Food access in captive *Ammotragus*: The role played by hierarchy and mother-infant interactions

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Short title: Dominance and food access in *Ammotragus*

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Abstract

An analysis of individuals' behavior when accessing a restricted food source (troughs) was carried out in a captive population of aoudad, *Ammotragus lervia*. Access to the troughs followed a strict hierarchical order, as higher ranking individuals fed before lower ranking ones. Unweaned male calves made use of the troughs from the age of two months, and female calves at the age of three months. Both fed from the troughs more frequently and for longer periods when their mother was present, which allowed them to make use of the troughs skipping the hierarchical order. Calves received fewer threats when in proximity to their mothers, particularly in high-ranking families. Mothers defended their calves from other herdmates more frequently when at the feeding area than in other areas of the herd; however, only sated mothers will let their calves feed freely from the troughs, as before that mothers showed an aggressive behavior even toward their calves. I conclude that maternal presence is necessary for aoudad calves to successfully feed from troughs, and that families holding higher social ranks benefit in getting access to this food source earlier in the day and are disturbed less than low-ranking families.

Key words: Access to Resources, Aoudad, Mother-Infant Relationships, Social Ranks, Ungulates

Introduction

In social species, when two or more individuals strive for the same resource (water, food, mates, resting place, shade…) conflicts of interest arise. These conflicts are solved

by means of agonistic-submissive encounters that are typically translated into dominance hierarchies, in which every individual in a group holds a social rank reflecting its position in the hierarchy [e.g., Scott, 1962]. Typically, high dominance status confers individuals preferential access to resources [e.g., Wrangham, 1981; Whitten, 1983; Cheney and Seyfarth, 1990]; thus, high-ranking individuals are expected to have higher reproductive success than low-ranking ones [e.g. Whitten, 1983; Gomendio, 1990; Cassinello and Alados, 1996; Cassinello and Gomendio, 1996; but see Packer et al., 1995].

It should be noted that when resources are patchily distributed dominant individuals can control access to them; thus, it is under highly restricted situations when social ranks become more evident [Harcourt 1987]. Under captive conditions, it is a common practice to provide food in a concentrated or limited space, i.e., by means of stalls or troughs filled periodically. This limited access to a food source causes a conflict of interests between the individuals living in a captive social group, so that a dominance hierarchy should show up [see Thouless, 1990].

In this paper, I investigated access to a restricted feeding source in a captive population of aoudad (*Ammotragus lervia*, Artiodactyla: Bovidae), paying particular attention to mother-infant interactions. This aoudad population has already been subject of previous studies on maternal investment and mother-infant conflict [see a review in Cassinello, 1998], as well as a recent comparison of suckling and grazing rates [Cassinello, 2001]; therefore it is an excellent choice to carry out a detailed study on mother-infant feeding behavior.

Ungulates are characterised by a strong mother-infant bond [Lent, 1974; Gubernick, 1981], which may last beyond weaning [e.g., Robbins et al., 1987; Green

and Rothstein, 1991; Rowell, 1991]. Weaned offspring may benefit from prolonged association with their mothers for protection against other herdmates and reduced intra-specific competition for food resources [Clutton-Brock et al., 1982; Green et al., 1989; Kojola, 1989].

Methods

Since 1975 an aoudad population has successfully bred in captivity at the Estación Experimental de Zonas Aridas (EEZA, CSIC), in Almería, south of Spain [Cassinello and Alados, 1996]. This population originated from just one male and one female captured in Western Sahara [Alados and Vericad, 1993]. Although intent of the EEZA is to eventually return this population to the wild, acute political difficulties in their historical range have precluded this.

Sampling was carried out from 1990 to 1992 in a herd made up of 17 males and 26 females at the beginning of the study, and 33 males and 43 females at the end of it. The study group was housed in a 950 m^2 enclosure (Fig. 1), covered by rocky ground and bare soil used by the animals for sand bathing [see Haas, 1959]. The individuals were identified by means of colored plastic ear tags. Birth date, sex, and identity of father and mother were known for each individual.

The animals fed on trusses of hay and standard cattle food pellets daily distributed by the EEZA staff in six rounded feeding troughs. The "feeding area" was defined as the area surrounding any of the six feeding troughs and from which an animal could access to them (around one meter distance) (Fig. 1). The feeding area also contained two drinking sources. An upper area was distinguished from a lower one,

98 both communicated by a middle area which consisted of a gradual slope (Fig. 1). Both
99 food and water were provided ad libitum.

100 Feeding behavior analysed here included time devoted to feed from the troughs
101 only, and not grazing on scattered forage along the enclosure [see Cassinello, 2001].
102 Sampling method have been described in detail elsewhere [e.g. Cassinello, 1996, 1997].
103 Focal sampling was used to record the behavior of mother-calf pairs during the
104 evenings, when mothers and calves were more active [Altmann, 1974; Martin and
105 Bateson, 1986]. Each sample being 20 min in duration. A "sampling period" consisted
106 of all focal samples carried out on a given day, in average 6 samples. Every female
107 which gave birth during 1990 and 1991 was sampled four times per week during her
108 calf's first two months of life; during the rest of the lactation period (the average
109 weaning age was 8.2 months), sampling was carried out 3 times in each 2-week period.
110 All the interactions that took place between a mother and her calf were recorded, as well
111 as any interaction between any of them and the other herdmates. The most conspicuous
112 agonistic behaviors were: horn display, butting, horn pushing, horn clashing, rush-
113 charge and subsequent withdrawal. More subtle behaviors included subtle horn displays
114 and gazes along with subsequent retreats by the infant [see, e.g., Galef, 1981;
115 Cassinello, 1996]. Feeding rate was measured as the proportion of time devoted to
116 feeding per sampling period following Hass [1990] and Cassinello [2001]. Threats rate
117 was defined as the percentage of visits by a given calf to the feeding area that resulted in
118 a threat from herdmates other than their mothers. The data analysed here were obtained
119 from the regular focal samples. Also, in those occasions when the fodder was provided
120 in the evening, before the regular focal sampling started a continuous recording
121 sampling allowed me to register all animals interactions when gathering at the feeding

122 troughs. The number of mother-calf pairs from which I have got information on their
123 behavior at the troughs is 18. The analyses of feeding area use by unweaned calves
124 included individuals up to six months of age in order to minimize any confounding
125 effect of weaning [Cassinello, 1997]. The maternal social rank was calculated and
126 monitored throughout the whole study, following a standard method used previously
127 [e.g. Cassinello, 1995, 1996, 2001]. The rank given to a particular individual
128 corresponded to the percentage of herdmates with a lower dominance status. Family
129 rank was defined as the rank of a given mother in a mother-calf pair. Finally, in order to
130 test whether the order of access to the troughs depended on the social rank, I
131 differentiated up to seven rank classes, from 1 to 7: high, mid and low-ranking adult
132 males, high, mid and low-ranking adult females, and juveniles.
133 Statistical analyses were two-tailed. Throughout the study parametric tests were
134 preferably used and non-normal dependent variables transformed: frequencies into the
135 form $\sqrt{(x+0.5)}$, rates into $\arcsin\sqrt{x}$, and age into its logarithm [see, e.g., Zar, 1984]. Data
136 for different calves from the same mother were considered as independent, because a
137 previous analysis of the intra and inter-group variance showed for all the behavioral
138 variables that the inter-group variance was not greater than the intra-group variance
139 [Cassinello, 1996, 1997, 2001].
140
141 **Results**
142
143 The high population density present in the study herd (0.05 ind/m^2 at the beginning of
144 the study and 0.08 ind/m^2 at the end) was associated with a high frequency of
145 interactions between all the individuals, and few chances for subordinates to escape

146 from aggression, although they were not involved in a higher number of aggressive
147 encounters than dominant individuals (Simple regression analysis between frequency of
148 aggression and social rank in adult females: R^2=0.003, N=22, P=0.82).

149 Food provisioning coincided with behavioral sampling on only 12 of 1565
150 sampling periods, so the analysis of access of feeding troughs was limited to these
151 samples. In all cases the highest ranking males would always feed first and monopolise
152 all the troughs, followed by mid and low-ranking adult males, then by high-ranking
153 females, mid and low-ranking females, and finally by juveniles; as shown by a
154 Spearman Rank correlation between the average rank class and the order of approach to
155 the troughs: rho=1.00, N=7, P=0.01. Calves did not follow this pattern as we will see
156 later. Also, in the great majority (92%) of the 3610 encounters observed at the feeding
157 troughs the subordinate individual let the dominant herdmate approach and feed, usually
158 without direct confrontation.

159 Calves were seen feeding from the troughs from the age of 74±8 days, which
160 was positively related to the age when calves started to feed on solid food (20±2 days;
161 Simple regression: R^2=0.28, N=18, P=0.02). Male calves fed from the troughs at an
162 earlier age (56±4 days) than did females (92±14 days; ANOVA: $F_{1,16}$=7.29, P=0.02).
163 Maternal social rank had no influence on this behavior (Simple regression for all calves:
164 R^2=0.005, N=18, P=0.78; Simple regression for males: R^2=0.03, N=9, P=0.65; Simple
165 regression for females: R^2=0.26, N=9, P=0.16).

166 Calf visits to the feeding area were significantly longer when their mothers were
167 present than when they were absent (mother absent: 0.09±0.02 min.; mother present:
168 2.33±0.15 min.; Paired t test: t=20.06, df=17, P<0.0001), and the average proportion of
169 time spent feeding from the troughs was therefore higher when calves were in the

presence of their mothers (Paired t test: t=26.63, df=17, P<0.0001, Fig. 2).

Aggressive responses directed towards calves by other herdmates occurred almost every time the calves entered the feeding area in the absence of their mothers (99%); when mothers were present, the frequency of threats was much lower (67%) (Paired t test: t=18.14, df=17, P<0.0001). There was also a negative relationship between a calf's family social rank and threats rate received from herdmates (Simple regression: R^2=0.25, N=18, P=0.03; Fig. 3).

The frequency of responses by mothers to other herdmates' threats at the troughs or elsewhere in the herd did not vary; however, mothers tended to respond more often to threats directed at their infants in the feeding area than in other circumstances or areas of the enclosure (Paired t test: t=3.30, df=14, P=0.005, Fig. 4; 3 mother-calf pairs excluded due to insufficient data).

A detailed analysis of mother-calf interactions while feeding from the troughs showed that after accessing to the trough, calf's attempts to feed were usually followed by agonistic responses by the mother toward it; this aggressive or non-tolerant behavior decreased with time at the feeding trough, as shown in Fig. 5 (ANOVA: $F_{4,85}$=46.69, P<0.0001; Fisher's PLSD post hoc test showed significant differences, P≤0.001, for all pair comparisons except for minutes 4-5).

Discussion

Aoudad is highly gregarious and its herds are characterized by relatively fixed hierarchies, closely dependent on sex and maturity: any male older than three years of age dominates all the females, whereas juveniles always hold lower ranks than any adult

194 [Cassinello, 1995]. The high population density of the study herd allowed dominant
195 individuals to easily control the feeding area. Under these circumstances, gaining access
196 to food resources was always under hierarchical control. This was already reported by
197 Katz [1949] in his pioneer work on the species. However, mother-calf pairs represent an
198 exception to this rule, as infants in their mother's presence feed from the troughs even
199 when higher ranking herdmates are still queueing and waiting for access. Similar
200 findings on feeding behavior mediated by the hierarchical status have been found in
201 other ungulate species, both when forced to compete for artificially concentrated food
202 resources [red deer, *Cervus elaphus*: Appleby, 1980; Hall, 1983] and when feeding
203 under natural conditions [woodland caribou, *Rangifer tarandus caribou*: Barrette and
204 Vandal, 1985; red deer: Thouless, 1990].

205 Aoudad calves start to alternate milk consumption with grazing early in life
206 [Cassinello, 2001]. At about two and a half months of age they start feeding from the
207 troughs, which is precisely when suckling rates substantially decline [Cassinello, 1996].
208 Moreover, males start using the feeding area at an earlier age than females, which is in
209 accordance with the greater time spent grazing by males at the age of two months
210 [Cassinello, 2001]. This is not surprising considering the higher energetic demand of
211 unweaned males compared to females in a highly sexually dimorphic species such as
212 this [see Clutton-Brock, 1991].

213 Mother's presence and behavior had a significant effect on calf visits to the
214 troughs. Calves spent more time feeding from the troughs when their mother was
215 present, calves received fewer threats when their mother was present (especially if their
216 mother was high-ranking), and mothers tended to react before agonistic behaviors
217 addressed to their calves at a higher frequency when at the troughs than in other

218 circumstances/locations. It is worth pointing out that the existence of a mother's
219 response to a threat did not necessarily imply that the encounter was won by her,
220 instead, it is a measure of the mother's willingness to defend her calf. Mother-infant pair
221 bonds are very strong in ungulates [e.g. Green et al., 1989], and calves tend to
222 synchronize their activities to those of their mothers as they mature [Lickliter, 1987],
223 especially "follower" species [e.g. Estes and Estes, 1979], such as aoudads. This could
224 partly explain why calves follow their mothers to the troughs, but a more evident benefit
225 obtained is the lower rate of threats suffered by calves when escorted by their mothers.
226 An interesting finding is importance of social dominance: high-ranking families
227 suffered from a lower rate of aggressions in the feeding area. This, along with their
228 higher priority of access to the feeding troughs, confers obvious advantages. Similarly,
229 Deutsch and Lee [1991] reported that high-ranking females of rhesus monkeys (*Macaca*
230 *mulatta*) are threatened less frequently while feeding than subordinates.

231 The onset of a behavioral conflict between mother and infant under a feeding
232 context has been widely studied in primate species [e.g. Rosenblum and Sunderland,
233 1982]. Apart from conflicts related to the amount of maternal investment (lactation)
234 allocated to the infant [Barrett et al., 1995], when foraging conditions are demanding,
235 mothers tend to agonistic responses or reject more frequently their offspring during
236 feeding time [Rosenblum and Sunderland, 1982; Andrews et al., 1993]. Here, I have
237 registered a progressively decreasing agonistic behavior of the mothers towards their
238 calves, which seems to corresponds with a satiety process after several minutes feeding
239 from the troughs.

240 These results may help in understanding the complex relationships within
241 ungulate family groups, namely, maternal effects, offspring requirements and

hierarchical roles played under limited resources. It should also help in establishing adequate housing conditions, which is a priority for any successful captive breeding program.

Conclusions

1.- Access to concentrated food resources in captive aoudads is determined primarily by the hierarchical status of the individuals.

2.- Maternal presence is necessary for unweaned aoudad calves to successfully feed from these resources, as threats directed to them decrease, enabling them to spend more time feeding.

3.- Families holding high social ranks benefit by getting access to concentrated feeding sources earlier and with fewer disturbances than low-ranking families.

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Figure Captions

Figure 1. Diagram of the 950 m^2 enclosure inhabited by the study aoudad population. Three promontory levels are distinguished: upper, middle and lower, with an unevenness (wall) of 1.5 m between upper and lower levels. Middle level actually refers to a gradual slope area from lower to upper.

Figure 2. Average (+SE) feeding rate (proportion of time feeding per sample period) of six months-old aoudad calves (N=18) observed inside the feeding area, in the presence or absence of their mothers.

Figure 3. Relationship between mothers' social rank and threats rate (threats per sample period) addressed to their calves while in the feeding area.

Figure 4. Average (+SE) frequency of mother's responses to herdmates threatening her calf inside the feeding area and in other locations of the enclosure (N=15).

Figure 5. Average (+SE) number of mothers' agonistic responses towards their calves while both were feeding from the troughs for feeding bouts which lasted 5 or more minutes (N=18).

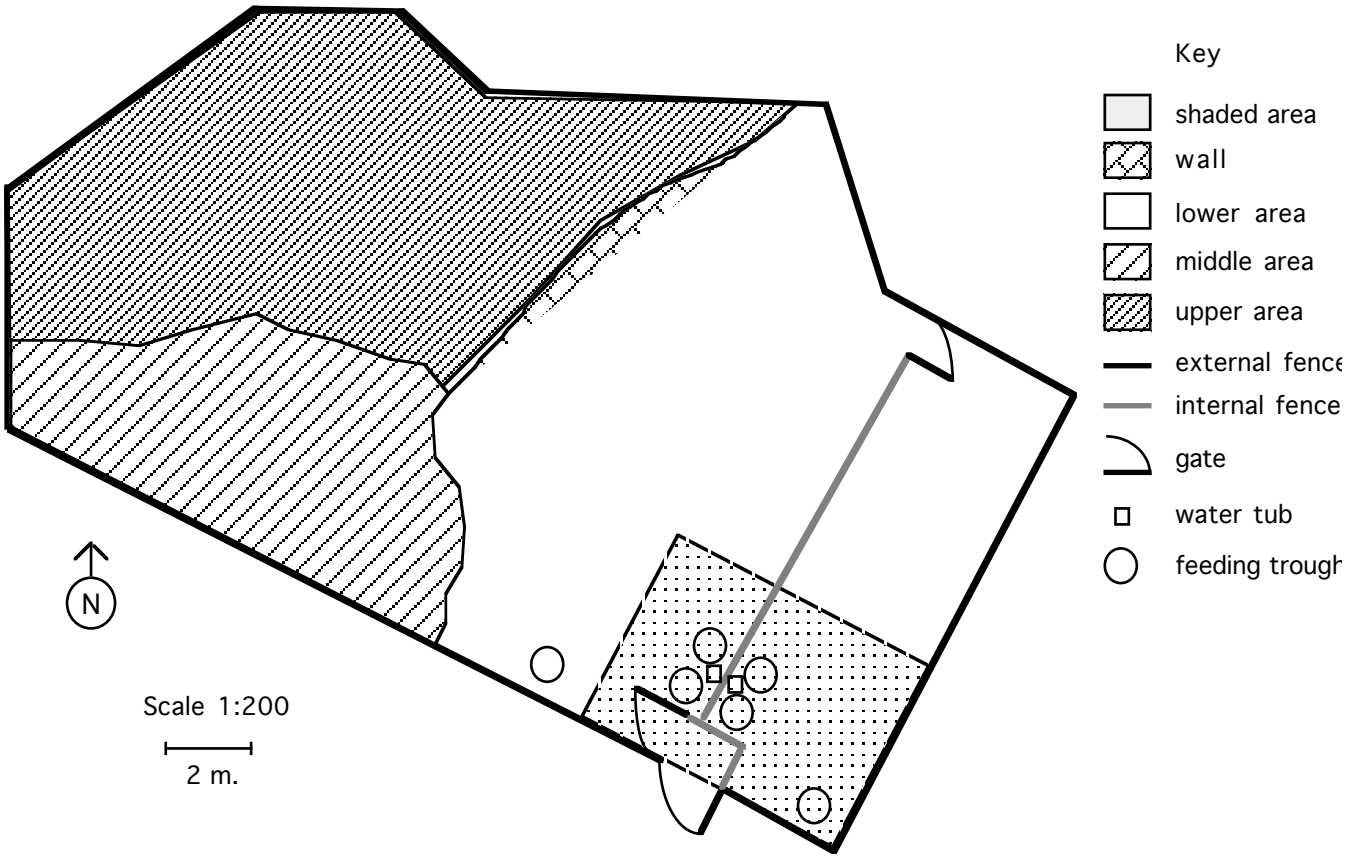
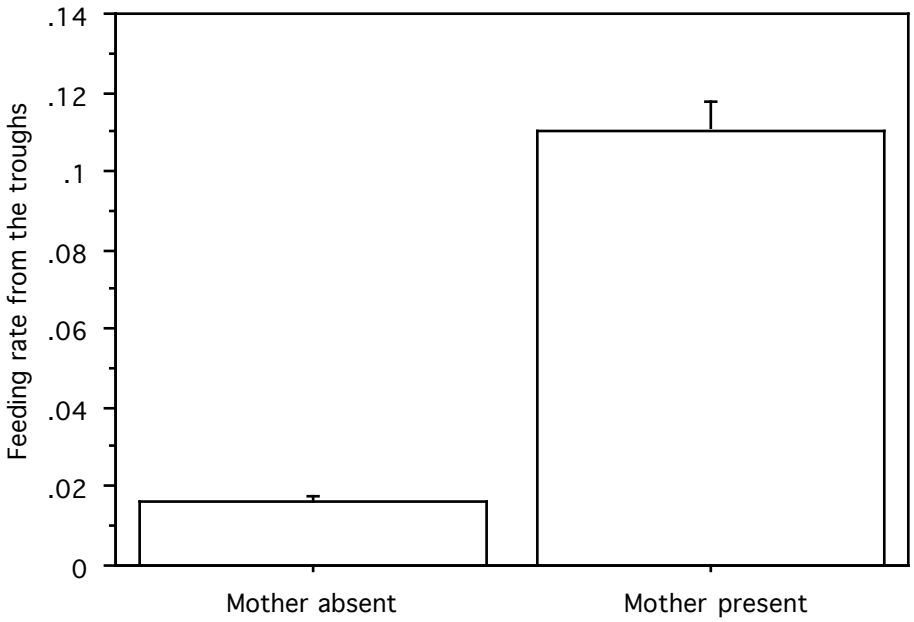


FIGURE 1 - J. CASSINELLO



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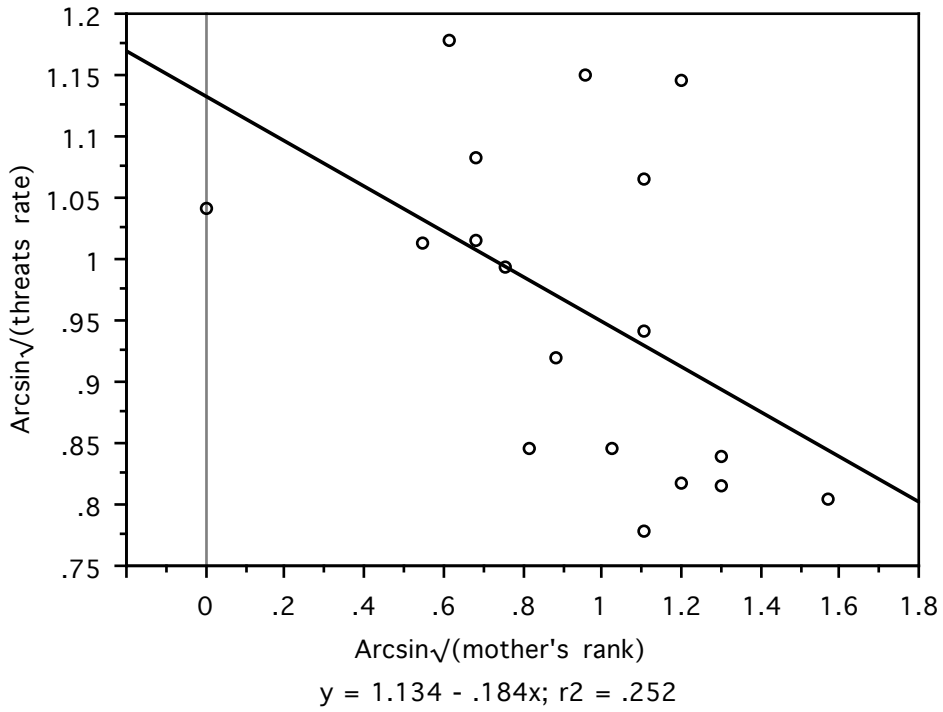

FIGURE 3 - J. CASSINELLO

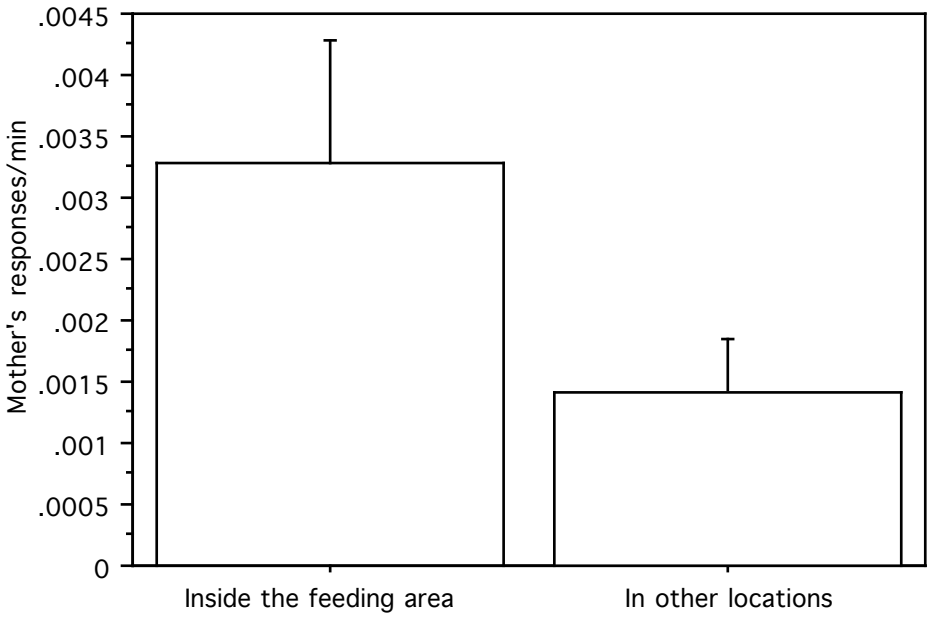

FIGURE 4 - J. CASSINELLO

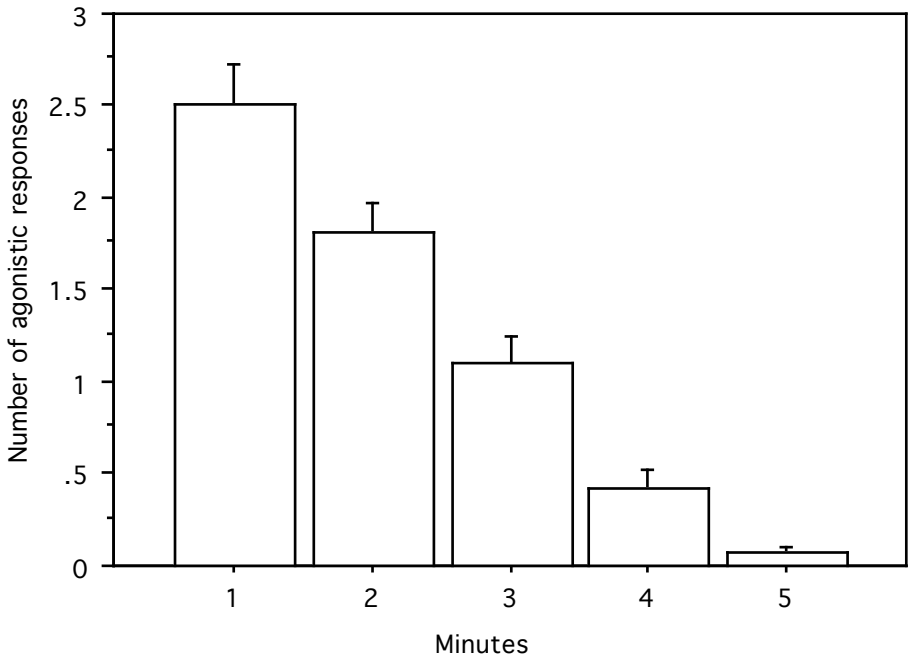

FIGURE 5 - J. CASSINELLO