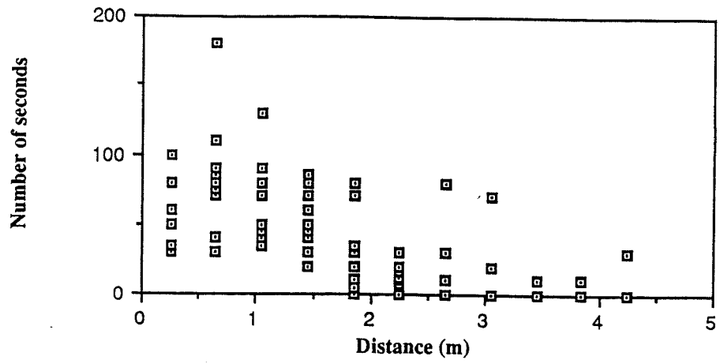
Figure 2 Time spent at various distances from a nearest neighbor (out of a possible 300 seconds).



HEAD BOBBING BEHAVIOR IN CTENOSAURA SIMILIS: VARIATIONS IN RATIO AMONG DIFFERENT-SIZED INDIVIDUALS AND BETWEEN MORNING AND AFTERNOON

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Abstract (L.T.)

Head bobbing in ctenosaurs (Ctenosaura similis) is a display of territoriality (Janzen, 1983). We found no significant change in the rate of head bobbing in ctenosaurs of the same size (small) between the morning and the afternoon. However, we did find a significant difference between the large and the small ctenosaurs when their bobbing rate for both time periods was compared. We attribute the large/small difference to the fact that the majority of the large ctenosaurs are males who aggressively defend their territories, possibly to show their (competitive) and reproductive fitness. In contrast, the small were females and smaller males who are less aggressively territorial. The non-significance of time of day on small ctenosaurs' head bobbing could be a result of the warm climate giving ctenosaurs a metabolic rate high enough to maintain a constant rate of head bobbing throughout the day. However, it could also be a result of other factors we could not control for, such as the lumping of small males and females into one category.

Introduction (G.Y.)

We studied head bobbing behavior in Ctenosaura similis through bobbing rate differences among individuals of different size and between morning and afternoon. Our first hypothesis was that large individuals would head bob more often than small individuals. Our second hypothesis was that average head bobbing rates would differ throughout the day.

Head bobbing is associated with defense of home and foraging patch territories and with intimidation of subordinate individuals (Janzen, p. 395, 1983). Like equivalent displays in numerous other species of animals, head bobbing is presumably an adaptive trait because it allows those individuals which partake in the behavior to estimate an opponent's strength before risking injury in a fight (Parker, 1974 in Krebs and Davies, 1987). It follows that larger, stronger individuals would threaten potential opponents more vigorously than smaller individuals. Because Ctenosaura similis is poikolothermic, as individuals warm themselves in sunlight, their general activity level may increase throughout the day, leading to increasing aggressive interactions. This could be demonstrated by increased head bobbing rates in afternoon as compared to morning, if a

metabolic rate does indeed limit aggressiveness in morning.

Methods (L.T.)

We followed individual ctenosaurs for thirty minute intervals and recorded the time of each head bob during this period. A head bob was defined as a series of 10-12 quick vertical jerks of the head. A pause of two or more seconds between the jerks separated 2 head bob events. Also, each time the subject ctenosaur changed his position we recorded the time, the distance it moved, and the approximate distance between the subject and its nearest ctenosaur neighbor. We categorized ctenosaurs into two categories:

1. large - which appeared to be primarily males with a much larger body (> 1.25m) and much larger spines.
2. small - which encompassed the smaller males (still with spines) and females which had much smaller, more flattened spines. (Janzen, 1983) (body size for both 1.25m).

We collected the morning data from 0800-1000 and each of us observed three subjects, for a total of nine observation periods. Our field site was the picnic ground near the hacienda, Palo Verde, Guanacaste.

We collected our afternoon data from 1430-1630 and conducted nine 30 min time intervals again. The picnic ground was unavailable due to the encampment of a large group of people there so we observed ctenosaurs around the OTS Field Station, Palo Verde, Guanacaste.

Results (A.S.)

The average head bobbing rates are summarized in Table 1. We found that there was a great difference in head bobbing rates between large and small ctenosaurs ($U = 56$, $n = 14$, $n_2 = 4$, $p < .001$). There was no difference in head bobbing rates among the small ctenosaurs between the morning and afternoon observations ($U = 33$, $n, = 6n_2 = 8$, $p > .05$). We could not compare morning and afternoon data for large ctenosaurs because we collected data from only one large ctenosaur in the afternoon.

Discussion (A.S.)

Although our sample size was small, there was a very large difference in head bobbing rates between the large and small ctenosaurs. Ctenosaurs are territorial, and our observations were conducted during the breeding season. It is likely that the males are more territorial and aggressive because of this.

There are, however, some factors that we did not take into account that may have influenced our results. Because the head bobbing is an aggressive behavior (Fitch & Hackforth, in Janzen, 1987), the distance to other ctenosaurs may have some effect on the rate. Our original plan was to estimate distance to nearest neighbor and correlate this to head bob rate. However, we found that we often did not see other ctenosaurs in the area until after the recording period, so we were unable to account for distance in our tests. We did note that the small ctenosaur that had the highest rate of bobbing had at least one ctenosaur within 2-3m. This was much closer than most of the other neighbors that we observed. The large ctenosaur with the highest rate also had several neighbors within 2-3m. For at least 1 male, we were able to see that there were no other ctenosaurs nearby. Possibly, large males bob often and small males and females bob only when another ctenosaur is near. This also could be related to the breeding season. If only large males had the opportunity to mate, it would be expected that they would be more aggressive and so bob more.

The ctenosaurs with the highest bob rate from each size group were from the afternoon group. The AM-PM difference for large ctenosaurs could not be tested because there was only 1 male in the afternoon. We also could not do an overall AM-PM comparison because we had more males in the afternoon.

It is possible that the small group should have been divided into male and female. We chose large and small at the beginning of the study because we were not certain that we could determine the sex. The large group was all male, but the small was definitely mixed. Females and small males might have had different rates. If females moved into the territory of males to breed, the females would be unlikely to strongly defend another territory or to experience territorial behavior from the males who would want to mate with them.

Another factor that might have affected head bobbing is proximity to the burrow. Ctenosaurs guard a territory around the burrow and therefore might show increased aggressiveness there (Fitch & Hackforth, in Janzen 1983). I noted that one small ctenosaur bobbed once after emerging from its burrow.

One last complication in our methods was the choice of study sites. The morning observations were made at the hacienda where the ctenosaurs are accustomed to people. In the afternoon, the area became unavailable to us because there were people picnicking in the area. We did observations at the OTS station*. Several ctenosaurs were frightened during observation. This, and the fact that, in general, the ctenosaurs may have reacted differently in our presence probably influenced the bobbing rates that we recorded.

*The ctenosaurs are fed at the hacienda and therefore are less frightened of humans than at the OTS Station.

Table 1 Ctenosaur Head Bobbing Rates (bobs/min)(sample sizes in brackets).

	small	large
1020-1200 hrs.	.005 [6]	.34 [3]
1400-1600 hrs.	.033 [8]	3.92 [1]
Total	.021 [14]	1.24 [4]

Literature Cited (A.S.)

Janzen, Daniel H. Costa Rican Natural History. University of Chicago Press, Chicago, 1983.

Krebs, J.R. and N.B. Davies, An Introduction to Behavioral Ecology, Oxford Scientific Publications, Boston, 1987.