The use of time and space by male and female gerbils exploiting a pulsed resource

Burt P. Kotler, Chris R. Dickman, Gideon Wasserberg and Ofer Ovadia

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Foraging theory postulates that interference is a foraging cost and affects patch exploitation and activity times. One such system contains two species of seed-eating gerbils inhabiting sandy habitats in the Negev Desert of Israel. Low population densities of the dominant species allowed us to examine the interaction between males and females of the subordinate species, *Gerbillus andersoni allenbyi*, as a function of interference and resource renewal. We used giving-up densities (GUDs; the amount of food left in a resource patch when a forager abandons the patch) in seed trays to quantify patch use by gerbils. By placing 6 trays at each foraging station and either presenting all 6 trays at the start of the night (pulse treatment) or presenting one tray at a station 6 times per night (renewal treatment), we were able to manipulate characteristics of resource renewal. We used radio telemetry to obtain an independent assessment of activity. Male and female *G. a. allenbyi* differed in their timing of activity, with males beginning earlier than females and remaining active later. This was most pronounced for the pulse treatment. For the renewal treatment, female activity in trays was more intense early in the night, but thereafter male activity was more intense. At the same time, telemetry showed that males and females did not differ in their total activity in or out of trays. This suggests that males begin their activity on the renewal treatment by exploiting the richest natural patches of seeds. Only later when these are depleted do they move to dominate the renewing seed trays. Finally, females exploited stabilized sand habitats more than did males, especially during the renewal treatment. Taken together, these findings suggest that male *G. a. allenbyi* interfere with foraging in females, causing temporal shifts in their use of space and resources.

B. P. Kotler, C. R. Dickman, G. Wasserberg and O. Ovadia, Mitrani Department of Desert Ecology, Jacob Blaustein Institute for Desert Reserach, Ben-Gurion Univ. of the Negev, Sede Boker Campus, IL-84990 Midreshet Ben-Gurion, Israel (kotler@ bgumail.bgu.ac.il). Permanent address CRD: Univ. of Sydney, School of Biological Sciences, Sydney, NSW 2006, Australia. Present address for GW: Dept of Wildlife Ecology, Univ. of Wisconsin, Madison, WI 53706, USA. Permanent address for OO: Dept of Life Sciences, Ben-Gurion Univ. of the Negev, IL- 84105 Beer Sheva, Israel.

Competition for scarce resources often plays a major role in determining population densities (Ritchie 1990), species interactions (MacArthur 1972), and community structure (Kotler and Brown 1988). Competition may be an indirect interaction among individuals through the exploitation and depletion of resources. Characteristics of individuals such as their encounter rate with resources and their handling times while harvesting resources

(elements that determine resource harvest rates), along with the energetic cost of pursuing and handling food items (Pulliam 1974), help to determine competitive ability in such scrambles (Vincent et al. 1996). Or, competition may be direct and involve aggression and interference (Pimm et al. 1985, Dickman 1991). Body size is one attribute that contributes to the ability of an individual to dominate its competitors and thereby to

monopolize the most profitable times and places (Frye 1983). Such interference can lead to territoriality (Kodric-Brown and Brown 1976), ideal despotic distributions of individuals across habitats (Morris 2003), and source–sink population structures (Pulliam and Danielson 1991) within species. Interference can also lead to segregation between species in space or in time and be pivotal in their coexistence (Rosenzweig and Abramsky 1986).

Foraging theory postulates that interference is a cost of foraging (Kotler and Brown 1988), and as such, it should affect exploitation of food patches and activity times. In general, a forager should exploit a resource patch until its harvest rate of resources in the patch (H) drops to equal its foraging costs (Brown 1988). Typically, these costs include energetic costs (C), predation costs (P), and missed opportunity costs (MOC) of foraging. But it can also include the costs of interference (I). Hence, a forager should exploit a patch until the following is true:

$$H = C + P + MOC + I \qquad (1)$$

A consequence is that an individual that experiences interference while exploiting a particular resource patch will find that patch more expensive to exploit. It will therefore leave that patch at a higher quitting harvest rate and higher resource density (often referred to as the giving-up density, GUD). In the extreme, interference may be so high as to help render the patch unacceptable. If interference is ongoing, the patch may never be exploited by a subordinate individual. Thus, interference can affect an individual's use of space. But if interference is active only when the patch is rich in resources, then the patch may later be profitable when the dominant, interfering individuals have left. Though the patch has been greatly depleted, a subordinate individual can still extract some profit from it providing that the individual's harvest rate is sufficiently high and its energetic and predation costs are sufficiently low. Thus, interference may affect not only an individual's place of activity, but also its timing.

One such system in which interference affects the use of time and space is comprised of two species of seed-eating gerbils that inhabit sandy habitats in the Negev Desert of Israel, Allenby's gerbil (*Gerbillus andersoni allenbyi*, 24 g) and the greater Egyptian sand gerbil (*G. pyramidum*, 39 g; Rosenzweig and Abramsky 1997). These species are known to compete intensively for seed resources and have been shown in controlled experiments to show intraspecific and interspecific density-dependent habitat selection and per capita activity times (Abramsky et al. 1990, Mitchell et al. 1990). The seed resources in this system are produced mainly by ephemeral annual herbs in the late winter and spring. Many of these seeds are exploited by migratory birds, along with resident gerbils, larks, and ants. But those

seeds that are not exploited soon after ripening quickly enter the seed bank in the sand. Then for the remainder of the year, winds out of the west–northwest blow nearly every day with enough force to redistribute sand and seeds. In this manner, wind action creates and renews seed resource patches that are then available to gerbils on a daily basis (Ben-Natan et al. 2004). These seed patches are then depleted daily by granivorous ants, birds, and especially, gerbils. The temporal variability in seed resources provides the axis of environmental heterogeneity that allows for the coexistence of the two gerbils. The body size difference between the two gerbil species provides for tradeoffs in harvest rates of seeds at high density, ability to interfere, and energetic cost of foraging and leads to a tradeoff in foraging efficiency at high versus low resource abundance. The result is temporal partitioning, with the larger *G. pyramidum* monopolizing the early, food rich (but risky) hours of the night through interference (Kotler et al. 1993, Ziv et al. 1993, Ovadia and Dohna 2003) and the smaller *G. a. allenbyi* using its lower energetic cost derived from a smaller body size (Linder 1987) to forage profitably during the later, food-poor (but safe) hours of the night (Kotler et al. 1993, 2002, Ziv et al. 1993). Interestingly, field experiments in which the presence of the larger *G. pyramidum* was controlled experimentally showed that interference from the larger species differentially affected males and females of the smaller species (Ovadia 1999). Specifically, the presence of *G. pyramidum* brought about a significant reduction in the aggression of male towards female *G. a. allenbyi*. Moreover, this pattern was associated with an increase in the body mass and in the survival of female *G. a. allenbyi*. This result suggests that interference can have effects between classes of individuals within a species.

An opportunity to examine intraspecific effects of interference in gerbils occurred in a particularly wet winter (1994–1995) at the Beer Asluj site in the Holot Mashabim Nature Reserve in the Negev Desert of Israel (the site of the research cited above), in which more than 2½ times the mean annual precipitation fell. A consequence of the heavy rains was the development of extensive soil crusts that stabilized nearly all the sand, and greatly reduced the population densities of *G. pyramidum*. This allowed us to study a natural community comprised almost solely of *G. a. allenbyi*, and permitted us further to examine the interaction of males and females as a function of intraspecific interference and resource renewal. We report on a field experiment in which we presented gerbils with resources that were renewed once at the beginning of the night or that were renewed repeatedly throughout. We quantified the timing of nightly activity and ranging behavior for males and for females in relation to these resources with the intent of seeing whether the relationship of males to females when only *G. a. allenbyi* is present is similar to

that of *G. pyramidum* and *G. a. allenbyi* when both are present.

Methods

We performed experiments at Beer Asluj, Holot Mashabim Nature Reserve, Negev Desert, Israel. The area contains mosaics of stabilized and semi-stabilized sand on longitudinal sand dunes. The dominant perennial plant species are *Artemesia monosperma* and *Retama raetam*. *Gerbillus andersoni allenbyi* was the most common rodent during these experiment, with *G. pyramidum*, *G. henleyi* (pygmy gerbil, 12 g), *Meriones sacrementi* (Buxton's jird, 120 g), and *Jaculus jaculus* (common jerboa, 55 g) also present, but rare.

In these experiments, we used two 2.56 ha grids on which we have studied the ecology of gerbils since 1986 (Brown et al. 1994). The grids contain a mix of stabilized and semi-stabilized sand habitats and are situated 100 m apart. For live-trapping, small Sherman traps were arrayed in 9×9 formation with 20 m between stations. Within the 9×9 layout, we used stations located at the intersections of evenly numbered rows and columns (4×4 layout with 40 m between stations) for seed tray stations. Of these, we chose eight stations on each grid to receive seed trays, spaced such that each evenly numbered row and column had two stations at which we placed seed trays.

We conducted three nights of live-trapping prior to the experiment, capturing a total of 67 different individuals of *G. a. allenbyi* in 137 capture events, but no *G. pyramidum* individuals. Male and female individuals of *G. a. allenbyi* were marked according to gender (removal of a single digit outer toe on either the hind left or right foot) to facilitate the identification of tracks in the seed trays (below). In addition, 3 male and 3 female *G. a. allenbyi* on each grid were fitted with radio telemetry collars (single-stage tags mounted on plastic cable ties with 10 cm whip antennae, weighing ~ 1.0 g; Biotrack, Wareham, UK) for a total of 12 radio-collared gerbils.

We provided seed resources to the gerbils using seed trays. The trays measured $60 \times 45 \times 2.5$ cm deep. We provisioned each tray with 3 g of millet seeds mixed thoroughly into 5 liters of sifted sand. Harvest rates of gerbils foraging in these trays fit a Holling's type II functional response disc equation, (Kotler and Brown 1990, Ovadia et al. 2001), and gerbils experience diminishing returns in harvest rates over time while exploiting a tray. Seed trays such as these provide a realistic approximation of natural food patches for gerbils (Lortie et al. 2000).

We wanted to know the rates of depletion of seed resources by gerbils during the course of the night as a function of resource renewal regime. At each station

chosen to contain trays, we arranged 6 seed trays like spokes on a wheel with the corners of adjacent trays touching to form a hexagram and the long axis of each tray radiating out from there (this reduces edge effects, if any). We divided the night into 6 evenly spaced time periods of 1½ hours each, and created different resource renewal regimes as follows. On one grid, we opened all seed trays at the beginning of the night (pulse treatment). On the other, we opened only one tray at a station in each time period (renewal treatment). In every time period, we visited each station. On the grid where we opened all trays at the beginning of the night, we selected a different tray at each station in each time period, identified tracks according to gender on that tray, and collected the remaining seeds from the tray. Revisiting stations and harvesting the next tray six times during the night gave us temporal snapshots of patch depletion. On the other grid, during each time period, we identified tracks according to gender on the opened tray at each station, collected the remaining seeds from the tray, and then opened the next tray. Seeds removed from a tray were returned to the lab, cleaned of sand and debris, and weighed to obtain the GUD. We repeated this for eight nights, rotating which grid received the pulse treatment and which received the renewal treatment each night. GUDs provide a measure of foraging effort and foraging efficiency and can be used to measure foraging costs (Brown 1988). Furthermore, gradual resource depletion and competition ensure that gerbils treat each night as a series of GUDs (Kotler et al. 1993, 2002).

We also used radio telemetry to obtain an independent assessment of gerbil activity. We did so by first establishing a line midway between the two grids, and then, during each time period on each night, locating each radio collared gerbil at least twice while standing at different fixed locations along the line. Bearings were taken using a hand-held 3-element yagi antenna and portable receiver (Titley Electronics, Ballina, Australia). Sequential bearings were taken 1–2 minutes apart to minimize movement error. We recorded time and direction and used these to triangulate an estimate of the animal's location to the nearest station. Pilot trials using stationary radio tags at the study site indicated errors of only ∀ 14 m at 100 m using two bearings and errors of ∀ 11 m using three. This allowed confident assignment of individuals to the nearest seed tray station, and also allowed us to estimate habitat use since we had previously classified each station by sand stabilization type (Brown et al. 1994). We also used modulations in the strength of the radio signal to classify the gerbil as active or resting. The strength of the signal and the apparent rate of the pulses emitted by its transmitter change rapidly and noticeably for an active gerbil because of movement of the antenna as the animal moves or digs (Kenwood 2001). Finally, we also used the radio telemetry data to estimate the ranging behavior of

each gerbil. We plotted each location of each gerbil each night using Arcview. Based on these, we estimated each individual's nightly "home range" using the minimum convex polygon method, along with overlaps in the "home ranges" of radio collared gerbils on each grid each night.

We ran the experiment during May 1996, and analyzed data using log-linear models of multi-way contingency tables and analysis of variance.

Results

Seed tray data

We analyzed GUDs from seed trays using repeated measures ANOVA, with gerbil sex, treatment, grid, and the interaction of treatment and sex as the factors and time period as the repeated measure (Table 1). Overall, males and females did not differ in GUDs. That is, on average, all gerbils regardless of their gender appeared to encounter an equally resource rich environment (between subjects effect of sex). Treatment did affect the amount of seeds left in a tray (between subjects effect of treatment; Fig. 1). Understandably, seed trays at stations receiving the pulse treatment had on average fewer seeds than those at stations receiving the renewal treatment since gerbils had more time to exploit most of those trays. At pulse stations, all seed trays were opened at the beginning of the night and only one was processed at each time period. Thus, only 1/6th of these trays were exposed to gerbil foraging for only one time period, and 1/6th were exposed for as many as six. At renewal stations, all trays were exposed to gerbils for only one time period. Nonetheless, treatment type did not cause one gender to experience richer trays than the other on average (between subjects interaction of sex and treatment). However, there were large effects of time (within subjects effect of time). The amount of seeds left in a tray decreased over the course of the night. This was true, even for seed trays at renewal stations, but the effect was most pronounced for seed trays at pulse stations (within subjects interaction of time and treatment; Fig. 1). More
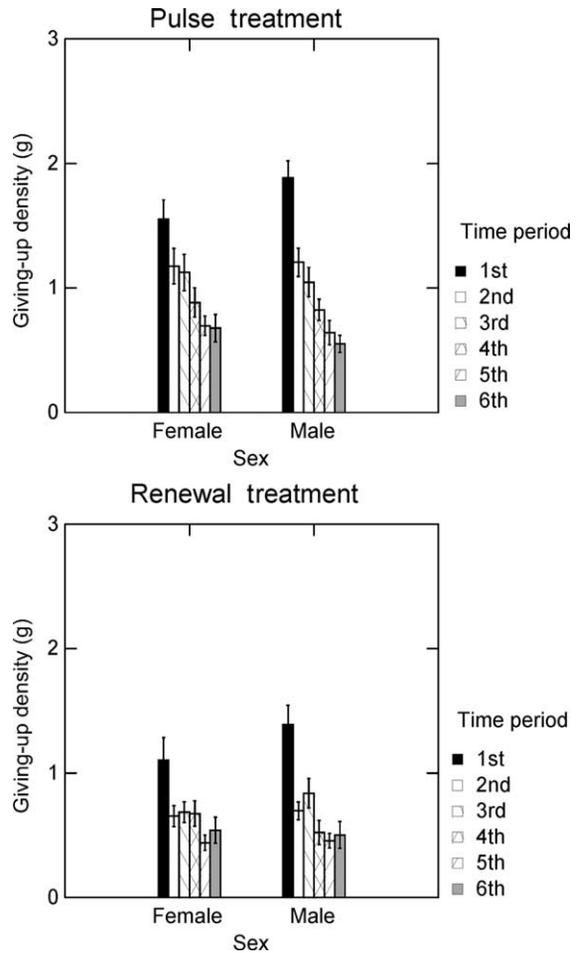

Fig. 1. Giving-up densities (g) for *Gerbillus andersoni allenbyi* (±SE) according to treatment (pulse or renewal), sex (male or female), and time period (1 to 6 from early to late).

interestingly, the sexes differed in the value of the seed trays they exploited over time (within subjects interaction of time and sex; Fig. 1b). This came about because males began foraging earlier in the night than did females (M.S. = 8.745, $F_{1,190} = 6.201$, p = 0.014) when seed trays were richer (M.S. = 2.421, $F_{1,190} = 5.334$, p = 0.022), and continued to forage later into the night

Table 1. Repeated measures ANOVA for giving-up densities of gerbils at seed trays.

Source	MS	df	F	p
Between Subjects				
Sex	0.386	1	0.431	0.522
Treatment	6.244	1	6.968	0.019
Treatment × sex	0.809	1	0.903	0.358
Error	0.896	14		
Within Subjects				
Time period	1.812	5	21.360	0.001
Time period × sex	0.258	5	3.041	0.015
Time period × treatment	0.316	5	3.729	0.005
Time period × sex × treatment	0.288	5	3.398	0.008
Error	0.085	5		

(M.S. $=5.219$, $F_{1,195} =4.033$, $p =0.046$), even though on average there was no difference in the time of foraging of males versus females (M.S. $=0.928$, $F_{1,491} =0.328$, $p = 0.567$; Table 2). Also, males spread their activity more evenly over the night, but females were most active at the beginning of the night and in the fourth time period. The treatment affected the differences in males and females in foraging over time (within subjects interaction of time, sex, and treatment). During the pulse treatment, males spread their activity evenly throughout the night, but females showed little activity until the fourth time period. During the renewal treatment, females showed more intense activity than males during the first two time periods, and males were more active than females thereafter.

Telemetry data

Telemetry data provided information on activity, movement, and overlaps in areas of activity between pairs of gerbils. In regards to activity, each time we located an animal, the modulation of the signal allowed us to find its location and classify it as active or inactive. We constructed a multi-way contingency table with treatment type, habitat type, time period, sex of the individual, and whether or not it was active as the factors. We tested for significance the various combinations of interactions involving treatment, habitat, time, and sex with activity using log-linear models (Table 3). Gerbils were more often recorded as active during the renewal treatment (treatment ×activity) and most active during time period 2 (time ×activity; Fig. 2). These results are consequences of gerbils being highly active early in the night and decreasing their activity later in the night as food is depleted during the pulse treatment, but retaining high activity during the renewal treatment (time × treatment ×activity). Across space, the areas with the most stabilized sand (habitat 1) received the least visits and the least activity (habitat ×activity), and the areas with less stabilized sand received relatively more activity, especially during the renewal treatment (habitat × treatment ×activity; Fig. 2). Nonetheless, females utilized the stabilized sand more than did males, especially during the renewal treatment (habitat ×treatment ×

Table 3. G-values for the significant interactions for the factors comprising the log-linear models of multi-way contingency tables for telemetry data of gerbil activity. The factors were treatment (pulse or renewal), sex (male or female), time period (1 to 6 from early to late), habitat (1 to 4 from most stable to most shifting sand substrate), and activity (active or non-active).

Interaction term	df	G
Treatment ×activity	1	28.13***
Time period ×activity	5	62.08***
Habitat ×activity	3	56.73***
Treatment ×time period ×activity	5	21.28***
Time period ×habitat ×activity	15	19.30***
Treatment ×sex ×habitat ×activity	3	23.52***
Treatment ×time period ×habitat ×activity	15	49.24***
Sex ×time period ×habitat ×activity	15	28.20*

***p <0.001, *p <0.05

gender ×activity) and earlier in the night (habitat × gender ×time ×activity; Fig. 3). There was also a significant habitat ×treatment ×time ×activity interaction, reflecting strong declines in activity over time on the looser substrates during the pulse treatment (Fig. 2).

The telemetry data allowed us to estimate movement over space by the distance between sequential locations of the same individuals on the same night. Distance moved was affected by habitat (M.S. $=2104.133$, $F_{3,386} =3.333$, $p =0.020$; Fig. 4), with animals located in habitats with more stabilized substrate moving longer distances by the next time period. There was also a treatment ×time interaction (M.S. $=2060.603$, $F_{4,386} = 3.264$, $p =0.012$), revealing that animals moved similar or shorter distances as the night progressed during the renewal treatment, but longer and longer distances as the night progressed and food was depleted (time periods 2–5) during the pulse treatment (Fig. 5). Also, gerbils differed strikingly in distance moved in the final time period under the different renewal regimes, with animals greatly increasing distances during the pulse treatment and decreasing distances moved during the renewal treatment. Nightly "home ranges" were calculated from the telemetry data to reveal further aspects of movement and use of space. However, neither treatment nor gender affected the size of the nightly "home range" or the overlap between pairs of individuals on the same grid.

Table 2. Average time period (SE) for first forage and last forage of the night at each station, and the amount of seeds remaining in the tray (i.e. the GUDs) (SE) following the first forage of the night and the last forage of the night at each station. Each night was divided into 6 equal time periods, each lasting 1½ hours. A value of 1.722 indicates that the first forage of the night occurred more often in time period 2 than time period 1. Values are given for male and female *Gerbillus andersoni allenbyi* for the pulse and the renewal treatments of seeds.

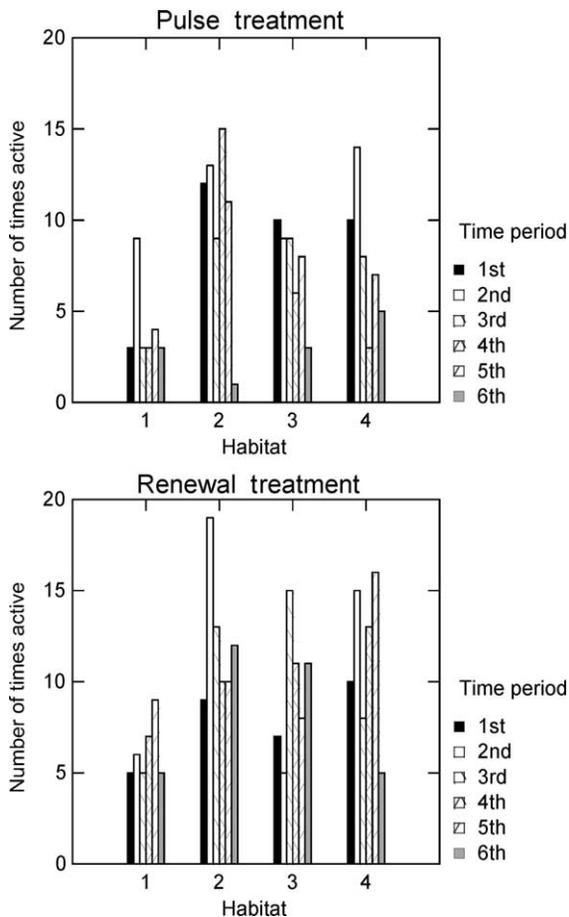| Treatment	Sex	First forage	First GUD (g)	Last forage	Last GUD (g)
Pulse	male	1.722 (0.141)	1.581 (0.117)	5.571 (0.108)	0.610 (0.071)
	female	2.212 (0.201)	1.385 (0.108)	5.148 (0.166)	0.722 (0.078)
Renewal	male	1.612 (0.159)	1.193 (0.111)	5.200 (0.174)	0.576 (0.079)
	female	2.000 (0.192)	0.923 (0.104)	5.000 (0.187)	0.571 (0.064)

Fig. 2. Number of times gerbils deemed active from telemetry signal according to treatment, habitat, and time period. Habitat type is scored from 1 to 4 in regards to sand stabilization. A score of 1 is most stabilized; a score of 4 is least.

Discussion

The results of our experiments provide support for the intraspecific effects of interference. In general, male *G. a. allenbyi* began their nightly activity earlier than females and remained active later. This pattern was most pronounced for the pulse treatment when all the experimentally supplemented seeds were provided at the beginning of the night in one very rich patch (six trays at a station), and gerbils were allowed to deplete them thereafter. This treatment most resembles natural dynamics of seed renewal and depletion where seed patches are renewed during daylight hours by wind action redistributing sand and seed and then depleted at night by foraging gerbils (Ben-Natan et al. 2004). In the renewal treatment, female activity in trays (moderately rich; one open tray at a time per station) was more intense early in the night, but thereafter male activity was more intense. At the same time, telemetry indicated that males and females did not differ in their total activity over the night in and out of trays. This suggests

that males began their activity early on nights of the renewal treatment by exploiting the richest natural patches of seeds. Only later when these were depleted did they move to dominate the renewing seed trays (renewed six times during the night, resembling those rare times during which the wind blows far into the night). Telemetry data also revealed that females exploited the stabilized habitats more than did males, especially during the renewal experiment. Gerbils prefer the semi-stabilized sand over the stabilized substrate (Abramsky et al. 1990, Ziv et al. 1995). In addition, in these experiments the majority of seed tray stations were located in the semi-stabilized sand habitat. The ability of males, but not females, to exploit seed trays early in the night during the pulse treatment and later in the night during the renewal treatment suggests that males directly reduce the ability of the subordinate females to access the richest resources. The relegation of females towards the stabilized habitat, especially during the renewal experiment, also suggests competitive inhibition. Taken together, the temporal and spatial differences in activity between male and female *G. a. allenbyi* in relationship to resource availability are most likely due to the ability of males to interfere with female access to resources.

If male *G. a. allenbyi* interfere with female *G. a. allenbyi,* what are the ecological consequences? At first glance, there appear to be none. Males and females do not differ in their average time of activity, nightly "home range" size, movement pattern, or even the average value of a resource patch visited. However, a closer examination of the data reveals several significant interactions involving time of night and sex. The most important involves the seeds remaining in trays and the treatment × time of night × sex interaction. Examining the value of seed trays visited by males and females during the pulse treatment reveals that males exploit resource patches more intensively early in the night than do females. This is when resource patches are richest and harvest rates highest. So, males appear to benefit by getting first access to resource patches when the benefits are the greatest. Just as *G. pyramidum* individuals when present can use interference to gain access to the richest patches at the best times and places (Kotler et al. 1993, Ziv et al. 1993), so too can male *G. a. allenbyi* when the larger species is rare or absent. However, while the use of interference leads *G. pyramidum* individuals to experience an environment that is on average twice as rich as that experienced by *G. a. allenbyi* individuals, *G. a. allenbyi* males interfering with *G. a. allenbyi* females benefit much less.

Interestingly, male *G. a. allenbyi* also continue to exploit resource patches long after females have stopped foraging. This is the reason that males and females do not differ in the average value of patches visited. But what might be the reason for this continued activity in males? Typically, the last forager to exploit a resource
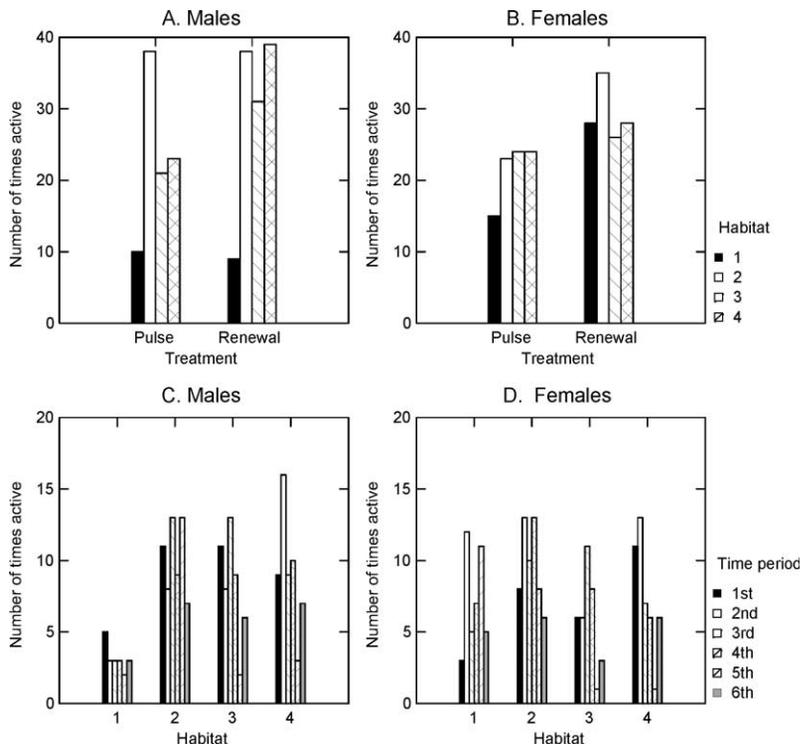
Fig. 3. Number of times gerbils deemed actie from telemetry signal according to sex for: a and b treatment, and habitat, and c and d time period and habitat.

patch is the most efficient forager with the lowest foraging costs or highest harvesting abilities. Aggression however may mask the effect of such patch use components on quitting harvest rate (Ovadia and Dohna 2003). Indeed, when patch quitting rates of *G. a. allenbyi* in allopatric populations were examined independently

Fig. 4. Distance moved between successive radio telemetry locations according to habitat occupied by gerbils in the first location.

of aggression, females had lower patch quitting rates than males (Ovadia and Dohna 2003). Moreover, when aggression was involved, the patch quitting rates of the dominant individuals was lower than that of subordinate ones (Ovadia and Dohna 2003). This suggests that in our study patch use behavior of females was strongly influenced by aggression by males who also had lower interference cost. Males are slightly larger than females, so it may be that they have higher harvest rates for a given density of resources in much the same way that *G. pyramidum* individuals have higher harvest rates (from significantly shorter handling times which conveys that largest advantage at high resource density when the foraging process is limited more by handling than by encounter) than *G. a. allenbyi* individuals (Kotler and Brown 1990, Ovadia et al. 2001). But no data actually exist to address this point. At the same time, it is unlikely that larger males have lower energetic costs of foraging than the smaller females; they likely have higher rates that would more than offset any harvest rate advantage. However, males may have lower interference costs. And, males may be defending depleted resource patches because of the potential of such patches to renew. In fact, we have observed dominant gerbils acting aggressively against subordinate individuals that approach seed trays that are completely empty of seeds. After the encounter, the dominant individual would then return to the tray and appear to sample it (O. Ovadia, pers. Obs.). Such action allows resource patches to renew from a higher initial value, and may allow a dominant male to
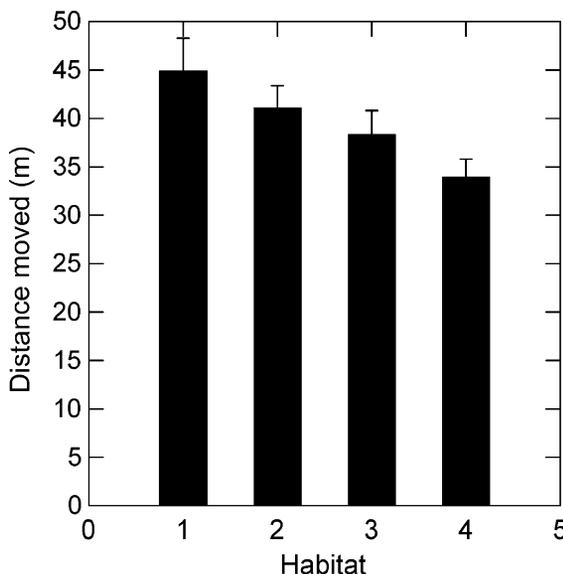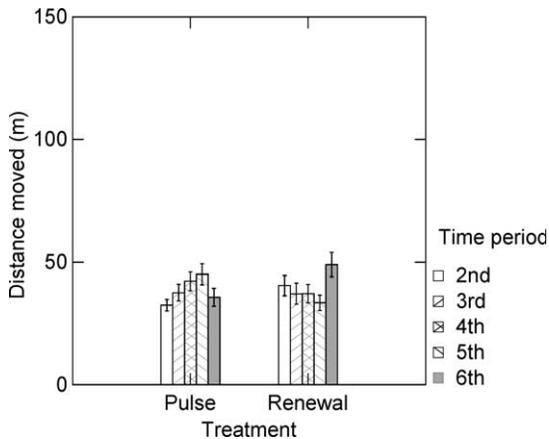
Fig. 5. Distance moved between successive radio telemetry locations according to treatment and time period.

reap more seeds the next day. Fox squirrels (*Sciurus niger*) and gray squirrels (*Sciurus carolinensis*) are known to base diet choice and patch use on similar considerations of future value (Kotler et al. 1999, Van der Merwe et al. unpubl.).

Characteristics of habitat and resource renewal helped to determine distance moved by gerbils. Animals located on more stabilized substrate moved greater distances by the next time period than those on more shifting substrate. Also, animals experiencing the renewal treatment showed different patterns of movement during the night than did those experiencing the pulse treatment. In response to the renewal treatment, animals moved long distances just before sunrise, but shorter and shorter distances coupled with intense activity during the times before. In response to the pulse treatment, animals moved longer and longer distances as the night progressed and resource patches were depleted; activity dropped while distance moved increased until foraging stopped. Both of these patterns may be related to availability of resources. Stabilized sand has a well developed soil crust, and the sand there is less prone to being blown by the wind. Consequently, the daily renewal of seed patches by wind action that is typical of semi-stabilized substrate is unlikely to occur in the stabilized sands or occurs less frequently. Gerbils foraging on stabilized sand are less likely to find profitable patches to exploit and may need to travel far and wide to do so. Similarly, gerbils traveled more and more in search of other profitable opportunities as the patch depleted. When patches renewed frequently during the night, but in small pulses (renewal treatment), gerbils started out the night searching extensively for better opportunities, but perhaps when none were found, settled into exploiting one or two patches intensively. These results seem to support a rule of thumb where gerbils that are successful in finding profitable patches restrict their search for new patches, while gerbils that

are unsuccessful or that find only poorer patches then move greater distances before resuming search for more patches.

Intraspecific interference is known in many systems. Perhaps most commonly reported is intraspecific interference in birds. This typically takes the form of territoriality and most often involves males interfering with males and females interfering with females (Beletsky and Orians 1987). However, in cases involving the defense of food resources, such as in hummingbirds defending a patch of flowers, interference can be directed towards all comers regardless of sex (Feinsinger 1976). Other cases of intraspecific interference include group-living mammals ranging from antelope to primates (Eisenberg 1981, Alcock 2001). In general, interference between males and females within a species occurs over access to resources and does not involve factors associated with reproduction or access to mates. In the present study, reproductive activity was not observed (breeding occurs typically in spring), and thus could not be invoked as a mechanism contributing to the observed results.

The experiments reported here examine the role of gender, habitat, and resource renewal on patch exploitation and the timing of activity in Allenby's gerbil. Males and females showed different patterns of patch exploitation and activity, and these suggest that males interfere with females. Intraspecific interference is common, especially in regards to territoriality and mating, but other aggression between males and females more typically involves access to food resources. In the case of Allenbyi's gerbil, such interference may be rare because of interspecific interference from the greater Egyptian sand gerbil, but as circumstances permit, may lead to modest gains in resource acquisition for males. In this instance, the response of individuals to competitors and resources involves a combination of search, exploitation, and interference.

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