



## Defense by exploitation in Negev gerbils

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### ABSTRACT

In this study, we addressed how frequently a non-traplining animal should visit food patches. More specifically, we investigate if non-traplining animals engage in a behavior called "defense by exploitation", which is characterized by an increase in visitation rates with increased intra-specific competition. We ran four tests with two gerbil species in the Negev Desert. Firstly, we measured patch use of *Gerbillus pyramidum* and *Gerbillus andersoni allenbyi*. We assumed that activity and competition would decrease through the night and that patch use would decrease with number of visits. Secondly, we measured how the number of visits to resource patches increased with the addition of individuals. Thirdly, we repeated this experiment, but instead removed individuals. Lastly, we conducted a simulation to compare these results against theoretical expectations. In the first test, we found support for defense by exploitation in *G. pyramidum*. The second and third test found no support. The fourth test found support for this increase visitation, but only if costs of locomotion are relatively small.

### 1. Introduction

Most animals revisit food patches, passing frequently through the same places when searching for food. The frequency and order of these visits connect an animal's habitat preference to its movement which are both fundamental topics in ecology. The former is a central aspect of ecology (Morris, 2003; Nathan et al., 2008), and the latter is a key point to individual survival. Despite its importance, visits were initially ignored in the first models of foraging theory (Charnov, 1976; MacArthur and Pianka, 1966), since it was commonly assumed, for simplicity, that the environment could not be depleted. Eventually, studies acknowledged that food can be limited, and that animals should revisit their patches. It was proposed that optimal visitation rates should be related to food renewal (Possingham and Houston, 1990). Animals should come back to a patch with such frequency that the patch would be fully renewed when the animal returns. This concept gave rise to an entire research topic focused on traplining species that visit patches in a fixed circuit (Thomson et al., 1997). Many studies in this subject addressed the optimal order of visits (e.g. Reynolds et al., 2013).

Patch visits are not determined solely by food renewal rates, nor it is only important for trapliners. One foraging ecology model predicted that animals may return to patches before resources are renewed (Erwin, 1989), and studies of traplining hummingbirds showed that competition increases visitation rates (Garrison and Gass, 1999; Paton and Carpenter, 1984). These increases in visits were thought to be a defense mechanism against competition (Paton and Carpenter, 1984).

Animals would try to exploit shared patches earlier and more quickly than their competitors. Exclusive patches would be visited later (Paton and Carpenter, 1984). This defense mechanism, based on shifting visitation patterns, was termed "defense by exploitation" (Paton and Carpenter, 1984). Although first discovered in trapliners, we expect that this defense may be employed by animals that visited patches in a less organized manner. Even if animals do not visit patches in an order, an increase in patrolling effort may keep competitors away. Thus, in this study, we ask whether defense by exploitation can be found in non-traplining animals.

Defense by exploitation is the pattern of interest, but resource defense theory offers alternative predictions that cannot be ignored. Resource defense theory suggests territorial defense is highest at intermediate population densities (Grant, 1993). At high population densities, the high cost on fighting for resources makes it less profitable, decreasing the use of territorial defenses (Grant, 1993). Under this theory, we can expect an alternative visitation pattern: a hump-shaped curve in visitation rates, with higher visitation *per capita* on intermediate densities.

Resource defense theory also provides a prediction to the intensity of resource consumption, which defense by exploitation does not. Under this theory, we would predict resource consumption to follow the same pattern as visitations. At first, small consumption with very low predator density, since there are not enough animals to significantly change resource density. At intermediate levels, there are enough animals to significantly depress resource levels and for competition to

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occur. At very high densities the consumption decreases, either because predators are too invested in fights and contests for the resource, or because the resource has become rare or extinct due to over-exploitation. Since we employ artificial food patches to test for defense by exploitation (see Methods), we can test for this prediction on resource consumption as a collateral.

In summary, we developed three hypotheses: 1) Increasing competition will lead to increased visitation rates to patches (defense by exploitation); 2) Increasing competition will create hump-shaped pattern in the number of visits (resource defense theory); 3) Increasing competition will create a hump-shaped pattern in resource consumption by patch (resource defense theory).

## 2. Materials and methods

To test these three hypotheses, we developed four tests. The first test was done in the field, test two and three on an enclosure and test four in a computer simulation. Through these four experiments, we estimated visits directly by videotaping trays or indirectly by using giving-up densities (GUDs; the inverse of resource consumption in a patch) to estimate it. Giving-up densities were also interesting on themselves as they allow testing the effect of competition on consumption.

We carried out the first test in the field to provide a realistic setting. However, we had to measure visits indirectly through GUDs. Doing so requires a design that makes it impossible to test if consumption has a u-shaped curve as predicted by resource defense theory. This design is based on measuring GUDs hourly throughout the night, and in a certain assumption: gerbils reduce their activity as resources are depleted through the night, (Ziv et al., 1993). That assumption implies two potential consequences. 1) Competition should decrease as the night advances, and 2) if gerbils are diminishing their foraging activity (instead of other alternative activities), they must either: reduce the number of patches visited while keeping visit duration constant; reduce the visit duration while keeping visits constant; or reduce both a little. Thus, for a given period of night there is a finite amount of time gerbils can forage, which should be split between patches. Based on these two conditions, we can measure competition as inverse of time since sunset, and the number of visits as directly proportional GUDs.

In the second test, we manipulated the number of individuals in an enclosure, and recorder number of visits between days. This allows us to test all three hypotheses, but it required an enclosure. Our enclosure was an outdoor semi-natural enclosure with one species of gerbil (*Gerbillus andersoni allenbyi*). In this experiment, we set up cameras and measured patch visits directly, in addition to measuring patch use. We also manipulated competition by adding rodents. We then tested whether the number of individuals increases the number of patch visits *per capita*.

In the third test, we repeated the same experiment as the second test with two key differences: We acquired *G. pyramidum*, allowing us to use both species, one on each side of the enclosure. We also started the experiment with a large population and removed rodents instead of adding. This allowed us to disentangle the effect of number of individuals from the effect of time (experimental day, i.e., experience).

In the fourth test, we conducted a computer simulation in which we created a landscape comprised of food patches. This allowed us to see the interaction of travel costs with competition. This information may help us to understand how distance between trays and other spatial features may influence the results of the previous experiments. In this virtual experiment, we tested whether energetic efficiency increases with the number of visits.

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

### 2.1. Test 1 — Field test

To test for our field hypothesis, we set up a study area in a sand

dune habitat at Kemahin, in the Negev Desert in Israel (34.4223 E, 30.9304 N, unprojected, WGS84). The area has low pluviosity precipitation (34–310 mm yearly; Israel Meteorological Service, 2017) and high variation in temperature (–5 to 46 °C; Yair et al., 2008). Vegetation is sparse, with scattered bushes and tufts of grass. We studied two common species of gerbils in the region: *Gerbillus andersoni allenbyi* (De Winton, 1902) and *Gerbillus pyramidum* (Geoffroy Saint-Hilaire, 1803). Both species are granivorous and compete for seeds made accessible by afternoon winds that blow and deposit them in wind shadows and depressions (Ben-Natan et al., 2004; Rosenzweig and Abramsky, 1986). *G. pyramidum* is larger and is known to competitively dominate *G. a. allenbyi* (Wasserberg et al., 2006; Ziv et al., 1993).

In this area, we set up a 4 × 3 grid, with stations separated by 20 m. At each station, we placed a plastic tray near a bush to serve as a food patch. In each tray, we thoroughly mixed 3 g of millet seeds into 3 L of sifted sand. Gerbils exploiting such trays experience diminishing returns in food consumption as they deplete the resource patch (Kotler and Brown, 1990). To measure patch use, we employed the giving-up density technique. To do so, we measured the amount of food left in the patch after an animal has quit foraging from the patch. Since foraging takes time, the lower the giving-up density the more time has been spent in the patch. We measured giving-up densities for trays made available to gerbils. All trays were available during the whole night (20:00 – 06:00) and they were renewed every two hours. During the renewing process, we collected giving-up densities resulting on density measures for each two-hour period in a night (20:00 – 22:00, 22:00 – 24:00:00 – 02:00, 02:00 – 04:00, 04:00 – 06:00). To renew trays, we started by approaching each tray at the end of a 2-hour period and recording which species of gerbil was the last to visit, based on tracks in the sand of the tray (similar to Garb et al., 2000; Kotler et al., 2002). If the tray had been visited and tracks were visible, we sieved the tray's sand to remove the remaining millet seeds, and replenish the tray with a new 3 g of seeds. We cleaned each seed packet (i.e. sand, dry leaves) and weighed the remaining seeds using an electronic balance (with precision of ± 0.005 g), to obtain the giving-up densities (GUDs). Non-visited trays were discarded. We collected data from 24 to 26 of April 2015.

To statistically test our hypothesis, we divided our data into trays last foraged by *G. a. allenbyi* and trays last foraged by *G. pyramidum*. For the former we used a linear regression with giving-up density as the response variable and the hour as the explanatory variable. Since we had more trays foraged by *Gerbillus pyramidum*, we used a generalized additive mixed model with giving-up density as the response variable, hour as a fixed variable, and a combination of station and day as a random factor. This method allowed us to consider the effect of station and day without restricting our inference to those specific days. In addition, it allowed us to model nonlinear effects without assuming a specific function. However, it requires a large sample size (> 100 samples) which prevented us from using the same approach on the *G. a. allenbyi* data (Zuur et al., 2009).

### 2.2. Test 2 — one-species enclosure test

For our second experiment, we used a semi-natural enclosure located on the Sede Boker Campus of Ben-Gurion University in Midreshet Ben-Gurion, Israel (enclosure dimensions: 17 × 34 × 4.5 m; coordinates: 30.8688 °N, 34.7925 °E; Fig. 1), from 05 to 14 of March 2016. This enclosure has 1 m tall rodent-proof concrete walls, with chicken-wire mesh extending the rest of the way up and enclosing the ceiling. Inside, a 1-m tall galvanized steel wall divides the enclosure into East and West halves. Another 1-m tall wall, of 1-cm hardware cloth, divides the enclosure into North and South halves. Together these divided the enclosure into 4 quadrants. In this experiment, plastic tunnels that bisected the wire-mesh fence allowed gerbils to move freely between north and south quadrants, separating the enclosure into east and west replicates. In each of the quadrants, we set up two lines of four trays,

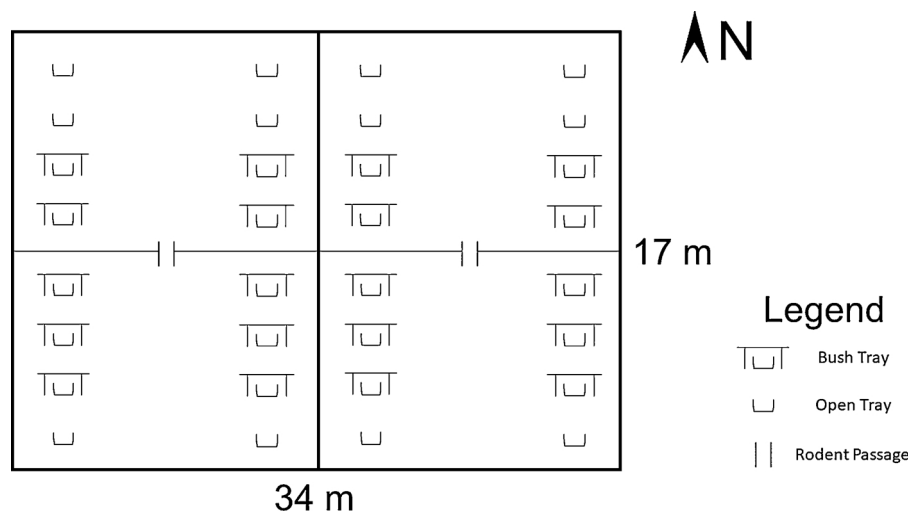


Fig. 1. Schematic representation of enclosure experiment (test 2 and 3).

running north to south. In the south quadrants, the 6 northernmost trays were covered by artificial bushes comprised of low-lying trellises topped with shade cloth, and the last two were in the open. In the north quadrants, the 4 southernmost trays were covered by artificial bushes, and the 4 northernmost trays were in the open. Trays were identical to those used in the field. Gerbils are known to prefer bush habitats (Kotler and Blaustein, 1995). Thus, this arrangement generates a safer region in the middle of the enclosure. We placed four CCTV cameras per quadrant (16 in total), with each camera positioned in a manner that its field of view included two trays, so the numbers of cameras were sufficient to record gerbil foraging at every tray. We placed cameras at the ground level, so that the bush would not interfere with recording gerbil foraging at the trays. Both trays were always visible by their respective camera.

We developed a motion detection algorithm to track gerbils and count the number of visits to each tray. First, videos were recorded by the CCTV system in 1-hour long files. We excluded any video segments before sunset. For every camera and every day, we picked the first video just after we finished working in the enclosure. In those videos, we manually drew a polygon around each tray. We used this polygon to split all videos in two files (one for each tray), to crop each file to fit the tray, and to place a black polygon to cover any area still outside the tray. That preparation prevented the motion detection from considering activity outside the tray. After that preparation, we split the videos into jpeg pictures, one for each second, converted them to gray scale, and used the background subtractor method to detect when movement occurred inside trays. A background subtractor compares the current frames with a background, which is updated by every frame using a specific learning rate. The background subtractor considers as a “movement” every pixel in the current frame that differs from the background by a value greater than a specified threshold. In this study, we used a learning constant of 0.9 and a threshold of 0.3 (in a 0 to 1 grayscale). We considered that a visit had occurred if at least one pixel detected movement. Further, to reduce the chances that camera malfunction would be counted as visits, we also excluded any visits that lasted less than five seconds. On the other hand, to avoid false negatives, we also considered gaps of one to two seconds between sequential visits as part of the same visit. All values were chosen manually as the ones that appeared to maximize gerbil detection and reduce false positives. To measure the accuracy of this process, ten video files were randomly selected, and the number of visits by gerbils were counted manually. The error mean and the root-mean-square error (RMSE) were calculated as measures of bias and precision, respectively. This software was developed in R 3.4.1 (R Core Team, 2016).

To begin the experiment, we released one *G. a. allenbyi* individual

on each side of the enclosure and recorded the number of visits to trays using the camera system. We also collected GUDs from seed trays each morning to validate hypothesis about GUDs in the enclosure. Every day, for 9 days, we then added an extra individual to each side, and repeated the procedure.

To test our hypothesis, we used a linear regression to infer whether the number of visits per capita increased with the number of individuals. Likewise, we used linear regression to test whether giving-up density increased the number of individuals using the tray, as well as the effect of type of tray (bush and open), quadrant (North of South), line (outer-west, inner-west, inner-east and outer-east), and their pairwise interaction as covariates.

### 2.3. Test 3 — two-species enclosure test

For the third experiment we used the same enclosure and followed the experimental design of the previous experiment. However, we started the experiment by introducing 10 *Gerbillus andersoni allenbyi* individuals on the East side and 10 *Gerbillus pyramidum* individuals on the West. All patches were prepared as described for test 1. However, after giving-up densities were collected, we did not reset the patches. Instead, we set 10 Sherman traps on each side, baited with millet seeds. The next morning, we removed one of the captured individuals from the experiment. The others were released on the spot. We then reset the trays with seeds, and continued with the experiment, now with one less individual on each side. In this experiment, we also changed the position of our cameras. Instead of setting each camera to view two trays, we moved them to each focus on a single tray in order to increase accuracy and facilitate processing by the motion detector.

With this new camera layout, pre-existing motion detectors could be used more easily. We thus changed the motion detection by using a background subtractor based on a mixture of gaussians (BackgroundSubtractorMOG2 in the OpenCV 2 library), and a different set of parameters. We set the learning rate to 0.001, the threshold to 50 (measured in a scale from 0 to 255), the minimum number of pixels to consider a visit to 10, and minimum length of a visit to 4.1 s (50 frames) and the minimum gap between visits to 4 s. This analysis was done in Python 2.7 and R 3.4.1 (R Core Team, 2016).

To test our hypothesis, we ran two linear regressions with visits as the dependent variable and number of individuals, habitat, and their interaction as independent variables. We ran one of these for each species. In addition, two linear regressions were performed on giving-up density data, one for each species. Giving-up density was the response variable and type of tray (bush or open), quadrant (north or south), line (outer or inner), number of individuals and their two-way

interaction were the independent variables. We later added the square of the number of individuals as an independent variable, since we observed a quadratic effect.

### 2.4. Test 4 — simulation

To allow us to better integrate the different scales of the field and the enclosure experiments, we created a spatially explicit foraging simulation in which we varied the intensity of competition and travel cost. In this simulation, time progressed in discrete steps. At step 1, we created a landscape comprised of 20 patches. Patches were all equidistant from one another and all initially contained 3 food resource items that differ in their energetic values. The three food resources contained three, two and one energy units respectively. In each time step, a forager could only harvest the most valuable resource within its patch. Thus, a forager experienced diminishing returns in its harvest rates when foraging on the same patch, with 3 energy units being harvested in the first step, 2 in the second, and 1 in the third. An “animal” was then put in a randomly selected patch. At every time-step, each patch had a chance of being removed, i.e. have the number of food resource items set to 0. That probability represents the competition costs, the chance that a competitor (not explicitly modeled) arrived first at the patch and foraged on it until there was no food left. After this patch exclusion, the animal randomly selected a patch among the ones remaining, moved to it (if it was not the current patch), and consumed the most energetically valuable food item present. This process continued until there were no more resource items available to the animal. At this point animal’s efficiency was calculated as:

$$\text{efficiency} = \frac{\text{energy}}{\text{travel costs} * (\text{number of moves} + 1)}$$

Where “efficiency” represented foraging efficiency, a ratio of energy gained over energy lost. “energy” represents the number of energy units consumed. “number of moves” represents the number of times the forager switched patches. “travel costs” is a constant that represent the cost of each movement in energy units. We ran this simulation with competition costs ranging from 0.1 to 0.9 with steps of 0.05 and travel costs ranging from 0.1 to 3.1 with steps of 1. For every combination of these two parameters, we ran 100 simulations, and constructed a linear regression between number of moves between patches and efficiency.

### 3. Results

In test 1, we collected a total of 137 giving-up densities of *G. pyramidum* and 31 of *G. a. allenbyi*. With these data, we found support for our defense by exploitation hypothesis in *G. pyramidum*. As night progressed individuals were more thorough in exploiting their patches ( $F = 12.72$ ,  $e. d. f. = 4.06$ ,  $P < 0.0001$ , Fig. 2). Under our assumption, that implies they were visiting fewer patches in periods with less competition. Hence, competition is correlated with the number of visits. However, we did not find the same result for *G. a. allenbyi* ( $F_{1,30} = 1.075$ ,  $P = 0.308$ ).

In test 2, we estimated 7783 visits by *G. a. allenbyi* individuals, a number which was slightly biased toward underestimation (mean error = -0.2, RMSE = 1.4832 visits per video). Contrary to the defense by exploitation prediction, the number of visits *per capita* showed a non-significant tendency to decrease with the number of individuals ( $t = -1.914$ ,  $d. f. = 3706$ ,  $P = 0.0567$ ). Regarding GUDs, we found that giving-up densities were density dependent and decreased with number of competitors ( $t = -6.330$ ,  $d. f. = 299$ ,  $P < 0.0001$ , Fig. 3). Therefore, neither resource defense or defense by exploitation were supported by this experiment

In test 3, we examined a total of 6498 visits (unbiased; mean error = 0, RMSE = 1.0000) and did not find support for our defense by exploitation hypothesis, for both species. Both species show a reduction in *per capita* rates (*G. a. allenbyi*:  $t = -0.0876$ ,  $d. f. = 1370$ ,  $P <$

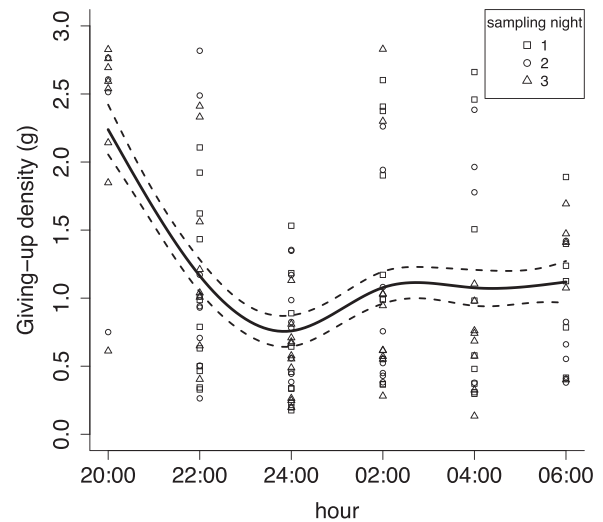


Fig. 2. Effect of night hour on the visitation rates of *G. pyramidum* in Kemahin (24–26 of April 2015). Visitation rate is represented here as giving-up density, the amount of food left on patch. Giving-up density is inversely related to patch use, which we assume is inversely related to number of visits. As animals visit fewer patches on the end of the night and previous studies suggest there is less competition on the end of the night, our result suggests visitation increases with competition.

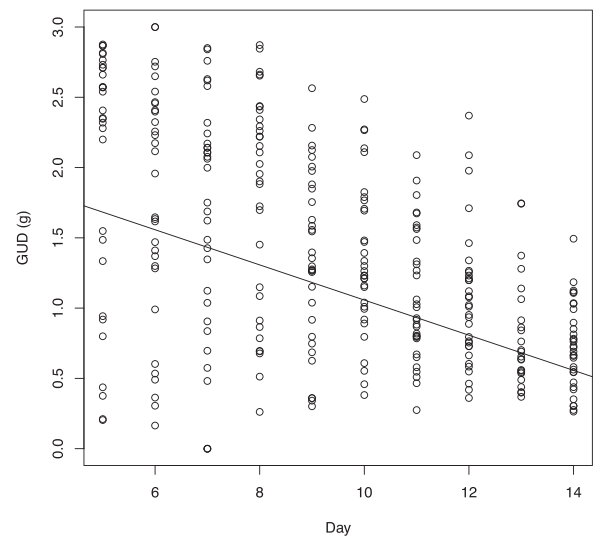


Fig. 3. Effect of density on the giving-up densities of *G. andersoni* in an enclosure in Sede Boker (05–14 of March 2016), where one individual was added per day. Visitation rate is represented here by giving-up density, the amount of food left on patch. Note the pattern is opposite to what was expected by our hypothesis, with number of individuals decreasing giving-up densities.

0.0001; *G. pyramidum*:  $t = -0.0297$ ,  $d. f. = 1352$ ,  $P < 0.0001$ , Fig. 4). However, the giving-up density pattern was more complex. It showed a u-shaped curve with the number of individuals (*G. a. squared*:  $t = 12.228$ ,  $d. f. = 150$ ,  $P < 0.0001$ ; *G. a. allenbyi*. linear:  $t = -12.439$ ,  $d. f. = 150$ ,  $P < 0.0001$ ; *G. pyramidum* squared:  $t = 10.947$ ,  $d. f. = 150$ ,  $P < 0.0001$ ; *G. pyramidum* linear:  $t = -10.747$ ,  $d. f. = 150$ ,  $P < 0.0001$ ; Fig. 5). Once again, all metrics failed to support the hypothesis of defense by exploitation, but we found support for a behavior compatible with resource defense theory on GUDs.

In test 4, we found support for both a linear increase or decrease of visits with competition, thus partially supporting defense by exploitation. Travelling has a positive effect on efficiency when competition is high and travel cost low. When competition and travel costs are high, then traveling more reduces foraging efficiency (Fig. 6). This suggests

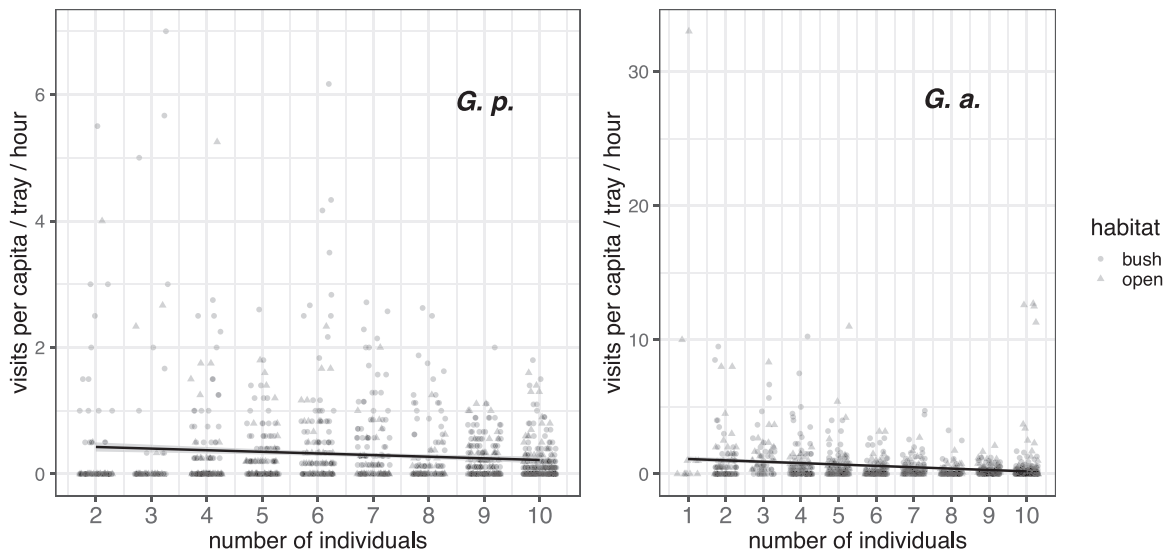


Fig. 4. Number of visits *per capita* per tray and per video of 1 h. Data refers to both *G. andersoni* and *G. pyramidum* in the second vivarium experiment, separated by habitat (bush or open). Note that it decreases with more individuals, the opposite of what is expected by our hypothesis. Points were randomly moved up to 0.3 units on the x-axis to facilitate visualization.

that travel costs play a key role in the benefit of revisiting to protect territories.

4. Discussion

Our results show mixed support for defense by exploitation, and our hypothesis of increased visitation with increased competition. In the field experiment (test 1), we found support for the larger *G. pyramidum* showing a defense by exploitation mechanism. However, this pattern disappears in the second enclosure experiment (test 3). *Gerbillus andersoni allenbyi* also did not show the behavior in either the field (test 1) or any of the enclosure experiments (test 2 and 3), adding to evidence against the hypothesis. Meanwhile, test 4 provides theoretical support for the hypothesis. We found that foraging efficiency can increase with greater number of visits, but this effect is conditioned on low travel costs.

Results for resource defense theory were also mixed. No tests

showed the predicted hump-shaped pattern between competition and visitation. Regarding resource consumption, only test 3 show the predicted hump-shaped. However, the same pattern does not hold in test 2, and cannot be tested in test 1. It remains unclear if resource defense theory can explain gerbil behavior, and if it is more successful than defense by exploitation in describing gerbil foraging.

The evidence refuting the defense by exploitation hypothesis suggests that results in the field might be caused by other factors than competition. Indeed, previous studies showed that patch use is affected by many aspects of animal behavior and its environment, which might be a confounding factor in our experiment. One of those effects is learning. Both gerbils may learn about the environment, which may increase their foraging efficiency (Berger-Tal et al., 2014). This implies that a patch can be foraged more thoroughly and still yield energetic profits, increasing patch use. This mechanism may help explain the decrease in GUDs from one day to the next in test 2, and the descending part in the u-shaped curve of test 3. However, it is unlikely that it would

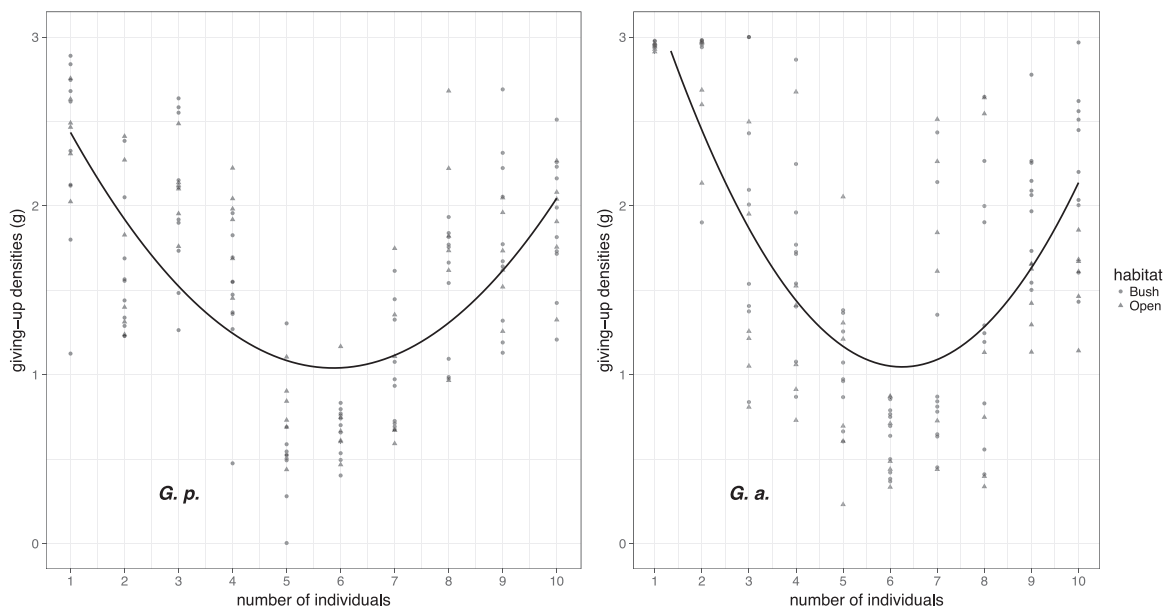
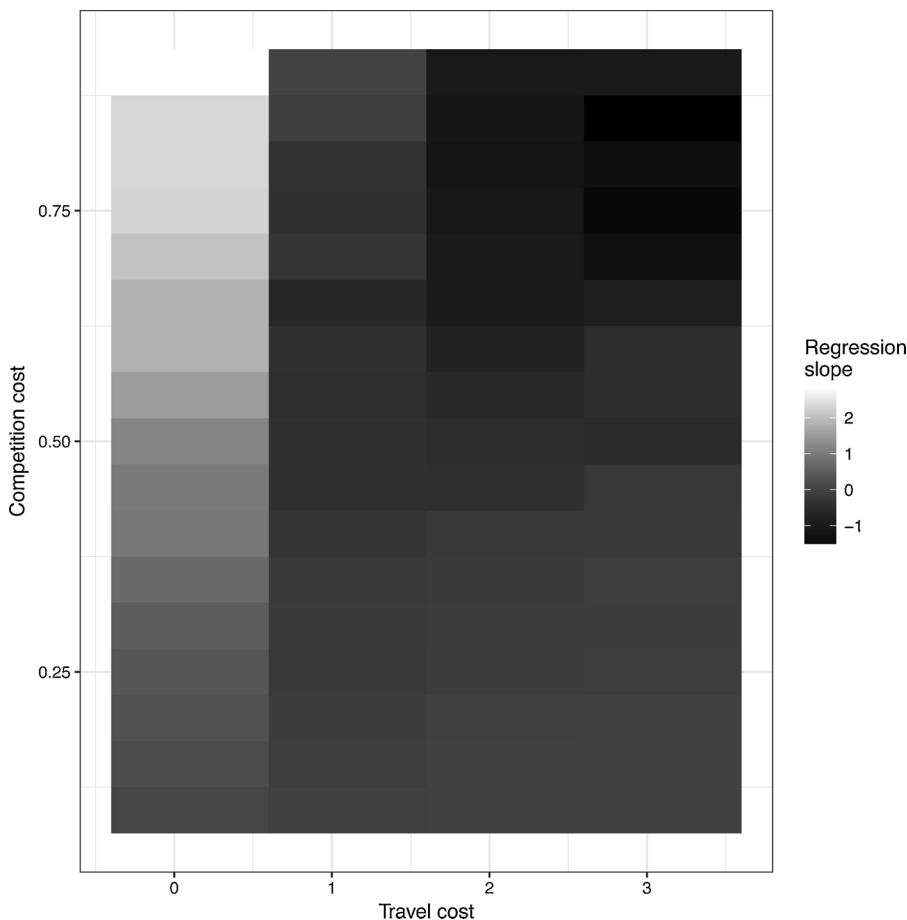


Fig. 5. Giving-up density of *G. andersoni* and *G. pyramidum* in the second vivarium experiment, separated by habitat (bush or open). Giving-up densities is assumed to represent number of visits. Note that it decreases with more individuals, the opposite of what is expected by our hypothesis.



**Fig. 6.** Mosaic plot indicating the slope of the relationship between number of visits and forager efficiency in different levels of travel costs and competition, in a simulation experiment. Supporting our defense by exploitation hypothesis, in high competition scenarios, visiting more patches increases foraging efficiency. However, this is only true for small travel costs (top left corner). For high travel costs competition decreases the efficiency of an animal that visits patches frequently.

decrease *G. pyramidum* GUDs in test 1. If patch use was increasing due to learning we would see a continuous trend, and the value at the beginning of one night would be lower than those at the end of previous one, which is not observed (Fig. 2).

Another potential drawback is our assumption being incorrect, and higher GUDs reflecting a decrease in overall activity. Theory indeed predicts that high competition costs can force an animal to reduce its foraging (Mitchell et al., 1990). That may explain why *G. pyramidum* had higher GUDs at the beginning of the night, since competition is higher during this period. However, this alternative contrasts with previous findings where gerbils *G. pyramidum* foragers early in the night (Kotler et al., 1993). Therefore, we find it an unlikely alternate explanation.

The last confounding effect to consider is interference. When facing high competition, gerbils interrupt each other's forage to dispute patches, resulting in patches being used less (Ovadia and Zu Dohna, 2003). However, this effect was not observed in *G. pyramidum* (Ovadia and Zu Dohna, 2003), which suggests it would play a small role in *G. pyramidum* results.

Test 3's result failed to support the defense by exploitation, however, giving-up density data is compatible with resource defense theory. The u-shaped patterns suggest that animals exploit patches more intensively in high population densities, but at a certain threshold, the costs of competition become too intense to bear and foraging decreases. We are not aware of any other study with similar results. This theory appears to be the most successful in explaining this pattern. Other studies can predict segments of this curve, such as decrease of GUDs (depletion due to competition, Mitchell et al., 1990) or an increase (interference competition, Ovadia and Zu Dohna, 2003; predation risk, Brown et al., 1988), but only resource defense has connected both. Resource defense theory explains both the decrease of GUDs (enough

animals are added to allow all patches to be depleted), and the high GUDs (large populations density in a relatively small enclosure leads to constant fighting). Thus, we add more evidence to list of several empirical studies corroborating this theory (e.g. Jensen et al., 2005; Rousseu et al., 2014)

In summary, we found support for resource defense theory (Test 3) and theoretical support for defense by exploitation (Test 4), with empirical support being constrained by assumptions (Test 1). These findings have several implications worth mentioning.

One of those implications is the extra support for animals increasing patch visits when facing competition, given our assumptions are correct. Hummingbirds are known to visit patches more frequently when facing competition, which reduces resource loss (Garrison and Gass, 1999; Gill, 1988; Paton and Carpenter, 1984). Our results also agree with theoretical models of home range. According to one of these models, the more predictable a patch, the less it should be revisited (Spencer, 2012). Since, more animals make it harder to predict resource abundance, it follows that visitation rates should increase with competition. Likewise, studies show that home ranges decrease with competition (Abramsky and Tracy, 1980; e.g. Bond and Wolff, 1999). If animals perform the same amount of activity, which could occur if they are foraging just enough to sustain themselves, this implies that they cycle more frequently among patches in their home ranges, increasing the number of visits. An increase in visits is expected and observed in non-traplining animals.

If competition increases visitation rates to patches, as our field studies suggest under our assumptions, there is one possible implication to its prey population. If the consumer species is a seed disperser, competition should enhance dispersal abilities by forcing the disperser to cycle more among patches. This might be important to conservation, if we consider the opposite trend. Removing an individual that provides

disperser services would also reduce the efficiency of the remaining dispersers, by releasing them from competition and reducing their need to move between patches. Coupled with frugivore susceptibility to hunting (Peres and Palacios, 2007), this mechanism suggests that dispersal services in a community are especially susceptible to hunting pressure.

Another potential effect is a consequence of ecological drift. With more visits, it is possible that animals will forage more frequently in patches, keeping prey standing crop lower. If prey population are kept in smaller numbers by more frequent visits of predators, more visits should increase their chances of extirpation due to ecological drift (Pimm et al., 1988). This implies competition can destabilize predator-prey interactions. This concept goes against classical predictions, where competition among predators tend to be stabilizing (Begon et al., 2006). To reconcile both, we argue that competition among predators is stabilizing if they limit each other's use of the patches. If they defensively overexploit their own patches, then competition will be destabilizing. Continuing this reasoning, territorial predators would have a greater tendency to create unstable communities, since territorial predators would be more likely to overexploit their resources. However, they may gain some stability if they change territory size (Carpenter et al., 1983; Dill, 1983; Smith and Shugart, 1987), which would reduce the pressure on prey population, making this effect amendable.

Defense by exploitation can also decrease species coexistence. If one species responds to another by increasing patrolling, it decreases the chances that a poorer competitor species can survive by using the environment when the first is not active. Therefore, it would inhibit coexistence through spatial lags, as observed in plant metacommunities (Holyoak et al., 2005). Indeed, we do not observe coexistence through spatial lags in gerbil communities. *G. pyramidum* is the superior competitor and it arrives to the patches first. *G. a. allenbyi* is forced into two behaviors. It forages low quality patches in habitats where *G. pyramidum* does not go (Rosenzweig and Abramsky, 1986), and feeds upon the remaining seeds in a patch following exploitation by *G. pyramidum* (Wasserberg et al., 2006).

In summary, *G. pyramidum* revisits more patches when more competitors are present. However, there is no evidence of the same behavior in *G. a. allenbyi*, despite their similar biology and environment. Our results agree with most of the literature in traplining animals, despite rodents not sharing this movement pattern. These results show that patrolling patches to reduce competition is not exclusive of animals with organized routes such as bees and hummingbirds. Such vigilance may pertain to other species, just in a less organized manner.

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