The Effect of Female Call on Male Howling in Red Howler Monkeys *(Alouatta seniculus)*

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*Howler (*Alouatta *spp.) females often produce loud calls together with the males. Sometimes these howls are not heard above the much louder male call, but on other occasions most of the howls are produced by the females. Observations indicate that female howls are aggressive. Females howl at other troop females and at extratroop females; they also sit close to their mates and howl at other males. I suggest that howling by the females with their mate is important in strengthening the pair bond whereby the male recognizes his infants and acts protectively toward them. Playback experiments of female howls elicited more response from the males than did recordings of male/female and male-only howls, supporting the hypothesis that females howl in order to incite competition among the males.*

INTRODUCTION

Howler monkeys *(Alouatta* spp.) are famous for their loud, continuous calls (Carpenter, 1934; Altmann, 1959; Chivers, 1969; Baldwin and Baldwin, 1976). These calls are usually dominated by males, but females also take part. The duration of male howls and contexts in which they are observed suggest that they are used to assess capabilities of their opponents (Sekulic, 1982a). Because female calls are much softer than those of the males (Baldwin and Baldwin, 1976), they have been given little attention.

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In the well-studied mantled howlers *(A. palliata)*, the howl of females is distinguished from that of males by its higher pitch (Baldwin and Baldwin, 1976; Eisenberg, 1976), but the contexts in which females howl have not been described. Recently, Sekulic (1982b) observed that in another species, the red howler *(A. seniculus)*, calls directed at a solitary female were produced primarily by troop females. In this species females, as well as males, often leave their natal troop when they attempt to form a new troop or join an already established troop (Rudran, 1979; Sekulic, 1982b). Troop females strongly resist intrusion by unfamiliar females. The aggressive behavior by the troop females during the production of howls indicated that they were used as an alternative to chases and fights (Sekulic, 1982b). Troop males often followed solitary females, and in the absence of aggression by troop females, many solitary females would have been integrated into established troops.

When solitary males enter a troop, dominant males, as well as females, are threatened, because new males kill unweaned infants (Rudran, 1979; Sekulic, 1981, 1982c,e). The dominant male, therefore, as well as the females, would be expected to act aggressively toward nontroop males. The howling of red howler females in different social situations is described in this paper, along with the results of an experimental investigation of the hypothesis that the female call elicits male howling.

MATERIALS AND METHODS

The study was a part of a long-term investigation of the ecology and behavior of *A. seniculus* at Hato Masaguaral, Venezuela (Mack, 1979; Rudran, 1979; Thorington *et al.*, 1979; Sekulic, 1981; Crockett, in preparation). Four troops with contiguous, overlapping home ranges were observed between August 1979 and August 1980. The daily and seasonal ranging patterns of the troops are described elsewhere (Sekulic, 1982d). The four troops varied in size from 9 to 13 individuals (Fig. 1), including one or two adult males and two to four adult females. Individuals were recognized by size, scars, facial characteristics and ear tags (Thorington *et al.*, 1979). Most of the daytime observations were made with 10×50 binoculars from a distance of 10 to 30 m. The durations of most roars were timed with a stopwatch; many were also tape-recorded.

Experimental Procedures

Tape recordings of howls were used to investigate the effect of female calls on male howling. Although experimental playbacks of recorded calls
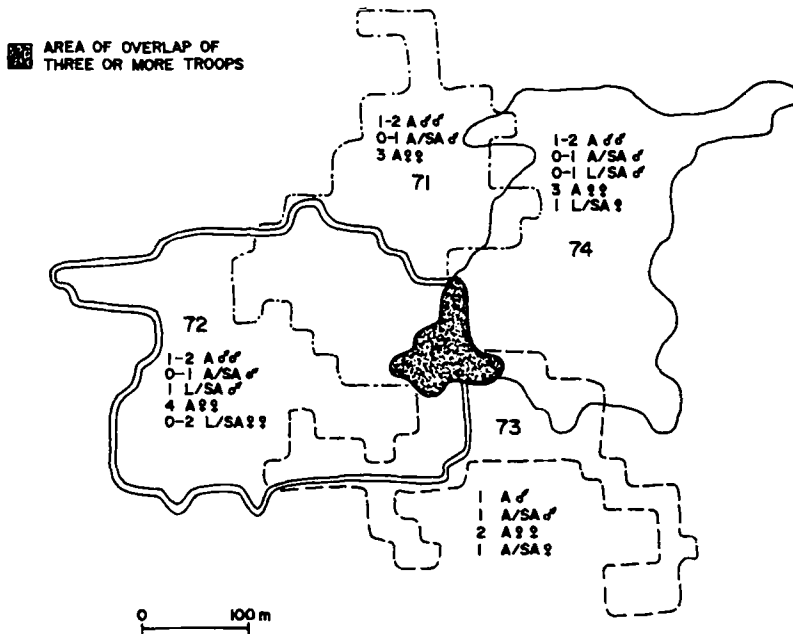
Fig. 1. Ranges of the four study troops and composition of the large juvenile to adult age class in 1979–1980: A, adult; S, subadult; L, large juvenile.

are most frequently used in bird studies (e.g., Falls and Brooks, 1975; Falls and McNicholl, 1979; Gish and Morton, 1981), they have also been successfully performed on primates (Chivers and MacKinnon, 1977; Waser, 1977; Robinson, 1979; Cheney and Seyfarth, 1980; Seyfarth *et al.*, 1980). These experiments offer a way of controlling at least some of the many variables that are encountered in the field. It has been suggested that loud primate calls are particularly well suited for experimental playbacks since they are frequently given out of sight of receivers (Waser, 1977). However, most red howler loud calls occurred when other troops or solitary individuals could be seen clearly (Sekulic, 1982a,b). During the daytime, roars usually were not preceded by roars of troops that were out of sight. The experiments were performed before dawn, therefore, when the monkeys were more likely to respond without seeing other monkeys. To prevent disturbance, the vehicle with the playback equipment was positioned near the sleeping tree the evening before the experiment. By playing recordings in the dark, the males could not see what elicited the call (playback). In particular, they could not distinguish whether female howls (playbacks) were "produced in response to" males or females. Another advantage of performing ex-

periments before dawn was that the monkeys were less likely to associate the presence of the observer with the playback.

Response to female playbacks was compared with response to male-only and mixed male/female calls. I performed a total of 45 howler playbacks, including 9 male-only, 9 female-only, and 13 mixed male/female calls recorded from neighboring troops and 14 male-only and mixed male/female calls recorded from nonneighbors. Since no other primate species occurred in the immediate vicinity of the studied troops, six control experiments were made using 1 min of a bird (limpkin, *Aramus guarauna*) call of similar amplitude. In order to prevent habituation, no troop was used in the experiment on successive days. In addition, the equipment was placed near the sleeping tree on 20 days when I came to the site before dawn but did not perform the experiment.

Calls were recorded using a Uher 4000 Report-L tape recorder and a Sennheiser MKH 816T directional microphone. A test call 1 min in duration was played back using the Uher tape recorder, a Nagra Kudelski DSM-monitor, and a Klipsch Heresy loudspeaker (frequency response, 50–17,000 Hz ± 5 dB). The loudspeaker was placed on the back of a vehicle and tilted slightly upward toward the monkeys. Two 12-V car batteries placed in series were used as a power source for the amplifier and the speaker. The vehicle was positioned between 38 and 58 m from the base of the tree where the monkeys were sleeping when they were near the area of overlap with three troops (Fig. 1). The experimental calls were played from the direction of the area of range overlap, and the experiments took place only when the monkeys slept within 200 m of this site. All the playbacks were conducted between 38 and 67 min before dawn.

Peak call amplitudes (as measured by a General Radio Type 1565-B sound-level meter, C-weighting) were taken of naturally occurring howler roars between 0500 and 0630 hr (Fig. 2), as well as of playback tapes at different distances from the loudspeaker (Fig. 3). It must be noted, however, that these are peak amplitudes; the actual intensity of each roaring bout varied as much as 14 dB. The measurements showed that a roar about 50 m away will reach an amplitude as high as 70 dB, while the playback tapes at this distance were only 61–65 dB. Sounds attenuate about 6 dB with every doubling of distance in a homogeneous, frictionless medium (Peterson and Gross, 1967). In natural environments, of course, attenuation is greater (e.g., Morton, 1975; Marten *et al.*, 1977). Thus, the playbacks probably sounded to the howlers as if they were produced at a location about twice the actual distance. Peak amplitudes of each playback, as heard by the monkeys, were estimated with the aid of Fig. 3 and the distance between the vehicle and the base of the tree in which the animals slept.

The playback was started if no near troop (within about 600 m) called for at least 3 min. A playback was considered valid if no near troop other
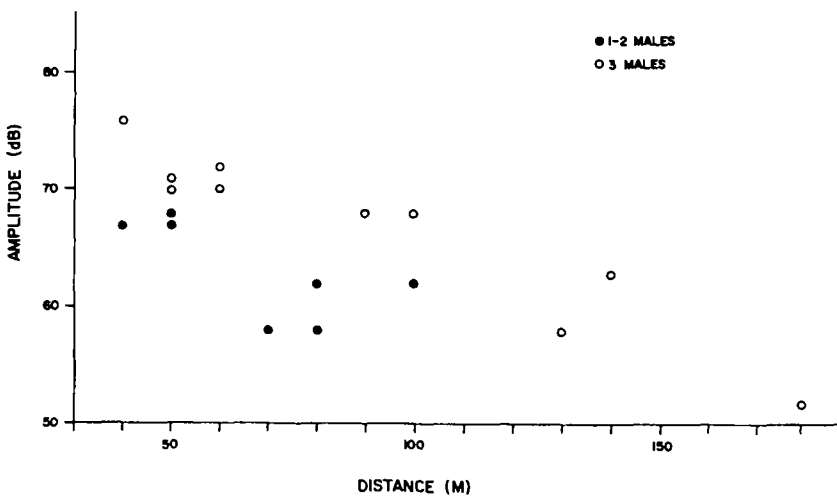
Fig. 2. Peak amplitude of naturally occurring howler roars by troops at different distances.

than the experimental troop called within the first 3 min following the beginning of the playback. Most playbacks and any vocal responses were recorded with a second tape recorder. All of the statistical tests were drawn from Siegel (1956) and Sokal and Rohlf (1969).

RESULTS

Excluding intertroop encounters, the contexts of daytime howling based on 2300 min of howling during daily observations are presented in Fig. 4. A total of 68.7% of these howls were directed at solitary individuals, 24.1% were elicited by interactions with troop members, 4.7% could not be identified, 2.4% were caused by disturbances (usually humans or dogs), and 0.1% were apparently caused by the onset of rain.

Howls initiated by one animal usually elicited immediately such a quick vocal response by at least one other individual that it was difficult to decide which animal had begun the call. Some members of a troop that were calling in synchrony sat close together and even embraced each other during the most intense howls, but others were more than 10 m apart. The term "howling with" is used to describe individuals that were touching each other while howling. The animals that were "howling at" one another were usually more than 5 m apart.

Sonograms of female howls are shown in Fig. 5. At low intensities females produce roars decreasing in frequency over 700 Hz (Fig. 5A), while
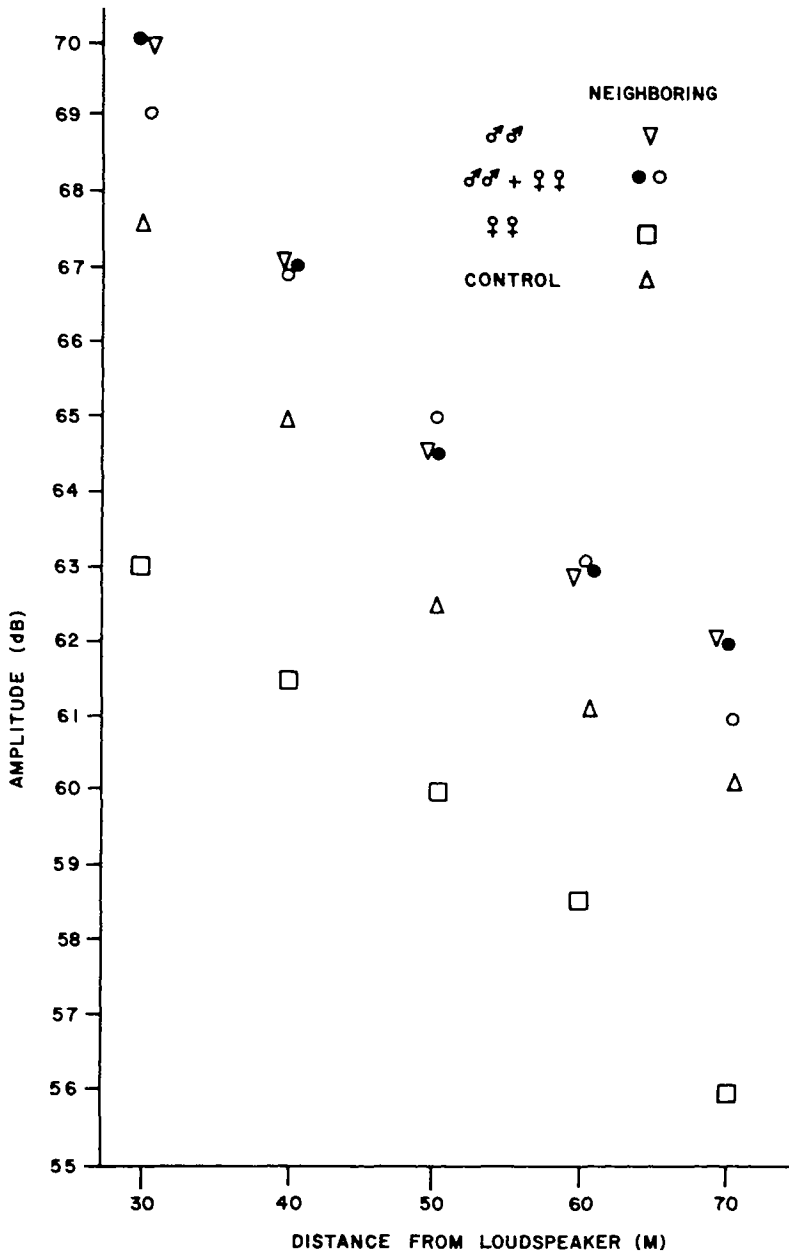
Fig. 3. Peak amplitude of the playback tapes and the control at distances of 30 to 70 m.
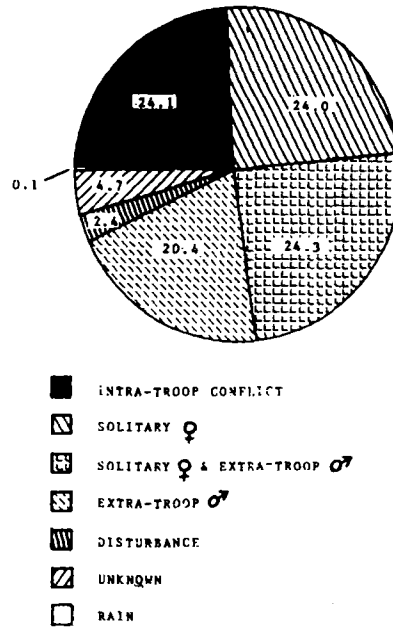
Fig. 4. Total roaring "contexts" (excluding intertroop encounters) based on 2300 min of roaring by four troops (see also Fig. 5).

highly aroused females produce 500-Hz harsh sounds without frequency modulation (Fig. 5B). Not only did troop females howl at solitary females, but also conflicts occurred among troop females when two females sitting next to each other howled at a third female. This was most evident in one of the study troops (74; Fig. 1) which included an adult female (No. 423) that had immigrated into the troop in 1978 (Rudran, 1979). She successfully raised one infant (Sekulic, 1981) and, at the onset of the present study, appeared to be a well-integrated member of the troop; she even handled a newborn infant belonging to another troop female. When she became receptive at the end of October 1979, however, the other two troop females that had young infants became aggressive toward her. Not only did female 423 become a peripheral animal during resting periods, but also she was displaced when she attempted to roar with the troop male (No. 412). On the rare occasions when she began to roar with the male, she repeatedly looked at the other females. The latter invariably approached within 2 min, often piloerected, to join the male in calling. Female 423 immediately moved 10-15 m from the calling animals and lay down. Occasionally, female 423 produced a short roar or a head-throw (an aggressive display) toward the other females. Sometimes she was joined by a large juvenile female that put
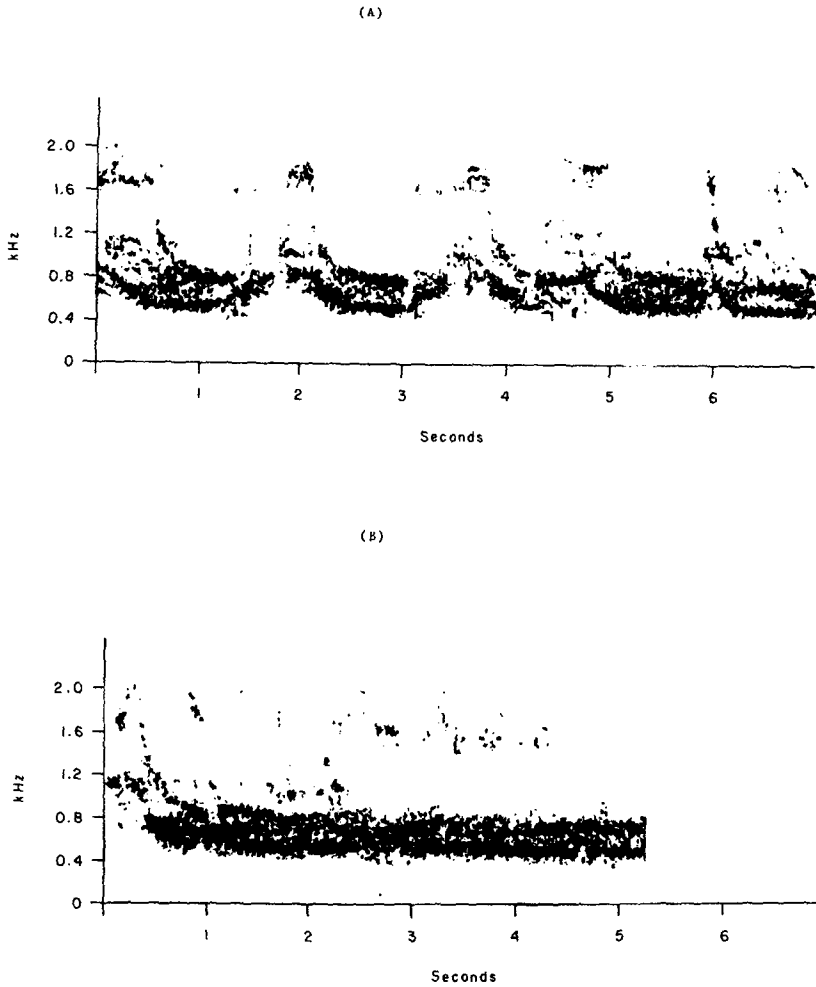
(A)

(B)

Fig. 5. Sonograms of (A) *A. seniculus* female roar at a moderate intensity (B) *A. seniculus* female roar at a high intensity.

her arms around her and roared vigorously, but female 423 called less at these times. On several occasions the troop females also roared directly at female 423 and displaced her from the tree. After female 423 had become pregnant, another male (No. 411) entered the troop. Female 423 continued to howl with male 412, while the other two females howled with male 411. These two females mated with the new male and the subsequent observations showed that they conceived shortly after male 411 had entered the troop (Crockett and Sekulic, 1982).
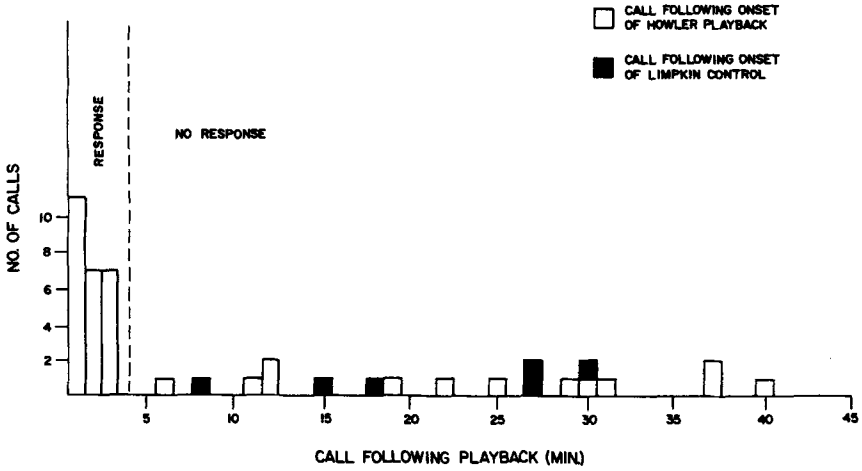
Fig. 6. Timing of calls by the experimental troop following the onset of the howler roar playbacks and controls. All calls that occurred within 3 min of the onset of the playbacks are considered "response."
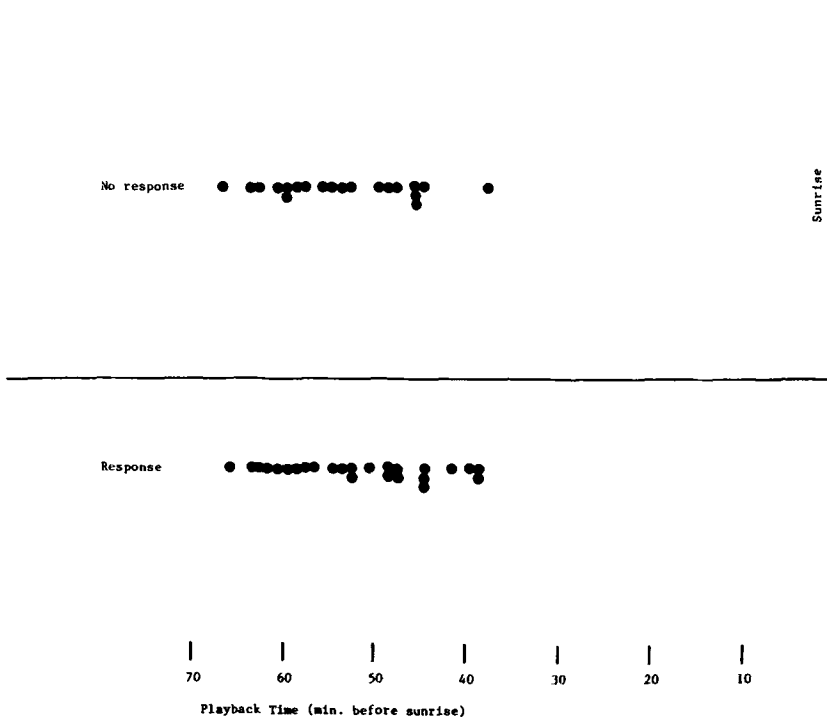

Fig. 7. Time of playback in relation to sunrise. Points indicate the number of minutes before sunrise of playbacks that resulted in vocal response and playbacks to which there was no response.

Howling by females directed at solitary males was seldom heard clear-ly because such calls were dominated by the much louder male howls. This was also the case during intertroop encounters, when adult females with in-fants usually stayed farther away from nontroop males than the other age/sex classes. The position changes of individuals and the intensity of their participation in howling, as well as visibility changes, made collection of any quantitative data difficult. Conflict among troop females, however, was also evident in troop 72 (Fig. 1), where the three females with infants howled with male 211 which had probably fathered all the infants (Sekulic, 1982e), while the fourth female (No. 223) first mated with male 212 two months before he ousted male 211. In the third troop where there was more than one adult male (troop 71), the females never howled with male 112, which emigrated from the troop in March 1980.

Unlike many other primates, which may move rapidly toward calls of a conspecific (e.g., Robinson, 1979; Waser, 1975), the red howlers do not leave the tree and usually shift their position only slightly as they move to higher branches and closer to other troop members. Such movements, however, could not be observed in the dark. Therefore, the only response to playbacks that could be monitored was vocal. The results are shown in Fig. 6. Overall, 25 of the 45 (55.6%) experimental playbacks were answered within 3 min of the onset of the experiment, while there was no response to the limpkin control during this time ($G = 8.85$, df $= 1$, $P < 0.01$). All of the responses were started by the males, but females usually joined within a few minutes. The median duration of responses was 7.57 min (range, 1.20–19.0 min). The duration of the calls, however, could not be taken as a meaningful measure of response because a neighboring troop countercalled on 11 occasions (44.0%) before the response to the playback terminated. These calls were significantly shorter when another troop did not countercall (median, 6.47 min; range, 1.20–13.50 min) than when another troop countercalled (median, 9.75 min; range, 4.83–19.0 min; $U = 46.0$, $n_1 = 11$, $n_2 = 14$, $P < 0.05$).

On 19 of the 20 days when I arrived at the vehicle without performing the playback, the control troop began to call 24.0 min (range, 1.0–81.0 min) following my arrival; on one occasion they did not call at all. The tendency to answer or not answer did not depend on the time of the playback in rela-tion to sunrise (Fig. 7; $U = 204.0$, $n_1 = 20$, $n_2 = 25$, $P > 0.1$).

The peak amplitudes of playback and control tapes at the distance from the loudspeaker where experimental subjects were located are shown in Table I. Overall, the peak amplitudes of the playbacks that were answered and those that were not answered were not significantly different ($U = 244.5$, $n_1 = 20$, $n_2 = 25$, $P > 0.05$) and there was no dif-ference between experimental and limpkin control amplitudes (Table I; U

Table I. Median Peak Amplitude of Playbacks (Ranges Are Shown in Parentheses), as "Heard" by the Howlers (see Text)

Playback tape (n)		Amplitude (dB)		Mann-Whitney
a	b	a	b	U test
Control, 6	Experimental, 45	64.0 (42.0–64.5)	63.5 (59.5–67.5)	118.5
Male/female, 13	Male only, 9	65.5 (60.5–67.5)	65.0 (63.5–67.0)	48.5
Male/female, 13	Female only, 9	65.5 (60.5–67.5)	60.5 (59.5–61.5)	4.5*

*$P < 0.001$.

$= 118.5$, $n_1 = 6$, $n_2 = 15$, $P > 0.05$). While there was no difference in amplitude between the male/female and the male-only playbacks ($U = 48.5$, $n_1 = 9$, $n_2 = 13$, $P > 0.05$), the female-only playbacks were significantly quieter than the mixed male/female calls ($U = 4.5$, $n_1 = 9$, $n_2 = 13$, $P < 0.001$). All the responses to female howls occurred within the first minute of the onset of the playback. Responses to male-only, mixed male and female, and female-only howls within the first minute of the onset of the playback are shown in Table II. There was a significant difference in response to the three types of playbacks ($G = 14.78$, df $= 2$, $P < 0.001$). The response to female-only calls occurred more frequently than the response to male/female mixed calls ($P < 0.005$, Fisher's exact probability test). Also, when there was a response, the males called more rapidly to known female playbacks than to known male/female calls ($U = 0$, $n_1 = n_2 = 8$, $P < 0.0001$). This result is observed in spite of the fact that the female-only calls were of significantly lower amplitude than the mixed calls of males and females.

Table II. The Effect of Male, Male/Female, and Female-Only Playbacks of Neighboring Troops Within the First Minute of the Onset of the Playback*

	Playback		
	Male only	Male/female	Female only
Response	1	3	8
No response	8	10	1
	$G = 14.78$, df $= 2$, $P < 0.001$		

*If countercalling did not occur within 1 min of the onset of the playback, the experiment was noted as "no response."

DISCUSSION

Howling by *A. seniculus* troop females can be divided into two categories: (a) calls directed at other troop females and extratroop females in which males rarely participate and (b) calls by some females directed at extratroop males in which troop males always take part.

Howling by troop females directed at solitary females has been described elsewhere (Sekulic, 1982b). Three possible reasons given for aggression toward solitary females were (a) limited food resources within the home range; (b) since there are limits on troop size for energetic reasons, protection of space within the troop for resident female offspring; and (c) prevention of access to mates.

The observations described in this paper indicate that howling at troop females may also occur to prevent access to dominant males; one troop female was regularly prevented from calling with the dominant male, while some females in neighboring troops were also occasionally displaced by other troop females from the vicinity of the males. Such conflicts between troop females appear to be most frequent among females at different stages of their reproductive cycles. Females howl with males with which they have most recently mated. While receptive females always support the dominant male, females with young infants support the males that apparently sired their infants (see Sekulic, 1982e) even when they are no longer dominant because new males are likely to kill their offspring. Two cases described in this paper clearly showed such conflict: in one troop a cycling female was repeatedly prevented by females with young infants from approaching the dominant male. Shortly after she conceived, another male entered the troop and mated with the two females but the pregnant female continued to support her mate. In another troop a pregnant female and two females with young infants continued to support an old male until he was ousted from the troop, while a cycling female mated with the new dominant male 2 months before the old male was ousted (Sekulic, 1982e). I suggest that howling by the females with their mates is important in strengthening the pair bond whereby males also form attachments to their infants and act protectively toward them. Howler males seldom actively protect infants (Sekulic, 1982e), but their presence near infants when threatening males are in the vicinity may deter infanticide (Sekulic, 1982b). In contrast to langurs (*Presbytis entellus;* Hrdy, 1977), pregnant red howler females do not solicit new dominant males.

It is interesting that the males responded at all to the calls directed at females. By calling alone, females could attract outside males and troop males may participate in order to communicate to neighboring conspecifics of the same sex monopoly over their mates. This function has also been suggested for the female song of the gibbon (Gittins, 1978).

Unweaned red howler infants are frequently at risk of being killed, not only by extratroop males that attempt to enter the troop (Rudran, 1979) but also by the resident males that are unlikely to be their fathers (Sekulic, 1981, 1982c,e). It would be advantageous, therefore, for a female to detect which male is more likely to remain dominant at the time when her next infant is born. The observations presented in this paper indicate that calling by the females elicits male calls, which are used in assessment of their opponents (Sekulic, 1982a). Since subordinate males are likely to emigrate, by inciting howling among troop and nontroop males a female could maximize the chances that weak troop males would be replaced before her next infant is sired and that her mate will remain in the troop when the infant is born. Copulatory calls of female elephant seals and some primates may also be used to incite competition among the males (Cox and LeBoeuf, 1977; Hamilton and Arrowood, 1978). Another option open to red howler females faced with weak troop males is emigration in search of a troop with a more fit male, as has been described for Tana river colobus *Colobus badius rufomitratus* (Marsh, 1979). However, this option does not seem to be open to *A. seniculus* females, as troop size is limited and entry into established troops is extremely difficult (Sekulic, 1982b).

During the daytime the males could see why females were calling, but this was not the case before dawn when I performed the playback experiments. The strong male response to female playbacks supports the hypothesis that female calls incite competition among the males. The male response to female calls may depend on whether or not a male can visually assess the threat from other males. If no other male is present in the vicinity, the response is weak. On the other hand, if another male is threatening the dominant male's access to a receptive female or is attempting to enter the troop, the competing males maximize the intensity and duration of their howls.

ACKNOWLEDGMENTS

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