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THE ESTABLISHMENT OF DOMINANCE AMONG FEMALE *CTENOSAURA SIMILIS* AND THE EFFECT OF EXPANDING TERRITORIES ON AGGRESSIVE ENCOUNTERS

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Abstract. We explored relationships between time of day, territory size, and aggression in female Ctenosaurs, *Ctenosaura similis*. We found that the females are spaced further apart near midday, when they are most active and their territory sizes are maximized. As inter-female distance increased, the number of aggressive encounters between females decreased. Aggressive encounters between females resulted in decisive dominance of one female over another, thereby establishing the dominance hierarchy that determines which females have access to the best basking and foraging areas. (JMH)

INTRODUCTION (ABS)

Territoriality and dominance hierarchies exist within harems of female *Ctenosaura similis* (Henderson and Fitch 1979). *C. similis* are most active during the hottest hours of the day, during which time their range and territory sizes reach their maximum extent (Henderson 1973). With this in mind, we hypothesized *a priori* that the mean distance between individuals and time of day should show a convex curvilinear relationship, the number of aggressive interactions and time of day a concave curvilinear relationship, and therefore, the number of aggressive interactions should be negatively correlated with mean distance between individuals.

The dominance hierarchies characteristic of female ctenosaur social structure is presumably established during aggressive encounters. These encounters are initiated by either a series of head bobs by one of the individuals, or by the pursuit of one individual by another. With this in mind, we formulated our third hypothesis, that an aggressive interaction between two females results in the establishment of dominance by one of the individuals.

METHODS (JMH)

We observed a group of ctenosaurs from 0715 to 1530 on 10 January 1992. The ctenosaurs were residing in a barn adjacent to the administration buildings of Palo Verde National Park, Costa Rica. All individuals observed were members of the same harem, which included approximately 20 females. Although the area which we observed included most of the group's range, ctenosaurs occasionally left the observation area.

Every half-hour, for each female in the group, the distance to the nearest female neighbor was estimated and recorded. Throughout the observation period, three observers in different locations recorded all visible aggressive encounters between females and the times at which they occurred. Each encounter was comprised of a series of stereotyped behaviors, which were also recorded. Temperature was recorded every 15 minutes.

Analyses were performed on data obtained between 0900 and 1500.

RESULTS (JJB)

The data for number of aggressive encounters and mean distance be

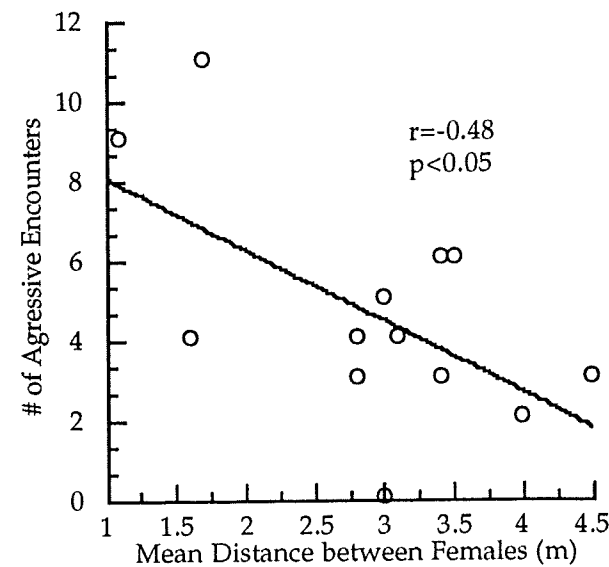
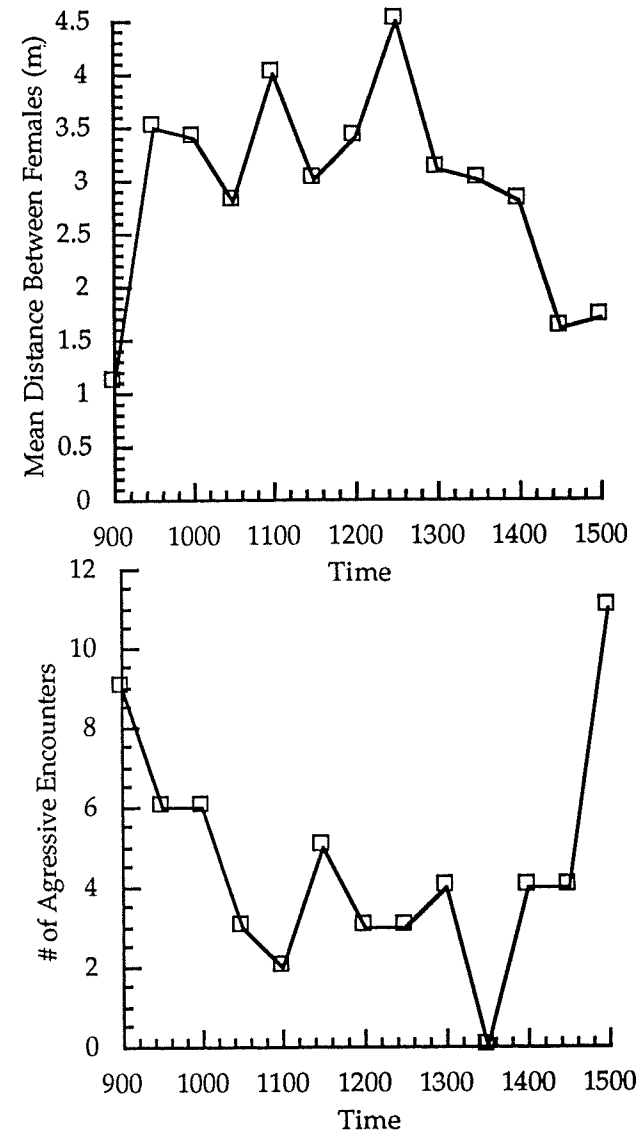


Figure 1. Aggressive encounters as a function of interfemale distance.

tween females are shown in Figure 1. The Spearman Rank Correlation coefficient between these two sets of data is -0.48 ($p < 0.05$). Thus, as inter-female distance increased, the number of aggressive encounters decreased (Figure 1).

To test whether encounters resulted in establishment of dominance, we recorded the number of resolved and unresolved encounters over a six hour time period. Forty-seven of 55 encounters were resolved, which differed significantly from an even (expected) distribution ($\chi^2 = 27.66$, $p < 0.001$).

The number of aggressive encounters shows a decrease from morning to mid-day, and then an increase in the afternoon (Figure 2). In contrast, mean distance between females was low in the morning, high at mid-day, and low again at night (Figure 2). Thus, an inverse relationship appears to exist.



DISCUSSION (ABS, JJB)

We attempt to explain the convex curvilinear relationship between mean inter-female distance and time as follows: As the size of a female's territory increases, so does the quantity of food resources that it has access to. However, the farther it ventures from its burrow, the greater the likelihood of predation. Therefore, during the hottest hours of the day, when an individual is most active and perhaps

most capable of escaping predators, it maximizes the size of its territory.

As the average territory size increases, the density of females decreases, and it is less likely that two individuals will come into contact with one another. This could explain the negative relationship between mean inter-female distance and the number of aggressive encounters (Figure 1).

Because dominance hierarchies exist within a harem of ctenosaurs, there must be a method to establish dominance. Between females, dominance is determined through aggressive encounters. A head bob or chase initiates an aggressive interaction. In response, the antagonized female may respond aggressively, by returning head bobs; subordinately, by fleeing; or may ignore the stimulus entirely. A returned head bob or multiple head bob sequences represent unresolved

interactions, and must escalate to a chase-flee/attack in order to become resolved. Our findings show that aggressive interactions frequently lead to the establishment or reinforcement of dominance. Dominance probably gives a female ctenosaur access to optimal foraging and basking areas.

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