Table 1: The time taken for Atta cephalotes to carry the two leaf treatments from the study site. (Corcovado, Costa Rica)

	Colony I		Colony II	
Trial #	Leaves cut by ants	Leaves Cut by humans	Leaves Cut by ants	Leaves Cut by humans
1	7	40	22	27
2	72	81	50	45
3	42	77	40	30
4	29	92	35	23
5	45	100	80	70
6	27	49	41	150
7	14	34	20	19
8	14	54	11	25
9	16	110	18	60
10	25	128	27	75
11	21	28	18	20
12	68	30	60	75
13	67	137	17	110
14	27	132	26	15
15	18	57	20	23
16	23	20	60	160
17	42	23	45	57
18	15	30	165	70
19	33	40	20	138
20	80	30	25	40
Means	34.25	67.10	40.00	61.60

TEST OF THE CENTRAL FORAGING THEORY IN JET CRABS

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Abstract (L.T.)

Our study focused on whether or not the Central Foraging Theory could be used to describe the feeding pattern of the JET crab. We found that the distance to the burrow of the nearest neighbor increased as burrow diameter increased. We also found a significant decrease in the number of holes as distance from the high tide line down the beach increased. We found an increase in the number of crab pellets on the beach as the distance from the high tide line increased, indicating that JET crab feeding increased as the distance from the high tide line increased. These results led to the rejection of the Central Foraging Theory as it applies to the JET crab. Instead, crab feeding and burrowing areas are spatially separated on the beach. Burrowing occurs closer to the high tide line while feeding occurs right above the low tide line.

Introduction (J.K.)

JET (Jon-Elizabeth-Tara) crabs build their burrows on the beaches of Corcovado National Park, Costa Rica, Central America. Are these burrows merely for defense, or are they also the center of the feeding area? This latter strategy is described by the Central Foraging Theory which states that an organism secures a feeding area around itself, so that traveling time and energy can be minimized between the protective lair and the feeding area.

Whether JET crabs centrally forage or not leads to several questions: How are JET crab (food organic matter in the sand) resources distributed on the beach and with what type of predators must JET crabs must contend?

To determine how JET crabs allocate feeding resources, that is, how they partition the beach with respect to each other, we devised the following hypotheses after our initial observations.

1. As distance to the nearest neighbor increases, hole diameter increases.
2. The number of pellets increases as distance down beach from the high tide line increases.
3. The number of holes decreases as distance down beach from the high tide line increases.

The first hypothesis implies that larger crabs secure larger feeding areas to fuel their greater energy demands; the second and third hypotheses imply that feeding areas are spatially separated, thus rendering the Central Foraging Theory inapplicable.

Methods (J.K.)

On the playa abutting the Sirena Station, Corcovado National Park, Costa Rica, we set up two sets of transects according to the following diagram. We conducted the entire study during the recession of the tide.

For each of the ten transects for both sites, we estimated the number of crab pellets (in groups of 10 pellets) as a reflection of feeding activity. We recorded the number of crab burrows, burrow diameter at the rim and the distance to the nearest neighboring burrow.

The observation portion of this study involved our observing the behavior of the JET crabs for 4.5 people - hours with the following foci in mind:

1. Aggressive interactions between different size crabs
2. Feeding areas of different size crabs
3. Uses of burrows

Results (T.G.)

Each of our hypotheses was supported in this experiment. Via a regression, Hypothesis One showed a positive relationship ($r^2 = 0.124$, $r = 0.352$, $p < 0.01$). Although we did not statistically analyze the data from Hypothesis Two because we did not have the means, a strong trend that supports the hypothesis was evident (figure 1a). Hypothesis three showed a negative relationship ($r^2 = 0.588$, $r = -0.765$, $p < 0.01$) (figure 1b). We also calculated the mean burrow diameter for each transect. The resulting trend demonstrated that burrow diameters show less variation and increase in size as they move farther from the high tide line (figure 2).

Discussion (L.T., T.G.)

In light of our results, the Central Foraging Theory does not apply to JET crabs. Originally, we felt that Hypothesis One" As hole diameter increases, the distance to the nearest neighbor also increase," might apply because larger crabs require more energy and hence more area in which to feed. We found, however, that these crabs do no feed in the vicinity of their burrows. Instead, they inhabit two distinct areas: one for feeding and one

for burrowing. The fact that there was a significant relationship between hole size and distance to nearest neighbor should therefore be attributed to other factors. Perhaps the different geographical and topographical features of the beach determine the location of their feeding or burrowing activity. We observed the crabs defending their burrows by preventing access to intruders or expelling any intruder who entered.

These observations suggest that the crabs defend some type of resource. If it is not food, then perhaps it is defense against other density related factors. They may be more at risk of predation or disease in areas of higher density. Therefore, it would be preferable to live in areas of low density which competing large crabs would better be able to maintain. This could indicate that they are competing for space. It should be noted that our r^2 value (0.12) for these data was low indicating that there are other variables involved. For example, it is possible that our data were skewed because a number of our large holes were those low down on the beach (see figure 2). Here the density is much lower and thus results in larger distances between large crab neighbors.

The significance of hypothesis two - "Number of pellets increases as distance down beach from high tide line increases, "reflects the fact that JET crabs feed in areas spatially separated from their burrows (see figure 1a and 1b). It is likely that the sand's nutrient level is higher in areas where the tide has just deposited organic matter. This explains why all sizes of crab forage together at the last stretch of hard packed sand during low tide. This suggests that food is distributed patchily and in an increasing gradient toward the water. However, because we did not measure the nutrient level directly, we cannot ascertain whether the food is actually distributed in patches or whether the crabs forage together for other reasons, such as safety from predation via the "many eyes theory."

Hypothesis Three, "Number of holes decreases as distance down beach from high tide line increases,"shows an inverse trend to Hypothesis Two. The highest number of holes is found in the transect closest to the high tide line (see Fig. 1a). Intuitively, it would seem that crabs would build their burrows near their feeding area. However, this is not the case. Perhaps, it would be too great an energy expenditure to dig new burrows following each tide. Instead, they have developed other defense mechanisms, such as cryptic coloration (sandy brown). We found that large crabs, however, are an exception to both these trends: they do build burrows near the feeding area (see figure 2), and they do not have cryptic coloration (they are bright red). It seems reasonable for them, therefore, that the energy cost of building a burrow could be outweighed by the benefit of increased protection from predation.

Our three hypotheses describe the foraging pattern of the JET crab. Rather than foraging centrally, the JET crabs feed in an area at the water's edge completely distinct from the area of burrows. Further study is required to determine the cause of this. We suggest examining the effects of the following:

1. sand geology and topography on location of activity
2. energy expenditure on burrow creation and relocation
3. predation risk on spacing of burrows
4. predation risk on foraging behavior
5. nutrient distribution on feeding activity

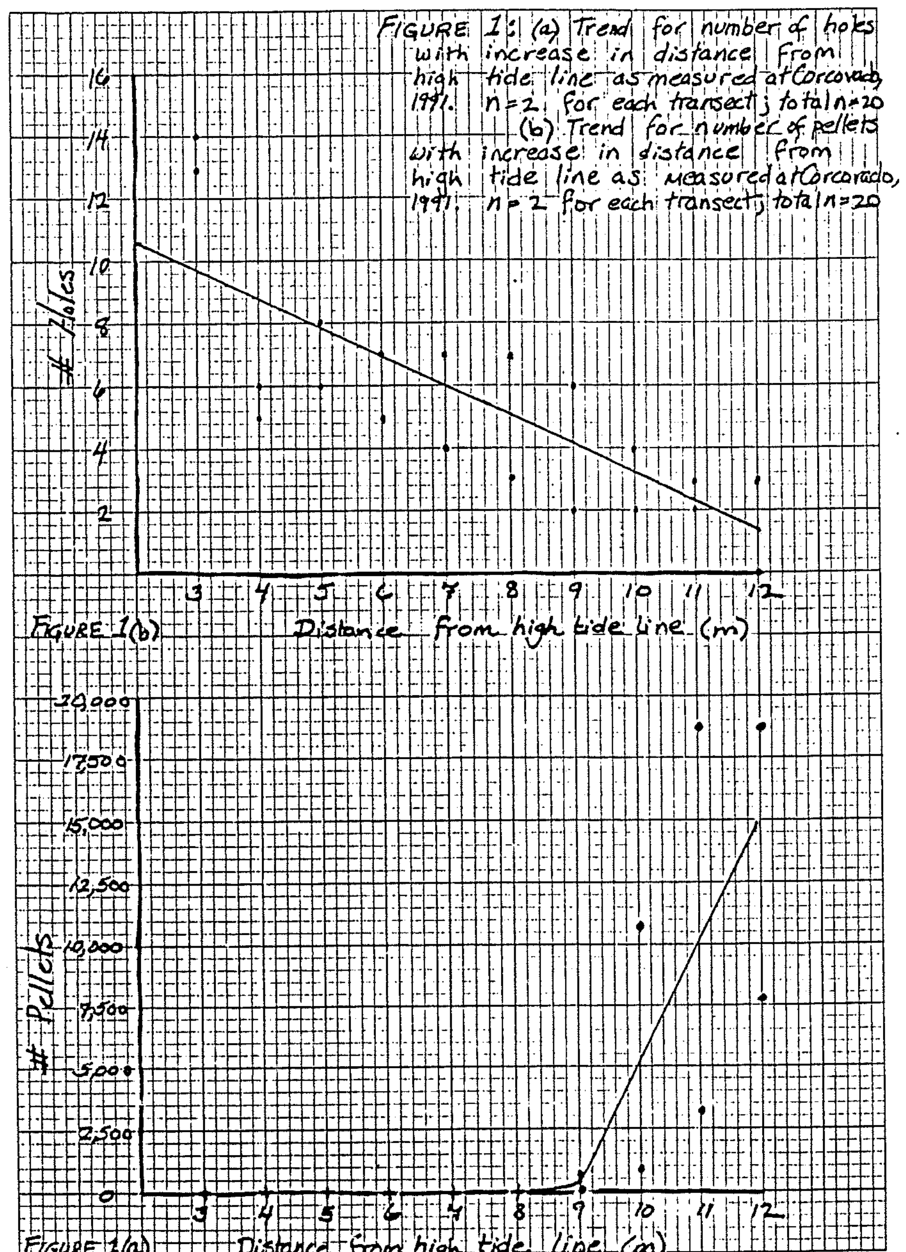

FIGURE 1: (a) Trend for number of holes with increase in distance from high tide line as measured at Corcovado, 1991. n=2 for each transect; total n=20
(b) Trend for number of pellets with increase in distance from high tide line as measured at Corcovado, 1991. n=2 for each transect; total n=20

+ = indicates two points at the same coordinates

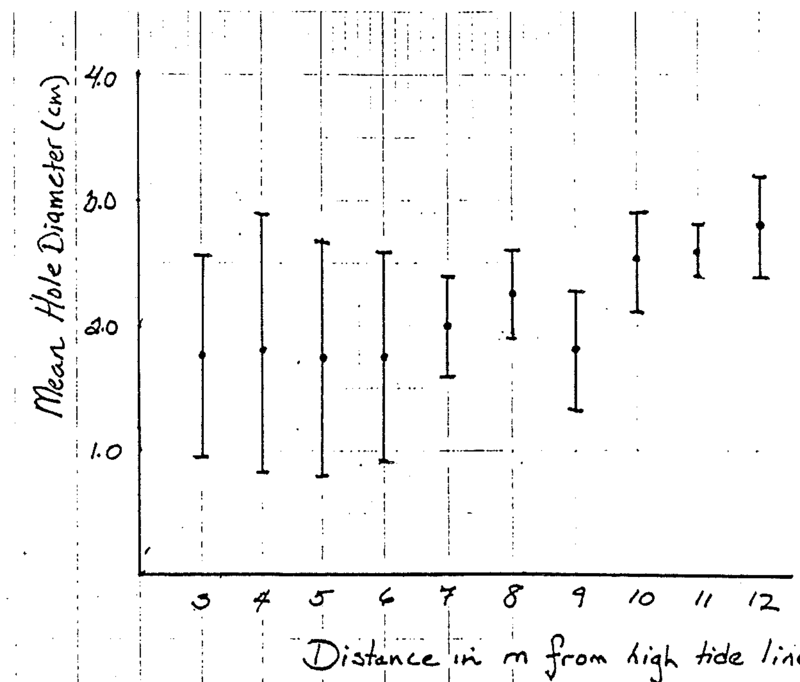

FIGURE 2: Trend for hole diameter with increase in distance from high tide line as measured at Corcovado, 1991. Each point represents mean of hole diameter for each transect. Bars show standard deviation for each mean. $0<n<14$. Total $n = 109$.