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EFFECTS OF SUBSTRATE ON FORAGING DECISIONS BY A  
NAMIB DESERT GERBIL



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We investigated the role of foraging and escape substrates on foraging decisions of a Namib Desert gerbil, *Gerbillus tytonis* (Rodentia), in the field. We used the giving-up density technique, which uses artificial seed trays to assess foraging decisions. We tested whether the foraging decisions made in the trays were an artifact of prior knowledge of a food source by comparing giving-up densities in trays that were randomly placed in different parts each night with that in trays that remained in fixed position throughout the experiment. There was no significant difference in giving-up densities between these two treatments, which suggests that prior knowledge of food location does not affect foraging decisions. We examined the preferences of gerbils for the different substrates using seed trays. The gerbils showed significant differences among habitats in the amount of seed taken and between new-moon and full-moon nights. They removed more seeds where the difference between the size of the seeds and the size of the sand substrate was large. This finding is congruent with the hypothesis that tactile discriminatory ability affects the foraging behavior of these rodents. Although these rodents alter their foraging behavior in response to predation risk, there was no significant difference in the amount of seeds taken in habitats differing only in the degree of compaction of escape substrates.

**Key words:** foraging behavior, predation risk, desert rodents, optimal foraging, *Gerbillus tytonis*

The factors that influence the foraging behaviors of desert rodents have been the subject of a great deal of investigation (Brown et al., 1979; Kotler and Brown, 1988). A number of studies have indicated that harvesting efficiency (e.g., Lawhon and Hafner, 1981; Price, 1983a, 1983b; Price and Heinz, 1984) and predation risk (e.g., Brown et al., 1988; Kotler 1984a, 1984b, 1984c; Kotler et al., 1991; Price et al., 1984) are major factors influencing foraging behavior, which in turn may influence habitat selection and the community dynamics of desert rodent species (Brown, 1989a; Kotler, 1984a; Price, 1983a).

Typically, the importance of predation risk is suggested by observations that desert rodents avoid moonlight because of increased predation risk from visually-orienting predators, such as owls (e.g., Dice, 1945; Kaufman and Kaufman, 1982; Kotler, 1984a). This has been shown experimentally by Kotler (1984a) by the addition of light sources, which decrease rodent activity. Desert rodents also feed close to cover to minimize exposure to predators (e.g., Christian, 1980; Hughes and Ward, 1993). Differences between species in the distances that they forage from cover has led Brown (1989a) to suggest this as a possible

- *G. tytonis*  
- foraging behavior  
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mechanism of coexistence; specifically, co-occurring species foraging at different distances from cover achieve niche separation via exploitation of different food patches.

Two factors that may affect foraging decisions are the ease with which an animal can extract food from a substrate (Price and Heinz, 1984) and the ability with which it can avoid predation there. A factor that has been shown to affect harvesting efficiency of desert rodents is tactile discriminatory ability (Bowers, 1990; Lawhon and Hafner, 1981; Price and Heinz, 1984). As size of sand grains approaches size of seeds, foraging efficiency declines, owing to reduced discriminatory ability. Price (1983a) has suggested that differences in the abilities of small and large rodents to differentiate between sand and seeds (large rodents usually are less efficient than small species) may lead to coexistence through separation of food or patch use. For example, large rodents may exclude small rodents from areas where there are great differences in size between seed and sand grain. Coexistence is achieved because the small species forage in areas where there are slight differences in size between seed and sand grain, where it is no longer profitable for large species to forage because of the latter's poor discriminatory abilities. Kotler (1984b) considered the interaction between harvest efficiency and predation risk to be an important determinant of community structure. Although laboratory studies have shown that the difference in size between sand grains in the foraging substrate and the seeds to be eaten may affect harvest efficiency (Lawhon and Hafner, 1981; Price and Heinz, 1984), there has been no field study of the importance of this factor. Field study matters because other factors, such as predation risk, may override the importance of the foraging substrate so it may not be manifested in field situations. To test whether foraging substrate affects foraging decisions, we compared the amount of food eaten in patches with sand similar and dis-

similar in grain size to the seed they were harvesting.

Escape substrate also may alter the risk of predation by affecting the escape velocity of the rodent. Because desert rodents escape their predators by dashing off at the last moment (pers. obser.), it is presumed that traction is important to facilitate escape. If escape velocity is retarded in loose sand, rodents may prefer to forage in habitats with compact sand to enhance avoidance of predators. The effect of escape substrate on foraging decisions can be determined by measuring the amount of seed removed from identical food patches that differed only in the degree of compaction of sand surrounding these patches.

To test the effects of both foraging and escape substrates on foraging decisions, we designed a series of experiments using a Namib Desert gerbil, *Gerbillurus tytonis* (mass = 28 g). This gerbil lives in partly-vegetated dune valleys in the sand sea of the Namib Desert. *G. tytonis* is subject to predation by a wide range of nocturnal predators in this exposed habitat. We have shown elsewhere (Hughes and Ward, 1993; Hughes et al., 1994) that this animal is subject to intense intra- and interspecific competition for food and space (with the striped field mouse, *Rhabdomys pumilio*); lowers the risk of predation by reducing activity on moonlit nights; exhibits preferences for specific microhabitats in ways that are congruent with choice based on predation avoidance (Hughes et al., 1994); makes foraging decisions in open areas congruent with the predictions of central-place foraging theory (Hughes and Ward, 1993). We, therefore, anticipate that the other foraging decisions they make will take into account the avoidance of predation and the maximization of foraging efficiency in the face of the high costs induced by competition.

To assess the foraging decisions of this gerbil in different foraging and escape substrates, we needed to provide uniform foraging opportunities in all aspects but that being tested. An effective way of providing

such opportunities is by measuring seed-tray giving-up densities (GUDs—Brown, 1988). Seed trays contain a single seed type of known quantity in a uniform foraging matrix (usually sand). The GUD approach for measuring optimal patch use assumes that a fitness-maximizing forager ceases to collect resources when the marginal benefit of foraging (=input) equals the sum of the foraging costs (=output). The marginal benefit of foraging is the energetic reward of the harvest while the marginal costs are the combined energetic costs of metabolism, risk of predation, and missed opportunity cost (i.e., the cost of not foraging elsewhere or not performing alternative fitness-enhancing activities). The GUD is the resource density at which a forager ceases to feed in a patch, i.e., when input = output. This translates into a foraging efficiency of one at the GUD (input/output = 1—Brown, 1989b).

For further elucidation of the assumptions of the seed-tray technique, see Brown (1988, 1989b), Hughes and Ward (1993), and Hughes et al. (1994). An important attribute of this technique is that gerbils foraging in the trays face diminishing returns to harvesting with increased time spent in the patch (Brown, 1988). The use of seed trays, therefore, mimics the situation in the natural environment where energy input is required for harvesting. Seed trays do not provide free food because rodents must search through the sand matrix as they would in their natural habitat. In addition, the millet seed used in the seed trays, although slightly larger than the average grass seed normally encountered by the gerbils, is within the range of seed sizes naturally available (Hughes, 1990).

#### MATERIALS AND METHODS

*Study site.*—The study site was an isolated island of vegetation, ca. 1.00 by 0.35 km in size, situated in an interdune valley between two parallel, linear dunes. It lay at the northern end of the sand sea of the Namib Desert, 5 km northwest of the Namib Desert Research Unit of Na-

mibia at Gobabeb (23°24'S, 15°03'E) and was separated by 1 km of sand dune and interdune plains from the usually dry Kuiseb Riverbed. Using capture-recapture techniques, we found that 62 gerbils were present at the site during this study (Hughes et al., 1994). date?

The vegetation at the study site consisted predominantly of the perennial grass, *Stipagrostis sabulicola*, and, to a lesser extent, the endemic nara melon, *Acanthosicyos horrida*, both of which occurred in distinct, monospecific clumps on sandy hummocks throughout the site. *S. sabulicola* is a spiky grass that grows in tufts and may reach a height of 2 m. Seeds are produced during summer after sufficient rain has fallen. Nara has leaves reduced to sharp thorns and grows in dense tangled bushes  $\leq 1.5$  m tall (Robinson, 1976) and several meters wide (Craven and Marais, 1986). Female plants produce melons that ripen in summer months (October to February) and commonly are eaten by rodents, ostriches, and jackals.

*Predators.*—Nocturnal predators at the study site included black-backed jackals, *Canis mesomelas*, which were regular nightly visitors (personal observation of tracks and animals), and spotted eagle owls, *Bubo africanus* (one pair observed roosting and foraging there for many years). Diurnal predators were predominantly raptors: pale chanting goshawks, *Melierax canorus*; rock kestrels, *Falco tinnunculus*. Reptilian predators present were the Namib sand snake, *Psammodon leightoni namibensis*, and the side-winding adder, *Bitis peringueyi*. No data are available on the abundances of these predators. For further details of the study site, see Hughes (1990) and Hughes et al. (1994).

*Giving-up densities.*—Twenty circular seed trays (45.0 cm in diameter and 2.5 cm deep), filled with 3 l of sifted sand into which was mixed 5 g of preweighed millet seed, were laid in pairs (separated by 1.5–2.0 m) in nara, grass, and open areas, at sunset. The following morning the sand was sieved, debris removed, and the remaining seed collected. We could differentiate the foraging behavior of the gerbil in the seed trays from that of the only other rodent foraging in this habitat, the striped mouse (*Rhabdomys pumilio*), by the latter's large footprints and larger body imprints left in the trays. This was seldom necessary because *R. pumilio* is diurnal and did not forage when the trays were in the habitat.

*Knowledge of seed tray location.*—Familiarity with the position of the seed trays may influence GUDs because the animals may remember where the trays are and, thus, pay little or no search cost for food supplies in a known location. This familiarity may reduce the overall cost of foraging in that habitat. If this is the case, animals might not be making foraging decisions in seed trays that reflect their assessments of the habitat at large. GUDs, in this instance, will not be determined on the basis of the average resource value for the habitat (an assumption of the technique). Thus, GUDs would be an improper indicator of the animal's foraging efficiency in that habitat. An effect of familiarity can be shown by significantly lower GUDs in trays that remain in place relative to those that are randomly placed in different locations within the habitat between nights. To test for this effect, an experiment was conducted on 3 nights (2 full-moon and 1 new-moon nights): one-half the seed trays (five pairs in each microhabitat) were moved to new positions (>20 m from original position); the rest remained in the same places as at the previous full- or new-moon experiment.

*Predation risk and habitat selection.*—To investigate habitat selection by gerbils, relative activity within each microhabitat was quantified by seed trays (20) in nara, grass, and open areas. The effect of predation risk on activity of gerbils was monitored by performing the experiment on full-moon and new-moon nights, making the assumption that increased lunar illumination is tantamount to increased risk of predation, particularly in deserts where cloud cover is minimal and infrequent (Kotler, 1984c; Price et al., 1984).

*Sand texture.*—Habitat selection by gerbils may be based on sand-texture differences between microhabitats (Price and Waser, 1985). To ascertain microhabitat differences in sand texture, a sand sample was taken from the top 5 cm of the substratum of 15 randomly selected sites in each of the three microhabitats (open, grass, and nara; total of 45 sites). Each sample was shaken through a series of Tyler sieves (2,000, 1,000, 500, 250, 90, and 63  $\mu\text{m}$ ) on an automatic sieve shaker for 10 min, after which the component fractions were weighed.

To test whether sand texture influenced the ability of gerbils to harvest seeds, two seed trays were laid at each of 30 stations. One of each pair of trays was filled with coarse sand while

the other was filled with fine-grained sand. These stations were divided equally among nara, grass, and open areas, and the paired trays were separated by a distance of ca. 15 cm. GUDs were compared between each pair of trays at each station. This experiment was conducted on 2 full- and 2 new-moon nights.

Sand texture, by varying in compaction, may influence a rodent's ability to escape predators. This was tested by laying paired seed trays containing similar sand texture, surrounded by sand of dissimilar grain size. Differences in the GUDs between the two trays reflect only differences in the rodents' ability to reach and escape from the food source.

For the harvest-ability and escape-substrate experiments, coarse sand was taken at random from open areas and fine sand from nara clumps. The sand was sieved to remove all food particles prior to the placement of millet in the trays.

Forty-two paired seed trays containing similar sand texture were laid in open areas only on a full-moon night. At each station, one tray was surrounded by fine sand to a depth of ca. 2 cm, extending 1 m around the tray, while the other tray was surrounded by coarse sand. GUDs in all trays were measured.

## RESULTS

*Knowledge of location of seed trays.*—GUDs from trays in altered positions were not significantly different from those trays whose positions remained fixed (Table 1), revealing that GUDs were unaffected by knowledge of location of seed trays. Table 1 presents the overall results (i.e., for all nights combined). We tested each night separately and obtained the same result. Congruent with previous tests (Hughes et al., 1994), GUDs among habitats were significantly lower in nara than in the open and significantly lower at new moon than at full moon.

*Sand texture.*—The relative proportion of the two largest fractions of the sand samples (125–250 and 250–500  $\mu\text{m}$ ) differed significantly among the three microhabitats (Fig. 1). The sand samples from open areas contained similar amounts of the two fractions while sand samples from grass and nara clumps contained less of the 250–500-

TABLE 1.—Summary table from analysis of variance for experimental tests of effects of position of seed trays on  $\log_{10}$  giving-up density  $\pm 1$ . Levels of factors are: position, seed trays of fixed location and those moved randomly within the habitat each night; habitat, open, grass, and nara; moon, new and full moon.

Source	Sum of squares	d.f.	Mean square	F	P
Position	0.018	1	0.018	0.842	0.360
Habitat	2.446	2	1.223	58.806	0.000
Moon	0.560	1	0.56	26.916	0.000
Position $\times$ habitat	0.033	2	0.016	0.788	0.456
Position $\times$ moon	0.028	1	0.028	1.322	0.252
Habitat $\times$ moon	0.274	2	0.137	6.586	0.002
Position $\times$ habitat $\times$ moon	0.015	2	0.007	0.350	0.705
Error	3.370	162	0.021		

$\mu\text{m}$  fraction and more of the 125–250- $\mu\text{m}$  fraction. Samples from nara clumps exhibited the strongest trend in this regard, i.e., they contained more of the finer subsample and less of the coarser subsample. Sand tex-

ture differed significantly among the three microhabitats. Open areas had coarser sand than did vegetated areas while nara clumps had finer sand than did grass clumps.

Pairwise analysis of GUD data (using

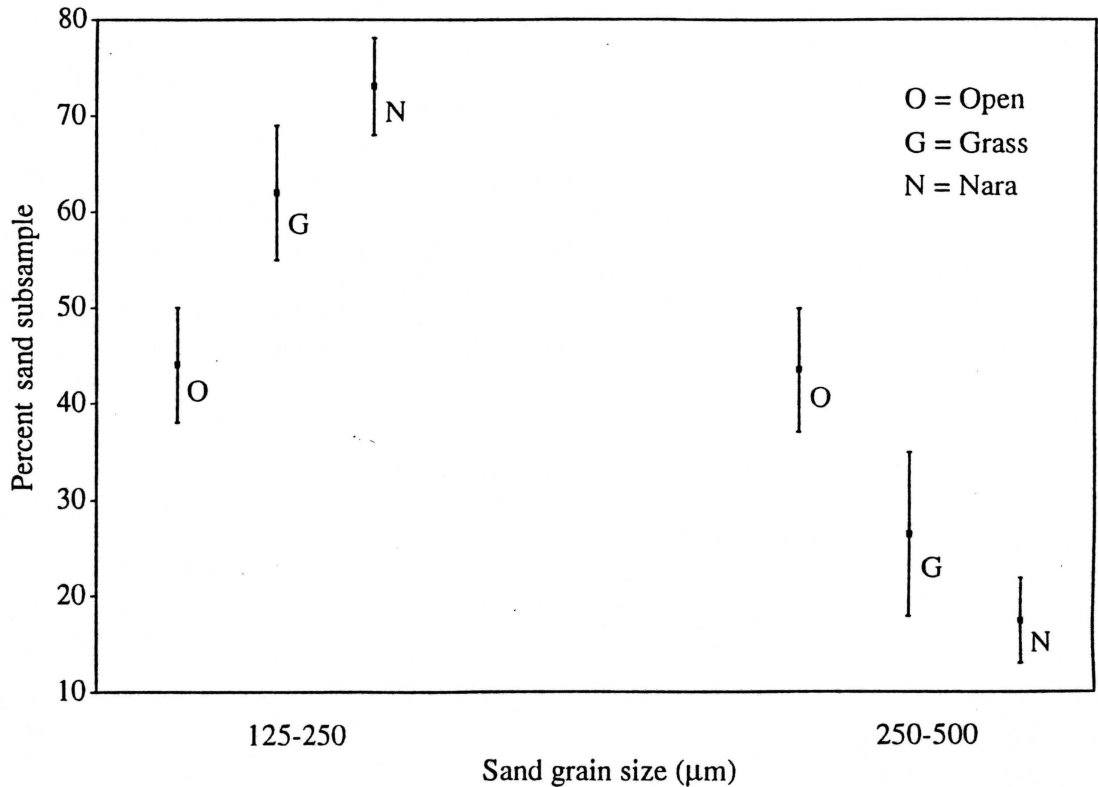


FIG. 1.—Differences in the percentage of 125–250- $\mu\text{m}$  and 250–500- $\mu\text{m}$  fractions in samples of sand from open (O), grass (G), and nara (N) microhabitats. Bars represent means and 95% CI.

TABLE 2.—The number of trays in which giving-up densities were lower in a particular foraging substrate. Giving-up densities were significantly lower in fine sand at both full ( $\chi^2 = 20.22$ ;  $P < 0.001$ ) and new moon ( $\chi^2 = 11.36$ ;  $P < 0.001$ ) when habitats were combined. When habitats were treated separately, this pattern was significant for new moon ( $\chi^2 = 13.22$ ;  $P < 0.01$ ) but not at full moon ( $\chi^2 = 2.04$ ;  $P > 0.05$ ).

Habitat	Full moon		New moon	
	Fine sand	Coarse sand	Fine sand	Coarse sand
Nara	12	6	12	5
Grass	13	4	11	8
Open	14	2	17	2

paired, adjacent trays, one of each pair with fine sand and the other with coarse sand) indicated a significant difference between the amount of seed harvested from trays containing fine and coarse sand. Lower GUDs occurred in trays filled with fine sand ( $\bar{X} \pm SE \log_{10} \text{GUD} + 1 = 0.316 \pm 0.019$ ;  $n = 114$ ) than in trays filled with coarse sand ( $0.338 \pm 0.022$ ;  $n = 114$ ). The results were significant across all microhabitats and at full moon (Wilcoxon signed-ranks test,  $Z = 3.25$ ,  $P < 0.01$ ) and new moon ( $Z = 3.80$ ,  $P < 0.001$ ). This also was evident within each microhabitat when new- and full-moon data were combined (open,  $Z = 3.80$ ,  $P < 0.001$ ; grass,  $Z = 2.66$ ,  $P < 0.01$ ; nara,  $Z = 2.07$ ,  $P < 0.05$ ). Gerbils exhibited

lowest GUDs in fine sand on new-moon nights.

Comparison of the number of trays in which GUDs were lower in a particular foraging substrate corroborates the pairwise Wilcoxon results (Table 2). GUDs were lower in trays with fine sand at both new and full moon.

When we used an analysis of variance to test the effects of foraging substrate, habitat, and moon on GUDs, the effect of substrate was not significant at the conventional level of  $\alpha$  of 0.05 (Table 3). We also separately tested for differences among nights with the same moonlight conditions and found the same results as presented in Table 3.

No significant difference was found between GUDs obtained from trays surrounded by either coarse ( $\bar{X} \pm SE \log_{10} \text{GUD} + 1 = 0.432 \pm 0.03$ ;  $n = 21$ ) or fine sand ( $\bar{X} \pm SE \log_{10} \text{GUD} + 1 = 0.473 \pm 0.03$ ;  $n = 21$ ;  $F = 0.974$ ;  $P = 0.33$ ). Of the 21 pairs of trays, GUDs were lower in eight trays surrounded by fine sand and in 13 trays surrounded by coarse sand ( $\chi^2 = 1.19$ ,  $d.f. = 1$ ,  $P > 0.10$ ).

#### DISCUSSION

*Knowledge of location of seed trays.*—It is of central importance to the validity of the GUD technique that decisions about foraging in a tray are made relative to the missed-opportunity costs of not foraging

TABLE 3.—Summary table from analysis of variance for experimental tests of effect of foraging substrate on  $\log_{10}$  giving-up densities + 1. Levels of factors are: substrate, coarse and fine sand; habitat, open, grass, and nara; moon, new and full moon.

Source	Sum of squares	d.f.	Mean square	F	P
Habitat	4.317	2	2.159	148.678	0.000
Moon	2.541	1	2.541	175.042	0.000
Substrate	0.043	1	0.043	2.984	0.086
Habitat $\times$ moon	0.462	2	0.231	15.912	0.000
Habitat $\times$ substrate	0.148	2	0.074	5.098	0.007
Moon $\times$ substrate	0.108	1	0.108	7.451	0.007
Habitat $\times$ moon $\times$ substrate	0.073	2	0.036	2.497	0.085
Error	3.151	217	0.015		

elsewhere in that habitat. Should animals remember the positions of the trays from 1 night to the next, they may favor them because no search costs are paid. Thus, the decision to forage in a particular tray may be independent of the consideration of the relative costs and benefits of foraging elsewhere in the habitat. Under such conditions, there would be no reason to expect that trays would represent an optimal foraging decision based on the animals' assessment of the value of the habitat. Surprisingly, this assumption of the GUD technique has not been tested previously. In this study, the absence of a difference between GUDs for trays with constant location and those randomly moved within the habitat each night confirms that this assumption of the GUD technique is valid for this species at this site. We suggest that all studies using this technique should test the validity of this assumption prior to experimentation.

*Sand texture and harvest rates.*—The GUDs of gerbils in this study differed among foraging substrates. Size of sand grains differed significantly among the three microhabitats; the finest sand occurred on nara clumps, and the coarsest in open areas, with grass clumps intermediate. GUDs were significantly lower in fine sand than coarse sand, which suggests that preference for nara clumps could be attributable, in part, to increased foraging efficiency in this microhabitat. This result is congruent with Price and Heinz' (1984) finding that harvesting efficiency declines as grain size approaches seed size and the hypothesis that foraging abilities of rodents in different substrates may play a role in determining habitat selection (Price and Heinz, 1984). The statistical nonsignificance of foraging substrate in the analysis of variance (Table 2) indicates, however, that this effect is relatively small and may be important only when habitats are relatively uniform. Analysis of variance, unlike the Wilcoxon test, does not treat the trays in pairwise fashion. Thus, high levels of variance between pairs of trays will mask

differences within pairs of trays. When habitats present spatially-heterogeneous foraging opportunities, as is usually the case, the effect of foraging substrate may be a relatively minor consideration to a forager.

The thorny nara plant also may be preferred because predator avoidance is more effective there (owls and jackals cannot penetrate the dense parts of this plant) and may contain more food because wind-borne seeds may be trapped in the sand hummocks that the plants grow on (Hughes, 1990). There may be no trade-off among these factors (predation risk, food availability, and harvesting efficiency); i.e., all three factors may make nara the best habitat to select.

*Influence of escape substrate.*—Gerbils did not alter their GUDs in different escape substrates. This indicates that either the difference between substrates in the cost of escaping is not large or there are other more important factors that override the importance of this factor. This result was particularly surprising in view of the ability of these animals to alter their foraging decisions relative to predation risk as measured by changes in moonlight and by changing the amount of food taken from seed trays with increasing distance from cover (Hughes and Ward, 1993). Brown et al. (1992) found that GUDs of *Gerbillus allenbyi* in rocky habitats were two to three times higher than GUDs of this species in adjacent sandy habitats. They suggested that the rock habitat surrounding a food patch may compromise the escape abilities of gerbils and, thus, they reduce their GUDs there. However, they did not control for escape substrate in an experimental design such as ours. Thus, they were unable to exclude other factors such as greater predation risk (more predators, fewer hiding places) in the rocky habitat. Experimental evidence of the importance of escape substrate to small mammals, therefore, is lacking.

The lack of importance of escape substrate in our study demonstrates the need to simultaneously examine a number of fac-

tors that may potentially affect foraging behaviors in field situations. Although many factors may be demonstrated to affect foraging behaviors in controlled laboratory situations, they may not play a role in the field because other factors may be of overriding importance.

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