A LONG-TERM STUDY ON THE BEHAVIOR AND SURVIVAL OF EARLY JUVENILE AMERICAN LOBSTER, *HOMARUS AMERICANUS*, IN THREE NATURALISTIC SUBSTRATES: EELGRASS, MUD, AND ROCKS

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ABSTRACT

An 8-month study on the behavior, growth, and survival of early juvenile American lobsters, *Homarus americanus*, was conducted in three different naturalistic habitats of mud, rocks with algae, and eelgrass. Fifteen narrow aquaria (10 cm wide) allowed visual observations of American lobster's activities in five replicates of each of the three habitats. After a 3-month acclimation period to establish "natural" benthic communities which entered through the water supply, three stage IV American lobsters were introduced into each aquarium. Observations were made on the settling, burrowing, activity, and feeding behavior of these lobsters.

American lobsters in eelgrass and rock habitats settled into the substrate more quickly, had burrows a greater percent of the time, and spent less time repairing their burrows than lobsters in mud habitats. The lobsters in eelgrass had a lower mortality rate than lobsters in either rocks or mud. None of the lobsters in any substrate were observed foraging for food outside of their burrows. However, the behavior of these American lobsters indicated that they were able to capture plankton drawn into their burrows by pleopod fanning. Six lobsters molted during the coldest part of the year when the water temperature was approximately 1° to 2°C.

Stage IV of the American lobster, *Homarus americanus*, is best described as transitional between larval and juvenile (Phillips et al. 1980). During this stage major behavioral changes take place, which coincide with the morphological changes occurring in the molt. These behavioral and morphological changes cause the stage IV lobsters to descend from the upper layers of the water column to the bottom where they build a burrow (Botero and Atema 1982; Ennis 1975).

Knowledge of the American lobster's behavior from the onset of settlement until they reach a size of approximately 20 mm in carapace length (CL) remains limited because juveniles of this size range have been found in the field only sporadically.

Several laboratory experiments sought to determine the substrate preferences of stage IV American lobsters. Howard and Bennett (1979) found that lobsters (*H. gammarus*) generally choose the largest size of gravel provided (approximately 20 mm in diameter), because larger rocks have more available space between them for burrows. If given a choice between a gravel substrate or a silt/clay substrate, American lobsters prefer the gravel (Pottle and Elner 1982). In choice tests, stage IV American lobsters preferred rocks with macroalgae, followed by, in order of decreasing preference, mud, rocks on sand, and sand. If not afforded a choice, the lobsters settled most quickly on the rocks with macroalgae, followed by rocks on sand, mud, and sand (Botero and Atema 1982).

MacKay (1926) recorded observations on the lobsters' ability to burrow in mud. Subsequently Cobb (1971), Berrill and Stewart (1973), and Botero and Atema (1982) have described the methods by which juvenile American lobsters make burrows in both mud and rocky substrates. No observations have been made on American lobsters burrowing into other substrates, such as eelgrass or peat.

Cobb et al. (1983) followed stage IV *H. americanus* for short periods of time following their release into the field. They observed behavior which may indicate that American lobsters test different substrates and continue moving if they are on unsatisfactory substrates such as sand or mud; however, only two lobsters were actually seen rejecting a substrate.

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None of the previous studies lasted for more than a few days, and long-term behavioral observations have never been recorded on early juvenile American lobsters. There are virtually no field data on simple life history parameters such as their preferred substrate, growth rate, diet, and behavior. It is unwise to proceed with experimental laboratory studies on an organism without having a descriptive life history background to provide context. Both Cobb (1987) and Fogarty (1987) recognized the need for more studies on the behavior and ecology of the postsettled prerecruits used in this study. At present it is difficult to gather such information in the field. However, this study was designed in order to provide such a background by carefully creating naturalistic habitats in the laboratory. We present quantified behavioral observations, survival, and growth of early juvenile American lobsters in three different substrates: mud, rocks, and eelgrass, over an 8-mo period.

MATERIALS AND METHODS

Fifteen "ant farm" aquaria (45 cm deep × 30 cm long × 10 cm wide) were constructed to optimize our ability to observe the American lobsters inside their burrows. Five of the aquaria were two-thirds filled with cohesive mud (particle size <0.06 mm) collected from mud flats in the Woods Hole, MA area. Five of the aquaria were two-thirds filled with rocks, collected from subtidal areas in such a way that a representative distribution of rock sizes was obtained (0.1–20 mm diameter). Some of the rocks in each tank had macroalgae *Coleus* (sp.) and *Fucus* (sp.), or both growing on them. Eelgrass collected from local eelgrass beds was placed in the last five aquaria; less substrate was used in these latter tanks so that the eelgrass leaves had room to grow.

The aquaria were randomly distributed in a system which provided running, unfiltered seawater at ambient temperatures seasonally ranging from 23° to 0°C. Plankton were always visible; also the three habitats occasionally had plankton blooms, during which algae and zooplankton were plentiful. The tanks were maintained on an ambient light/dark regime with a light intense enough to keep the eelgrass alive. Removable, opaque, black plastic was placed around each aquarium to the level of the substrate to ensure that the lobster burrows were dark. To establish "natural" benthic communities, the tanks acclimated from 20 July until 16 October 1982, before beginning the experiment.

Stage IV American lobster siblings from the hatchery at St. Andrews, New Brunswick, Canada were introduced, one per day into each aquarium for 3 consecutive days. Thus, the total number of lobsters at the start of the experiment was 45, 15 per treatment. Observations were recorded continuously for the first half hour after each introduction and then for the following 1.5 hours; observations were recorded by scanning (taking an instantanious reading of the lobsters' behavior) every 10 minutes. Observations were made of the following: 1) location of the animal in the aquarium, 2) motion (walking, swimming, or resting), 3) burrowing activity (pleopod fanning, bulldozing, or digging), and 4) shape, size, and location of final burrow. This procedure was similar to that used in the substrate choice tests done by Atema et al. (1982).

During the first introduction of American lobsters into several of the tanks, mud crabs, *Neopanope sayi*, immediately consumed them. The mud crabs were subsequently removed and new American lobsters were placed into these tanks.

After the American lobsters had been introduced into each of the 15 tanks, long-term observations began of each lobster in each tank at intervals ranging from daily to twice per week. The observation periods were at different times during the day with 5.1% during the dark period, although it was difficult to see the lobsters in low light because of the cryptic nature of some burrows. There was a total of 195 observations periods. Each lobster that was visible was watched for at least one minute; if the lobster was active, observations lasted until the activity ended. However, for the quantitative analysis of lobster activity only the first minute of observations were used. A total of 495 hours of observations were made averaging 11 hours per individual lobster. For each lobster we recorded 1) the location of the lobster in relation to its burrow, 2) whether the lobster had molted, 3) the lobster's activity, and 4) the shape of the burrow (with a quick sketch). The activities observed are described in Table 1.

The experiment lasted approximately eight months, from 21 October 1983 to 1 July 1984. The lobsters were not fed during that time; we assumed they would find food from the communities in which they lived. At the end of the experiment, the surviving lobsters were weighed and their carapace length was measured. Additionally, the sediment in each tank was sieved through a 1 mm screen, and all organisms were collected, weighed, and identified to the genus or species level.

TABLE 1.—Description of the different activities observed throughout the experiment.

Activity	Description
Rest	No movement for at least 30 seconds. Grooming was not considered movement, and was not recorded separately from rest.
Pleopod fan (PPF)	Movement of the pleopods; if the fanning was being used to repair the burrows, i.e., sediment was being moved, then the activity was recorded as burrow repair.
Burrow repair (BR)	Any activity which caused sediment to be moved, including bulldozing (pushing sediment foward with the claws spread apart), pleopod fanning, and digging (loosening sediment by pushing claws into it).
Investigate (INVEST)	Standing at the entrance of the burrow with antennules out and antennae flicking.
Feed	Eating anything larger than 1 mm. Activity that looked like filter feeding was not included in this category (it was part of the pleopod fan). It is discussed in the text.
Walk	Walking on the sediment. Does not include "walking" in the burrow.
Swim	Swimming in the water column.

RESULTS

Burrowing

The American lobsters in the eelgrass and rock substrates started burrow construction more quickly than the ones in the mud substrate (1 way ANOVA, Newman-Keuls test, $P < 0.05$). There was no significant difference in the time to initial burrowing between lobsters in eelgrass and lobsters in rock substrates (Table 2A).

American lobsters used the same methods to make burrows in eelgrass as in mud and rocks. They typically started at the base of an eelgrass plant and then established a burrow under the rhizomes by pleopod fanning and bulldozing. The burrows usually had two openings although burrows were seen with from one to six openings. These openings were smaller and more difficult to see than similar openings in mud or rock substrates. Although lobsters in all substrates had burrows for the majority of the observations, because their burrow had collapsed, the lobsters in the mud substrate were without a burrow for a greater percent of the observations than the lobsters in the eelgrass or rock substrates (arcsine transformation, 1 way ANOVA, Newman-Keuls test, $P < 0.05$, Table 2B). For this analysis the lobster had to be visible; if neither the lobster nor its burrow were visible during a given observation period, that observation was excluded from the analysis.

Activity

American lobsters were not seen to forage outside of their burrows. If a lobster had a burrow, it was never seen outside of that burrow in any of the treatments during the entire experiment. During the day periods, these lobsters were seen in their burrows 1,503 times, and outside of their burrows 0 times. Therefore, by using sampling theory, one can calculate that the lobsters were spending at least 99.8% of their time during light periods in their burrows (binomial distribution, $P = 0.05$). During the night periods lobsters were seen in their burrows 103 times, outside of their burrows 0 times. Therefore, the lobsters were spending at least 97.0% of the time in their burrows during the dark (binomial distribution, $P = 0.05$). The difference between the night and day percentages is a function only of the greater number of observations made during the day.

The cumulative times that the American lobsters spent at various activities were influenced by sub-

TABLE 2.—(A) The average time in minutes that it took each lobster in the eelgrass, rock, and mud treatments to start construction of their burrow (eelgrass vs. mud and rocks vs. mud, $P < 0.05$). (B) The percent of observations throughout the experiment during which the lobsters in each substrate did not have a burrow. N varied from 160 to 68, depending on how many lobsters were visible (eelgrass vs. mud and rocks vs. mud, $P < 0.05$). (C) The average weight, in grams, and the carapace length (CL), in mm, of the lobsters in each treatment at the end of the experiment.

	A	B	C	
	Time to burrow	No burrow	Weight and	CL
Eelgrass	7.92 ± 2.02	4.70 ± 1.7	4.95 ± 0.95	18.15 ± 1.25
Rock	11.92 ± 3.22	3.82 ± 1.22	3.18 ± 0.16	15.22 ± 1.34
Mud	49.17 ± 14.08	12.2 ± 3.7	3.22 ± 1.23	15.85 ± 1.92

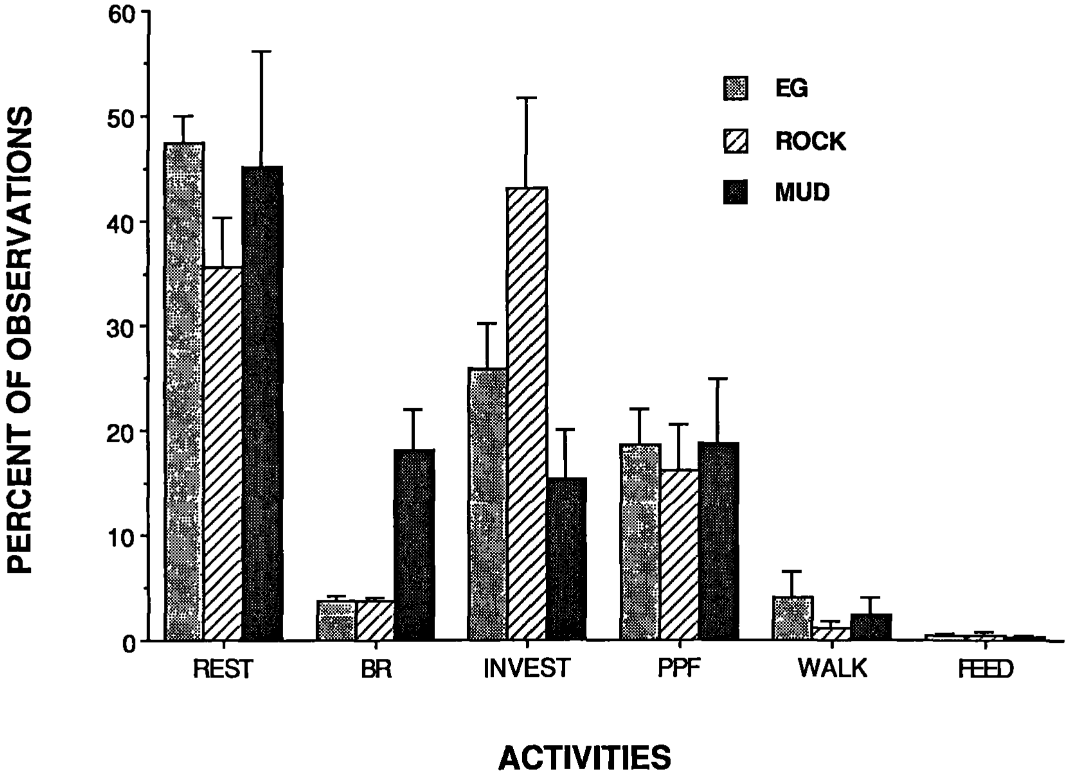

FIGURE 1.—The percent of observations in which the American lobsters were engaged in each of the listed activities. BR: eelgrass vs. mud, $P < 0.001$. Invest: eelgrass vs. mud and rock vs. mud, $P < 0.05$. N varied from 160 to 68.

strate (Fig. 1). The lobsters in the mud substrate spent a significantly greater percent of their time repairing their burrows than the lobsters in either eelgrass or rocks (arcsine transformation, 1 way ANOVA, Newman-Keuls test, $P < 0.001$). Based on percent of observations, the lobsters in mud spent significantly less time investigating than did the lobsters in rocks (tests as above, $P < 0.05$). There was no significant difference, however, between the percent of observations spent investigating in the mud vs. the eelgrass, or in the percent of observations spent investigating in the eelgrass vs. the rocks.

Based on the percent of observations, the time the lobsters spent resting and pleopod-fanning was considerable (18–45%) in all substrates and did not differ between them. Walking was only observed when a lobster did not have a burrow. Feeding occurred only on the few occasions when some edible object landed close enough to the burrow so that the lobster could reach it without entirely leaving its burrow. Twice lobsters were seen catching swimming amphipods at the entrance to their burrow.

American lobsters were observed creating a current by pleopod-fanning, which was seen to draw plankton through their burrows. During these periods the lobster stood with its clawed limbs held up and apart. The mouth parts, particularly the second and third maxillipeds moved rapidly, and the first pair of walking legs were often brought up to the mouth. Occasionally the lobster would jerk forward and snap its claws. All of the above-mentioned appendages are covered with various types of setae (Factor 1978), which could help the lobsters to catch the plankton both by "filtering" with their maxillipeds, claws, and first walking legs, and by seizing the plankton with their claws. These observations, supported by Lavalli and Barshaw (1986) and Barshaw (in press) show that American lobsters are able to catch plankton while remaining in their burrow.

Mortality

There was an initial mortality of the American lobsters in all habitats followed by no deaths in the winter and another die-off in the spring (Fig. 2). The mortality rate for American lobsters in eelgrass was significantly lower than those in the mud or in the rocks (arcsine transformation, linear, least-square regression, r^2 = 0.75 eelgrass, 0.86 rock, 0.94 mud, comparison of slopes, $P < 0.001$).

Molting and Size

At the end of the experiment there was no significant difference in the size of the lobsters between habitats, although the American lobsters in eelgrass tended to be larger (Table 2C). There was also no significant difference in the number of observed molts between treatments. We observed molting by six lobsters during the coldest part of the year when the water temperature was between 1° and 2°C.

Possible Prey

The biomass of American lobsters (>1 mm) was not significantly different among treatments, but the biomass of American lobsters in eelgrass tended to be higher (ANOVA, Newman-Keuls test, $P < 0.01$, Table 3). There were fewer different genera residing in the mud habitats, with the greatest diversity in rock.

DISCUSSION

Initial observations showed that stage IV American lobsters started to burrow more quickly in eelgrass and rock habitats. While several investigators have shown that American lobsters choose rocks over mud (Howard and Bennett 1979; Pottle and Elner 1982; Botero andAtema 1982), no choice experiments have used eelgrass as a substrate. Likewise, in this experiment we have not directly shown that the lobsters prefer the eelgrass substrate because they were not offered a choice. Speed of settling would be indicative of a preference, however, if the method that lobsters use to choose a substrate is to keep swimming if the habitat is unsuitable, but settle if it is suitable. Such behavior was observed in laboratory experiments by Botero and Atema (1982). Indications that lobsters keep swimming over unsuitable substrates was also observed by Cobb et al. (1983) in the field.

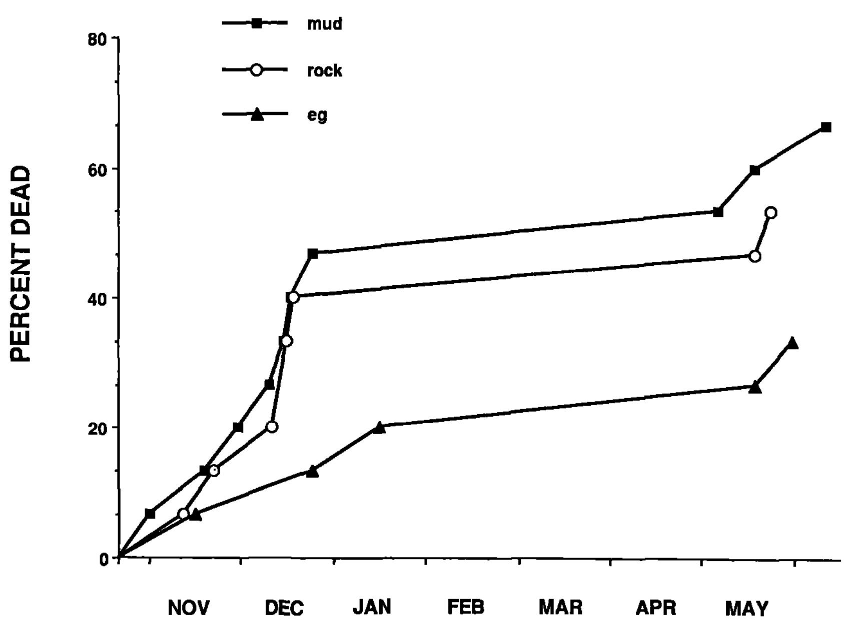

FIGURE 2.—The cumulative percent of American lobsters that died in the three treatments, each point represents a day when a lobster died. Fifteen lobsters per treatment were present at the beginning of the experiment. Eelgrass vs. mud and eelgrass vs. rock, $P < 0.001$.

TABLE 3.—Average biomass (wet weight) and species list of organisms larger than 1 mm living in the sediment of each treatment at the end of the experiment.

Treatment	Bivalve	Polycheate	Other
Eelgrass:	Mean biomass per tank = 8.2 ± 2.7 g		
	Mercenaria mercenaria	*Capitella* (spp.)	Sipunculoidea
	Yoldia (spp.)	*Clemenalla* (spp.)	(*Golfingia gouldi*)
		Glycera (spp.)	
		Lumbrineris (spp.)	
		Neris (spp.)	
		Spiondae (gen.)	
		Terebellida (gen.)	
Rock:	Mean biomass per tank = 3.28 ± 1.07 g		
	Andora ovalis	Chrysopetalidae	
	Andora transversa	(*Dysponetus pygmaeus*)	Sipuculoidea
	Mercenaria mercenaria	*Nephytidae* (spp.)	(*Golfingia gouldi*)
	Mucoma (spp.)	*Nereis* (spp.)	Crustacea
	Yoldia (spp.)	*Phyllodocdae* (gen.)	(*Neopanope sayi*)
		Sapella (gen.)	
		Terebellida (gen.)	
Mud:	Mean biomass per tank = 4.4 ± 1.07 g		
	Geukendia demessus	*Glycera* (spp.)	
	Solemya velum	*Nephtys* (spp.)	
	Yoldia (spp.)	*Nereis* (spp.)	
		Orbiniidae (spp.)	
		Terebelleda (gen.)	

The mud substrate appeared to be the least suitable of the three tested since American lobsters in eelgrass and rocks were without burrows for less time than those in mud. However, even in the mud habitat the lobsters had burrows for an average of 87.8% of the observations (Table 2B). The three substrates used in this study were chosen partly because of their differences, yet the lobsters managed to build and maintain burrows in all three substrates for eight months. This result clearly shows that early juveniles have flexible behavior and modify it to adapt to different substrates.

The way that the American lobsters partitioned the amount of time they spent on different activities was also affected by the substrate in which they lived. While lobsters in eelgrass and rock habitats spent little time repairing their burrows, lobsters in mud spent considerable time on repair (Fig. 1). This result is consistent with the characteristics of the three substrates. Eelgrass stabilizes the underlying sediment (decreases erosion) by baffling the water currents with its leaves and binding the sediment with its roots (Scoffin 1970); rocks, although usually found in areas of stronger currents, provide a ready made solid roof; mud, however, is more easily disturbed (Rhoads and Young 1970). If one lobster did not have a burrow in the mud tanks, its walking often destroyed the other lobsters' burrows.

The extra time that the American lobsters in mud spent repairing their burrows was subtracted mainly from investigation time (Fig. 1), perhaps because there was not as much prey in the mud for the lobsters to detect, so this activity was the most expendable. No significant differences were found between the time budgets of the lobsters in eelgrass and the lobsters in rocks; however, the lobsters in eelgrass spent more time resting than investigating, while the opposite was true of the lobsters in rock substrate.

The American lobsters in the eelgrass had a lower mortality rate than those in either mud or rocks. This result could have been due to the greater biomass of possible prey animals living in the eelgrass habitat, and/or the greater complexity of the eelgrass habitat, which in essence separated the lobsters and ameliorated the effects of high density. Seagrass beds in nature have also been shown to have a greater biomass of species living in them than the biomass of species living in less complex substrates such as mud or sand (Orth 1973; Thayer et al. 1984).

The lower mortality rate of lobsters in eelgrass led to a greater number of lobsters per tank in this treatment. Higher concentrations of lobsters have been shown to cause slower rates of growth in lobster living in fairly unnatural substrates (Cobb and Tamm 1974). In this study, the American lobsters in eelgrass were not smaller perhaps also because the eelgrass substrate ameliorated the effects of higher density. We did not observe any differences in the activity budgets of the lobsters owing to higher density (Fig. 1).

This study shows that early juvenile American lobsters differ dramatically in their behavior from older lobsters. They seldom, if ever, forage for food outside of their burrows, but instead remain inside of them. This was true even though there were no predators present other than other juveniles.

The lobsters' main activities within their burrows reflected their needs. Because they did not forage outside of their burrows, all of the early juveniles' nourishment must have been found inside of their burrow, or within reach of the entrance. Lobsters could forage on polycheates, meiofauna, and on any other organisms residing inside their burrows or draw plankton in by pleopod-fanning. In this study lobsters were seen to catch swimming amphipods at the entrance to their burrow, and Berrill (1974) observed similar behavior. Besides resting, the lobsters mainly "investigated" for anything edible in the entrance of their burrow and pleopod-fanned to draw in plankton. If they were forced to burrow in a relatively unstable substrate, such as mud, they spent a significant amount of time maintaining that burrow.

The claws of early juvenile American lobsters are smaller and weigh less relative to the abdomen than those of older lobsters, and, by external appearance the two claws are not differentiated from each other. Furthermore, the speed of the tail flip reflex is faster at sizes smaller than 20 mm carapace length (Lang et al. 1977). These morphological characteristics along with the behavioral results from this study, and field observations that juveniles become easier to find at a carapace length of 20–40 mm (Cooper and Uzmann 1980; Able et al. in press), indicate that the juvenile stage of the American lobster can actually be divided into two substages: 1) the early juvenile stage, spanning settlement to the time until claws begin to differentiate, during which period the lobsters seldom, if ever, leave their burrow; and 2) the late juvenile stage, starting when the claws are differentiated and become larger in relation to the abdomen and ending with sexual maturity. At this stage, the lobsters start to forage for food outside of their burrows, and behave more similarly to adults (Cooper and Uzmann 1980; Able et al. 1988).

We suggest the following scenario for the life history of early juvenile American lobsters. After settling onto a suitable substrate the lobsters build a burrow where they remain for the duration of the "early juvenile" substage. By catching food, both in the substrate around their burrow entrance and by drawing plankton into their burrow by pleopod-fanning, the early juvenile lobsters manage to survive without foraging outside their burrow.

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