risk, then gerbils should show a more even use of patches across safe and risky microhabitats (i.e. similar GUDs in bush and open microhabitat patches). In this situation, individuals may be forced to allocate more time to feeding in riskier open patches due to higher competition costs.

2. Materials and methods

All experiments below are compliant with Ben Gurion University IACUC guidelines.

2.1. Study area

We conducted our study over 10 days in March 2018 and for an additional three replicates of 10 days each during February and March 2019, for a total of 4 complete replicates. We set up our experiments in a large outdoor vivarium (17 × 34 × 4.5 m) exposed to natural environmental conditions (Embar et al., 2014). The study was conducted on the Sede Boker Campus, Ben-Gurion University located in the Negev Desert of Israel (30°52′N, 34°47′E). The vivarium is sub-divided into four equally sized quadrants (8.5 × 17 m) that are separated by rodent proof fences (Bleicher et al., 2016; Embar et al., 2014). The floor of the vivarium is comprised of loess soil covered with a deep layer of sand into which gerbils readily dig and establish their burrows (Embar et al., 2011).

2.2. Data collection

For this study we used adult female Allenby's gerbils that had been trapped in the same field location, thus, likely experiencing similar environmental conditions, food availability, and predator presence. All trapped gerbils were maintained in our climate-controlled animal room in individual boxes (30 cm × 20 cm) prior to the experiment. Allenby's gerbil is a commonly occurring desert rodent in the Negev Desert that has been extensively studied as a model organism for community dynamics (Abramsky et al., 1996; Kotler and Brown, 1990) and responses to perceived predation risk (Bleicher et al., 2016; Kotler et al., 1992). We injected the gerbils subcutaneously with uniquely numbered barcoded radio-frequency-identification PIT tags to identity each gerbil. PIT tag readers built into feeding trays and coupled with a data logger (see below) allowed us to record for each patch: the number of visits, the time and duration of each visit, the identify of each visitor, and the total time spent in a patch by all foragers. For each replicate of the experiment, we released 12 gerbils into one quadrant (habitat one) and 6 gerbils into the another (habitat two). To test whether gerbils responded to increased intraspecific competition by shifting their use of foraging patches to a habitat with fewer competitors, we allowed gerbils to move between habitats and foraging patches through an automated tunnel system. The tunnel (27 × 9 × 10 cm) comprised an open-ended plastic rectangular box through which gerbils could move from one habitat to the other. The tunnel was equipped with an automated gate that responded to the gerbil's unique PIT tag identification number and was programmed to allow selected individuals with pre-determined PIT tag numbers to move through by unlocking the gate. Gerbils moving through the tunnel were required to push the gate open to access the other side. A dual PIT tag reader was connected to the ends of the tunnel system to record the identity of each gerbil that moved through the tunnel, the time of movement, and the direction of movement. From this and the pit tag readers under each foraging patch, we could determine the nightly distribution of gerbils across the two habitats. For all replicates, one week prior to the study we released the gerbils into the vivarium and habituated them to the artificial food patches and the tunnel system.

We recorded the distribution and movement of gerbils over 10 nights, replicated 3 times, with an initial distribution of 12 and 6 individuals located across habitats one and two, respectively. To remove any idiosyncrasies associated with individual quadrants we also rotated the starting densities of gerbils (i.e. habitats one and two) between the quadrants alternating between replicates. The distribution of gerbils was defined as the ratio of the number of gerbils located (from the unique PIT tag numbers) in habitat one divided by the number of gerbils in habitat two on a nightly basis. We selected three individual gerbils from each habitat and programmed the tunnel system to allow only these individuals to move through the tunnel. Therefore, for each habitat, only three individuals were free to move between habitats while remaining individuals were free to move within habitats. This ensured that the distribution of gerbils resulted from the directional movement of individuals in response to increased intraspecific competition and not from random movement of all individuals (i.e. Brownian motion) between quadrants over time.

To determine whether the foraging effort of gerbils within patches reflected their distribution across the quadrants, we recorded gerbil' GUDs in artificial food patches. GUDs provide a measure of feeding effort within patches in response to the perceived costs of foraging at that patch by recording the amount of food remaining in a patch after an animal has abandoned it (Brown, 1988; Carthey and Banks, 2015). This in turn provides an index of an animal's quitting harvest rate (residual predation risk) within patches (Brown, 1988; Kotler et al., 1991; Schmidt et al., 1998). Differences in foragers' quitting harvest rates reflect habitat-specific differences in predation risk managed through time allocation (Brown, 1999).

Each artificial patch comprised a plastic tray measuring 30 × 30 × 5 cm filled with 3 litres of sifted sand into which we mixed 6 g of millet (*Pennisetum glaucum*) seeds. We set up 8 evenly distributed artificial foraging patches within each habitat, for a total of 16 patches per replicate. The matrix of sand provides diminishing returns to seed harvest rates for foragers as they deplete the patch (Kotler et al., 2010). The average daily metabolic rates (ADMR) recorded for Allenby's gerbils are 22.30 (Kj day^{-1}) with millet seeds providing 18.83 (Kj g^{-1}) of gross energy (Degen, 2012). Therefore, the average gross energy available per gerbil per night was 100.42 (Kj g^{-1}), thus ensuring that gerbils were provided with sufficient food within each habitat per night to meet their daily energetic needs.

Following each experimental night, we recorded which patches the gerbils had foraged in and sifted the remaining millet seeds to obtain their GUDs (Embar et al., 2014; Kotler et al., 2001). To replicate landscape features within the gerbils' natural habitats of bush and open microhabitats, we covered four artificial patches in each quadrant with a low-lying wooden trellis (76 × 60 × 16 cm) covered in black shade cloth and topped with cut brush to simulate a bush. We further placed four artificial patches per quadrat in the open. The PIT tag readers associated with all 16 artificial foraging patches allowed us to calculate the cumulative amount of time each gerbil spent in each patch per night within each habitat. From this, we were able to calculate the cumulative duration gerbils spent feeding from the artificial patches, which along with the GUDs, allowed us to estimate handling time and attack rates from Holling's disc equation and generate quitting harvest rate curves for the gerbils (Kotler and Brown, 1990; Kotler et al., 2010).

Holling's disc equation (Holling, 1959) describes resource harvesting for a forager, i.e., $\partial \mathbf{N}/\partial \mathbf{t} = (\mathbf{a \times N}) / (\mathbf{1 + a \times h})$, where N is the GUD, t is the time spent foraging, a is the attack rate based on the foragers search time and encounter rate, and h is the handling time required by the forager to process and consume the food item. By integrating the above equation over patch residency from initial to final resource density and solving for t, we obtain the following equation that can be used to estimate handling time and attack rate parameters and describe gerbil risk management behavior (Kotler and Brown, 1990): $\mathbf{t = 1/a(LN(Initial/GUDs) + h(Initial - GUDs)}$. Attack rate (a) and handling time (h) are estimated by regressing time in the patch against LN(Initial/GUDs) and (Initial - GUDs), respectively, using the known initial amount of food in a resource patch (6 g of seed), the final amount (GUD), and the cumulative time gerbils spent exploiting each patch (Kotler and Brown, 1990). To avoid negative coefficients obtained from the linear regression of Holling's disc equation, we used a constant handling time of 22.883 s/g estimated in previous trials (see Kotler et al., 2010). As harvest rate is a direct function of the density of food in a patch, we can utilize GUD as an index of an animal's quitting harvest rate (Schmidt et al., 1998). Curves of different slopes indicate different levels of vigilance, with shallower harvest rate curves reflective of slower harvest rates for any given seed density indicating greater vigilance. If foragers have similarly sloped harvest rate curves, but GUDs vary, this indicates differing use of time allocation for risk management, with lower GUDs reflecting greater time allocation to feeding (Kotler et al., 2010). Quitting harvest rate curves provide an effective method for visually portraying how animals use time allocation and vigilance to manage predation risk while foraging from resource patches (Kotler et al., 2010).

2.3. Data analysis and statistics

To compare the mean distribution of gerbils across the habitats over time, and the nightly distribution of gerbils across habitats one and two (ratio of gerbils located in habitat one divided by the number of gerbils located in habitat two), we ran Kruskal-Wallis tests for non-parametric data, with gerbil distribution as the dependent variable and night as the explanatory variable. To compare gerbil GUDs in foraging patches across quadrants each night, we used a generalized linear mixed effects model (GLMM) with Gamma errors (Zuur et al., 2009). Gerbil GUDs served as the dependent variable, while habitat (one and two) and microhabitat (bush and open patches) served as explanatory variables including interactions between variables, and patch position (1–8) was nested within habitat. Nights were included as a random factor.

3. Results

Despite beginning with twice as many gerbils in one habitat than in the other, there was no significant difference in the mean number of gerbils located across the habitats of foraging patches over time, with an average ratio of 9.1 and 8.9 gerbils located across foraging patches in habitats one and two, respectively ($X_{1,180}$ = 0.02, P = 0.870). Although, the proportion of gerbils located nightly within habitats fluctuated around the IFD ratio over time, this was not significantly different ($X_{10,18}$ = 10.00, P = 0.440; Fig. 1). That is, gerbils quickly reached and maintained an IFD.

As expected for animals selecting habitats according to an IDF, patch use by gerbils did not differ across habitats, but did across microhabitats within habitats according to the risk of predation. In particular, mean gerbil GUDs did not significantly differ between habitats one and two over time ($X^2_{1,610}$ = 0.13, P = 0.716; Fig. 2; Table 1). Furthermore, gerbils preferred foraging in bush patches rather than open patches ($X^2_{1,610}$ = 42.13, P < 0.001), and this did not differ between the two habitats ($X^2_{1,610}$ = 1.13, P = 0.286; Table 1; Fig. 2). The results of patch location nested within habitat indicates that the use of patches by gerbils did not differ for the two habitats ($X^2_{7,\ 610}$. = 0.92, P = 0.996).

Comparing how gerbils traded off time allocation to foraging with remaining vigilant within patches across the two habitats changed during the course of the experiments as animals moved and more closely approximated an IDF. During days 1–3 of the trial, gerbils in habitat one (higher starting density) allocated more time to foraging and had lower levels of vigilance (steeper quitting harvest rate curve; Fig. 3a) than gerbils foraging in habitat two (lower starting density), thus tending towards lower GUDs. Similarly, during days 4–6 of the trial, gerbils in habitat two employed greater levels of vigilance than individuals in habitat one, however, they allocated more time to foraging than during days 1–3 and thus GUDs decreased (Fig. 3b). Finally, by days 7–10, gerbils in habitat two further increased their time allocation to foraging and decreased their investment in vigilance behavior, thus GUDs evened out even further between the two habitats (Fig. 3c).

4. Discussion

Competition for resources is a key factor driving animal foraging decisions (Mitchell et al., 1990; Valeix et al., 2008), habitat use

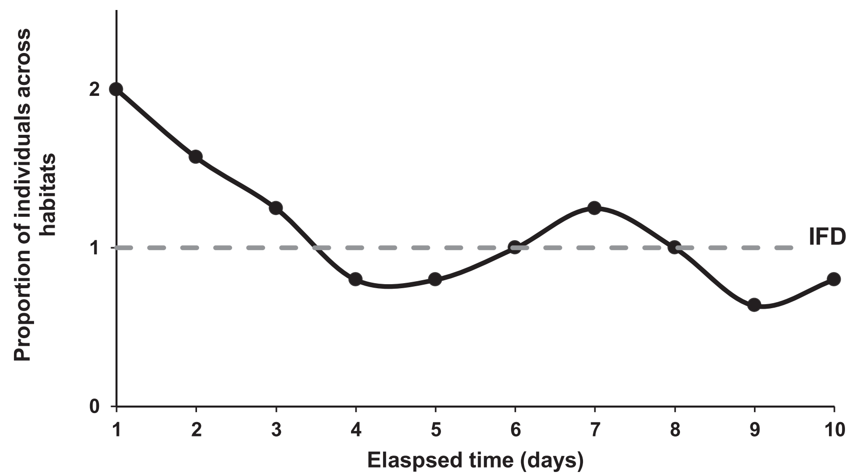

Fig. 1. Ratio of gerbil individuals located in foraging patches across habitats one (12 starting gerbils) and two (6 starting gerbils) over time in relation to the Ideal Free Distribution ratio of 1 (dotted grey line).

(Abramsky et al., 1998; Hanski, 2007), and patch use within habitats (Berger-Tal et al., 2015; Brown, 1988). Competition is not mutually exclusive to other factors contributing to how animals make these decisions, such as predation risk (Brown, 1999), resource distribution (Abrahams, 1986; Kennedy and Gray, 1993), and the availability of habitat features (Shrader et al., 2008; Valeix et al., 2010). Thus, it may be difficult to tease apart the individual factors contributing to decision making processes. This study provided an opportunity to control for some of these factors and determine if under conditions of high intraspecific competition, Allenby's gerbils established a distribution over time that follows the IFD model.

Over time, gerbils responded to increased intraspecific competition within foraging patches across the two habitats by shifting their use of space and selectively foraging in patches with fewer competitors. Thus, over time the average number of gerbils found within patches across habitats equalized, and the gerbils' distribution conformed to an IFD as predicted. However, while they established an IFD based on the average distribution of individuals, gerbils did not always remain static in habitats that offered equal rewards/payoffs once located. Instead gerbils continually moved between and within habitats, and thus they viewed their environment as fine-grained and fluctuated their inter and within-habitat resource patch selection over time (Morris, 1992; Van Beest et al., 2010).

One possible explanation for why gerbil numbers fluctuated between habitats on a nightly basis is that there existed a lag effect between the arrival and departure of gerbils from foraging patches. If gerbil patch use conformed to the assumptions of the original IFD model then travel times between foraging patches would be negligible and involve no costs (Fretwell and Lucas, 1969; Kennedy and Gray, 1993). However, travel times and costs are widely associated with foraging animals moving between patches (i.e. optimal foraging theory; Charnov, 1976), and studies building on the original IFD model have acknowledged these additional costs (Tregenza, 1995). Therefore, nightly fluctuating gerbil densities recorded across the habitats may reflect this movement of gerbils in search of new foraging patches in response to high levels of intraspecific competition. Furthermore, as the gerbils likely do not have perfect knowledge of their environment there will be a lag effect before the gerbils perceive any changes in nightly competition intensity within habitats (Rosenzweig, 1981). For example, this was observed for a population of *Daphnia*, that due to perceptual constraints constantly shifted their vertical distribution at low population densities despite reaching an equilibrium distribution (Maszczyk et al., 2018). In another example, male guppies with imperfect knowledge of their habitat, continued to move between feeding areas despite reaching an IFD distribution over time (Abrahams, 1986). Furthermore, Spencer et al. (1996), showed that variability in individual forager perception can significantly affect the distribution of foragers, with quicker, more perceptive individuals able to monopolize more profitable food patches compared to individuals with greater perceptual constraints.

Another factor that could explain this observation is that high levels of interference competition were driving individual foragers to continuously seek out new foraging patches to avoid aggressive interactions with competitors (Berger-Tal et al., 2015; Hughes et al., 1994; Rosenzweig et al., 1997). This is particularly well documented for Allenby's gerbils that have high recorded levels of interference competition among individuals (Abramsky et al., 1998; Berger-Tal et al., 2015) and very rarely share a foraging patch with conspecifics once located (Ovadia and zu Dohna, 2003). For example, Berger-Tal et al. (2015), investigated the role of intraspecific competition in Allenby's gerbils and found that strong interference competition leads to a tragedy of the commons scenario, where the overall fitness of the group is reduced through individual investment in competitive behaviors. Allenby's gerbils foraging together invested less time in feeding than individual foragers, and dedicated more time to monitoring competitors, leading to pairs of foraging gerbils having reduced foraging success compared to individuals (Berger-Tal et al., 2015). Rosenzweig et al. (1997) recorded in the absence of predation risk that Allenby's gerbils' patterns of patch use and dispersal reflected high levels of intraspecific competition, with individuals aggregating only at low densities and in the presence of predators in order to increase safety through dilution effects. Therefore, there are high costs of interference competition for competing gerbil foragers within patches, with reduced foraging success for both competitors (Berger-Tal et al., 2015). As such, it is likely that the foragers in our study avoided these competitive interactions with conspecifics and continuously searched for patches with fewer or no other competitors to reduce the cost of this negative interaction (Dall et al., 2001; Ovadia and zu Dohna, 2003; Scharf et al., 2008).

Comparing the quitting harvest rate curves of gerbils across the two habitats revealed an interesting pattern of patch use and risk management. Generally, gerbils in the initially lower density habitat had higher levels of vigilance and allocated less time to feeding, even after densities had equilibrated. In contrast, gerbils in the initially higher density habitat allocated more time to foraging while spending less time vigilant. A possible explanation for these initial vigilance differences between habitats is that higher initial competitor densities in habitat one resulted in elevated levels of interference competition among individuals and increased familiarity with potential competitors. Dominant individuals that early on excluded subordinates from patches through aggressive interactions might then be expected to continue to

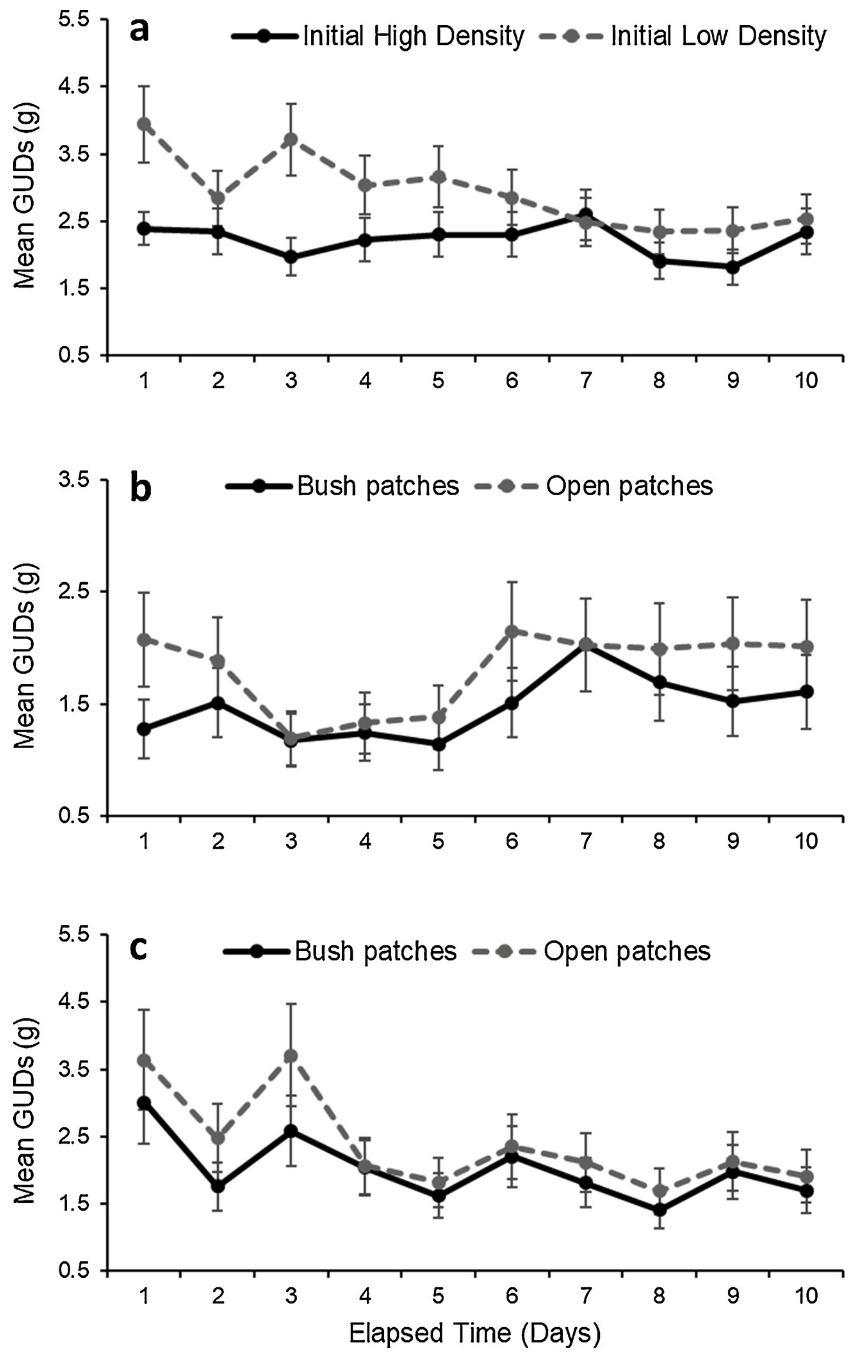

Fig. 2. Giving-up-densities of gerbils over time (days) comparing **a)** the two habitats with initial starting gerbil densities of 12 in habitat one and 6 in habitat two and **b)** bush and open patches in habitat one and **c)** bush and open patches in habitat two. Bars represent SE.

Table 1
Generalized linear mixed effects model (GLMM) comparing gerbil giving up densities (n = 610) between habitats one and two (initially high and low starting gerbil densities, respectively), microhabitats (open and bush patches), including interactions between variables and patch location (1–8) nested within habitat.

Variable	Chisq	DF	P
Habitat	0.13	1	0.716
Microhabitat	42.13	1	< 0.001
Habitat X Microhabitat	1.13	1	0.286
Habitat (Patch)	0.92	7	0.996

maintain dominance over these patches despite the population distribution arriving at an IFD (Berger-Tal et al., 2015). It is possible that dominant gerbils occupied burrows in close proximity to certain foraging patches and retained control over these patches, (Berger-Tal and Kotler, 2010). Therefore, the increased feeding effort and reduced vigilance in feeding patches in habitat one may reflect this, with surrounding individuals of lower competitive rank avoiding dominant competitors which then could allocate more time to foraging and less time to social vigilance and aggressive interactions (i.e. chases; Ovadia, 1999). Furthermore, Ovadia and zu Dohna (2003) observed that Allenby's gerbils with high competitive ranks (i.e. dominance) had lower rates of aggressive interactions once they occupied a patch and thus could dedicate more time to foraging with reduced interference costs. Subsequently, subordinate individuals displaced by stronger

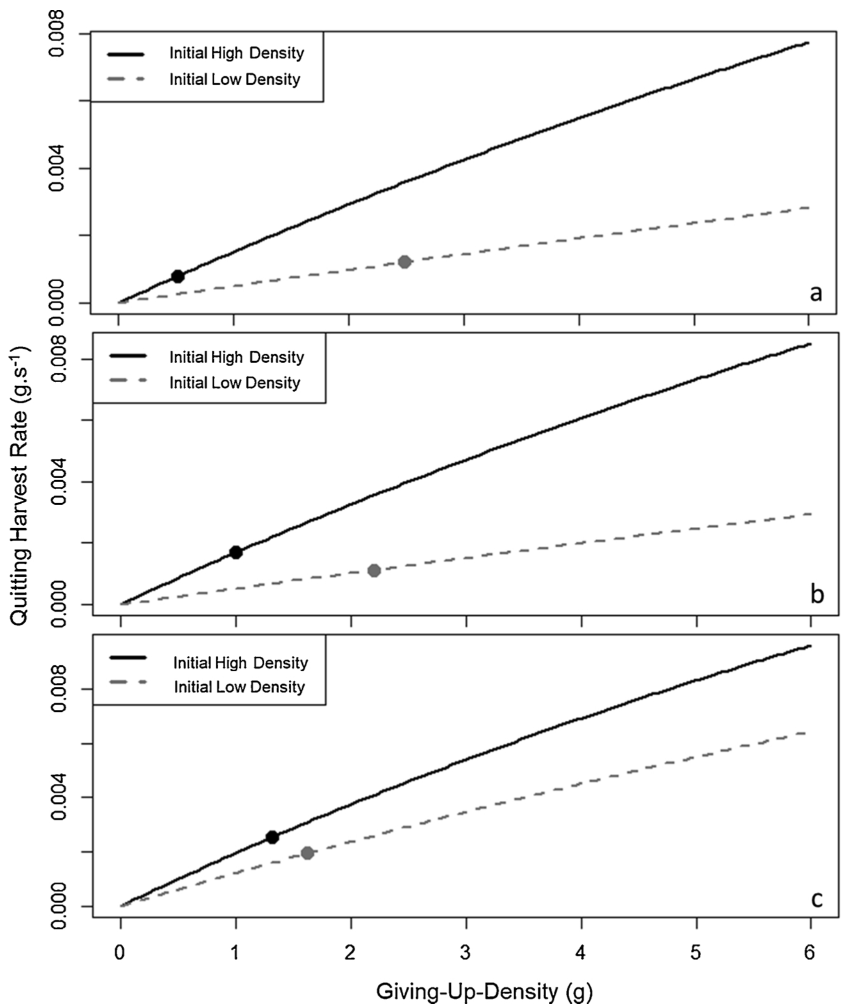

Fig. 3. Quitting harvest rate (QHR) curves for the foraging gerbils comparing habitat one (12 starting gerbils) and habitat two (6 starting gerbils) during a) Days 1–3, b) Days 4–6 and c) Days 7–10. The average giving-up-densities are represented as points on the plot curves.

competitors abandoned and avoided those patches and instead travelled in search of new patches where competition was reduced (Ovadia and zu Dohna, 2003). It is also possible that the reduced vigilance recorded reflected the greater starting density of gerbils in habitat one, where gerbils increased their individual foraging effort at patches due to a greater density of competitors at the expense of lower vigilance. However, as gerbils rarely share patches once located (Berger-Tal et al., 2015), engaging in chasing behavior (Mitchell et al., 1990), the observed pattern likely reflects the monopolization of patches by dominant competitors.

In contrast, in habitat two, fewer competitors initially led to reduced levels of interference competition (i.e. fighting, chases). As such, the establishment of a dominance hierarchy (i.e. patch monopolization) would have taken longer with a greater number of shared patches where individuals may have employed social monitoring (i.e. vigilance) to observe rivals. For example, Berger-Tal et al. (2015) found that Allenby's gerbils had a 50% reduction in foraging success in the presence of a single competitor and reduced time allocation to foraging to watch conspecifics. However, with the arrival of new individuals, density-dependent competition for food, interference competition, and the likely rate of patch monopolization increased. Hence, over days 7–10 we observed that the quitting harvest rate curves recorded for gerbil foragers between the two habitats evened out as individuals in habitat two allocated more time to foraging and less time to vigilance. As such, it is possible that a foraging hierarchy may have been established with dominant individuals holding control over certain foraging patches, with subordinate individuals seeking to reduce intraspecific competition by continuously shifting their use of foraging patches between habitats (Ovadia and zu Dohna, 2003).

It is possible that higher gerbil vigilance rates in habitat two may reflect increased levels of perceived predation risk within those foraging patches. However, as predation risk was low and constant across habitats and giving-up-densities evened out across foraging patches over time, the higher levels of vigilance likely reflect increased social monitoring of conspecifics in patches with multiple competitors instead.

The foraging effort of gerbils at patches should reflect their distribution across habitats as competition for food varies with competitor density. As the mean distribution of gerbils evened out, as predicted, differences in the mean GUDs of gerbils between habitats reflected this distribution and equalized over time. However, gerbils still preferentially fed from and achieved lower GUDs in bush patches rather than open patches. This suggests that although predators were absent, gerbils still retained a higher perception of predation risk when feeding in the open. This supports previous findings comparing Allenby's gerbils use of microhabitats in which they perceive bush microhabitats to be islands of relative safety compared to open areas (Abramsky et al., 1996; Embar et al., 2014; Kotler et al., 1992). Therefore, even in the absence of predators and in the presence of high levels of intraspecific competition, gerbils continued to display this innate preference for the bush patches through increased foraging effort and lower GUDs. As such, patch use patterns by gerbils continued to be influenced by the need to reduce perceived predation risks, despite the higher foraging costs associated with multiple competitors.

To conclude, our study provided an empirical approach to testing how density-dependent intraspecific competition shapes the foraging behavior and patch use patterns of Allenby's gerbil. In line with the original IFD model, the average number of individuals across foraging patches between habitats equalized over time, and this was further reflected in the evening out of giving-up-densities in patches across habitats. Contrary to the original IFD model assumptions, gerbils did not maintain a static distribution across foraging patches, but their use of patches across and within habitats fluctuated on a nightly basis. High levels of interference competition may provide an explanation for this behavior, with subordinate individuals shifting their use of foraging patches to minimize negative aggressive interactions associated with more competitive individuals (Ovadia and zu Dohna, 2003; Scharf et al., 2008). It appears less energetically costly to increase travel times between foraging patches than incur high energetic costs through increased interference competition (i.e. chases and possible risk of injury). Additionally, travel time lag effects between the arrival and departure of individuals likely affected the gerbils perception of changes in competition intensity, which combined with their likely imperfect knowledge of the environment may also have contributed to changes in their nightly distribution between and within habitats. Understanding how intraspecific competition affects the distribution of individuals across foraging patches is important as it strongly influences individual foraging decisions and thus the marginal value of feeding from a particular patch in the presence of competitors.

Acknowledgments

We would like to thank Stuart Summerfield for his contribution in developing the RFID and tunnel system employed. Jorge Menezes and Joel Brown provided helpful comments on the manuscript. Four anonymous reviewers and Douglas Morris provided constructive comments on the manuscript. This work was supported by the Israel Science foundation [grant number: 976/14]. DFM received financial support as a receipient of a postdoctoral fellowship from the Jacob Blaustein Center for Scientific Cooperation. This is publication 1038 from the Mitrani Department of Desert Research.

References

Abrahams, M.V., 1986. Patch choice under perceptual constraints: a cause for departures from an ideal free distribution. Behav. Ecol. Sociobiol. 19, 409–415.
Abramsky, Z., Rosenweig, M.L., Subach, A., 1998. Do gerbils care more about competition or predation? Oikos 75–84.
Abramsky, Z., Strauss, E., Subach, A., Riechman, A., Kotler, B., 1996. The effect of barn owls (Tyto alba) on the activity and microhabitat selection of Gerbillus allenbyi and *G. Pyramidum*. Oecologia 105, 313–319.
Berger-Tal, O., Embar, K., Kotler, B.P., Saltz, D., 2015. Everybody loses: intraspecific competition induces tragedy of the commons in Allenby's gerbils. Ecology 96, 54–61.
Berger-Tal, O., Kotler, B.P., 2010. State of emergency: behavior of gerbils is affected by the hunger state of their predators. Ecology 91, 593–600.
Bleicher, S.S., Brown, J.S., Embar, K., Kotler, B.P., 2016. Novel predator recognition by Allenby's gerbil (*Gerbillus andersoni allenbyi*): do gerbils learn to respond to a snake that can "see" in the dark? Isr. J. Ecol. Evol. 62, 178–185.
Brown, J.S., 1988. Patch use as an indicator of habitat preference, predation risk, and competition. Behav. Ecol. Sociobiol. 22, 37–47.
Brown, J.S., 1999. Vigilance, patch use and habitat selection: foraging under predation risk. Evol. Ecol. Res. 1, 49–71.
Carthey, A.J., Banks, P.B., 2015. Foraging in groups affects giving-up densities: solo foragers quit sooner. Oecologia 178, 707–713.
Charnov, E.L., 1976. Optimal foraging, the marginal value theorem. Theor. Popul. Biol. 9, 129–136.
China, V., Kotler, B.P., Shefer, N., Brown, J.S., Abramsky, Z., 2008. Density-dependent habitat and patch use in gerbils: consequences of safety in numbers? Isr. J. Ecol. Evol. 54, 373–388.
Creel, S., Schuette, P., Christianson, D., 2014. Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. Behav. Ecol. 25, 773–784.
Dall, S.R.X., Kotler, B.P., Bouskila, A., 2001. Attention, apprehension and gerbils searching in patch. Ann. Zool. Fenn. 38, 15–23.
Degen, A.A., 2012. Ecophysiology of Small Desert Mammals. Springer Science & Business Media, New York.
Dolman, P.M., 1995. The intensity of interference varies with resource density: evidence from a field study with snow buntings, Plectrophenax nivalis. Oecologia 102, 511–514.
Embar, K., Kotler, B.P., Mukherjee, S., 2011. Risk management in optimal foragers: the effect of sightlines and predator type on patch use, time allocation, and vigilance in gerbils. Oikos 120, 1657–1666.
Embar, K., Raveh, A., Hoffmann, I., Kotler, B.P., 2014. Predator facilitation or interference: a game of vipers and owls. Oecologia 174, 1301–1309.
Fretwell, S.D., Lucas, H.L., 1969. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheor. 19, 16–36.
Hanski, I., 2007. Spatial patterns of coexistence of competing species in patchy habitat. Theor. Ecol. 1, 29–43.
Hochman, V., Kotler, B.P., 2007. Patch use, apprehension, and vigilance behavior of Nubian Ibex under perceived risk of predation. Behav. Ecol. 18, 368–374.
Holling, C.S., 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. Can. Entomol. 91, 293–320.
Hughes, J.J., Ward, D., Perrin, M.R., 1994. Predation risk and competition affect habitat selection and activity of Namib Desert gerbils. Ecology 75, 1397–1405.
Kennedy, M., Gray, R.D., 1993. Can ecological theory predict the distribution of foraging animals? A critical analysis of experiments on the ideal free distribution. Oikos 158–166.
Kotler, B.P., Ayal, Y., Subach, A., 1994. Effects of predatory risk and resource renewal on the timing of foraging activity in a gerbil community. Oecologia 100, 391–396.
Kotler, B.P., Blaustein, L., Brown, J.S., 1992. Predator facilitation: the combined effect of snakes and owls on the foraging behavior of gerbils. Ann. Zool. Fenn. 29, 199–206.
Kotler, B.P., Brown, J., Mukherjee, S., Berger-Tal, O., Bouskila, A., 2010. Moonlight avoidance in gerbils reveals a sophisticated interplay among time allocation, vigilance and state-dependent foraging. Proc. R. Soc. Lond. B. 277, 1469–1474.
Kotler, B.P., Brown, J., Oldfield, A., Thorson, J., Cohen, D., 2001. Foraging substrate and escape substrate: patch use by three species of gerbils. Ecology 82, 1781–1790.
Kotler, B.P., Brown, J.S., 1988. Environmental heterogeneity and the coexistence of desert rodents. Annu. Rev. Ecol. Syst. 19, 281–307.
Kotler, B.P., Brown, J.S., 1990. Rates of seed harvest by two species of gerbilline rodents. J. Mammal. 71, 591–596.
Kotler, B.P., Brown, J.S., Hasson, O., 1991. Factors affecting gerbil foraging behavior and rates of owl predation. Ecology 72, 2249–2260.
Lima, M., Ernest, S., Brown, J.H., Belgrano, A., Stenseth, N.C., 2008. Chihuahuan Desert kangaroo rats: nonlinear effects of population dynamics, competition, and rainfall. Ecology 89, 2594–2603.
Lima, S.L., Bednekoff, P.A., 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. Am. Nat. 153, 649–659.
Lynch, E., Northrup, J.M., McKenna, M.F., Anderson, C.R., Angeloni, L., Wittemyer, G., 2014. Landscape and anthropogenic features influence the use of auditory vigilance by mule deer. Behav. Ecol. 26, 75–82.
Maszczyk, P., Babkiewicz, E., Czarnocka-Cieciura, M., Gliwicz, Z.M., Uchmański, J., Urban, P., 2018. Ideal free distribution of Daphnia under predation risk—model predictions and experimental verification. J. Plankton Res. 40, 471–485.
Mitchell, W.A., Abramsky, Z., Kotler, B.P., Pinshow, B., Brown, J.S., 1990. The effect of competition on foraging activity in desert rodents: theory and experiments. Ecology 71, 844–854.
Morris, D.W., 1987. Spatial scale and the cost of density-dependent habitat selection. Evol. Ecol. 1, 379–388.
Morris, D.W., 1992. Scales and costs of habitat selection in heterogeneous landscapes. Evol. Ecol. 6, 412–432.
Ovadia, O., 1999. Integrating Behavioural Responses of Individual Gerbillus allenbyi and G. Pyramidum (*Rodentia: Gerbillinae*) with Their Measured Population Responses. Beer-Sheva: Ben-Gurion University of the Negev.
Ovadia, O., zu Dohna, H., 2003. The effect of intra-and interspecific aggression on patch residence time in Negev Desert gerbils: a competing risk analysis. Behav. Ecol. 14, 583–591.
Rosenzweig, M.L., 1981. A theory of habitat selection. Ecology 62, 327–335.
Rosenzweig, M.L., Abramsky, Z., 1985. Detecting density-dependent habitat selection. Am. Nat. 126, 405–417.
Rosenzweig, M.L., Abramsky, Z., Subach, A., 1997. Safety in numbers: sophisticated vigilance by Allenby's gerbil. P. Nat. Acad. Sci. 94, 5713–5715.
Scharf, I., Filin, I., Ovadia, O., 2008. An experimental design and a statistical analysis separating interference from exploitation competition. Popul. Ecol. 50, 319–324.
Schmidt, K.A., Brown, J.S., Morgan, R.A., 1998. Plant defenses as complementary resources: a test with squirrels. Oikos 81, 130–142.
Shrader, A.M., Brown, J.S., Kerley, G.I.H., Kotler, B.P., 2008. Do free-ranging domestic goats show 'landscapes of fear'? Patch use in response to habitat features and predator cues. J. Arid Environ. 72, 1811–1819.
Sih, A., 1998. Game theory and predator–prey response races. In: Dugatkin, L.A., Reeve, H.K. (Eds.), Game Theory and Animal Behavior. Oxford University Press, Oxford, pp. 221–238.
Spencer, H.G., Kennedy, M., Gray, R.D., 1996. Perceptual constraints on optimal foraging: the effects of variation among foragers. Evol. Ecol. 10, 331–339.
Tregenza, T., 1995. Building on the Ideal Free Distribution, Adv. Ecol. Res. Elsevier.
Valeix, M., Chamaillé-Jammes, S., Fritz, H., 2007. Interference competition and temporal niche shifts: elephants and herbivore communities at waterholes. Oecologia 153, 739–748.
Valeix, M., Fritz, H., Matsika, R., Matsvimbo, F., Madzikanda, H., 2008. The role of water abundance, thermoregulation, perceived predation risk and interference competition in water access by African herbivores. Afr. J. Ecol. 46, 402–410.
Valeix, M., Loveridge, A.J., Davidson, Z., Madzikanda, H., Fritz, H., Macdonald, D.W.,

2010. How key habitat features influence large terrestrial carnivore movements: waterholes and African lions in a semi-arid savanna of north-western Zimbabwe. Landsc. Ecol. 25, 337–351.
Van Beest, F.M., Mysterud, A., Loe, L.E., Milner, J.M., 2010. Forage quantity, quality and depletion as scale-dependent mechanisms driving habitat selection of a large browsing herbivore. J. Anim. Ecol. 79, 910–922.
Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Modelling for Nested Data, Mixed Effects Models and Extensions in Ecology With R. Springer.