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# SEASONAL DIFFERENCES IN TERRITORIAL BEHAVIOR BY GOLDEN JACKALS IN BANGLADESH: HOWLING VERSUS CONFRONTATION

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Responses of golden jackals (*Canis aureus*) to broadcasted howling were investigated in rural Bangladesh. Two hypotheses were tested: that the howl response shows the same annual trends reported for other *Canis*, being high during the season of pairing-mating when territories are being established, and low during the denning season when there is a risk to vulnerable young from advertising the location of their den to rival conspecifics; that the frequency of approach responses (confrontation) varies inversely with howl responses and is higher during denning when howling is low. Results support both hypotheses and are consistent with the primary function of howling being as a passive means of territory maintenance whereby dominant animals advertise their locations to facilitate mutual avoidance between groups and thereby reduce accidental confrontation.

**Key words:** *Canis aureus*, jackals, howling, passive territory maintenance, approach, denning, Bangladesh

Group howling by canids (Lehner, 1978; McCarley, 1975) is believed to function primarily as a passive means of territory maintenance whereby neighboring groups mutually advertise their locations over sufficiently long distance so as to warn each other and nonterritorial transients where to avoid (Joslin, 1967). The strongest evidence to support a territorial function for howling is from Harrington and Mech (1979). They showed that howl responses by wolves (*Canis lupus*) were by territorial pack members and not transients, that they were initiated by alpha males, and that responsiveness was associated with defense of young or carcasses of prey. Annual trends in both spontaneous and elicited howling have been reported for wolves (Harrington and Mech, 1978, 1979; Joslin, 1967), coyotes (*C. latrans*; Okoniewski and Chambers, 1984) and black-backed jackals (*C. mesomelas*; Skead, 1973). Peaks in responsiveness oc-

cur during the annual reproductive cycle when pairing and mating take place, and following abandonment of dens when family groups become more mobile and use rendezvous sites within their territories (Fig. 1). Howling diminishes at the end of the reproductive cycle when young are fully mobile. Howling also is low at the time of denning when it might endanger immobile young by signaling the location of their den site to rivals or other predators (Joslin, 1967). Killing of young at the den site by conspecifics has been reported for coyotes by Camenzind (1978). A dynamic state of conflict and avoidance, therefore, seems to occur among neighboring territorial groups, which probably is mediated by the changing need to compete for resources.

Presently, there is no direct evidence that howling acts as a passive means of territory maintenance (i.e., to reduce confrontation). It is necessary to determine whether howl-

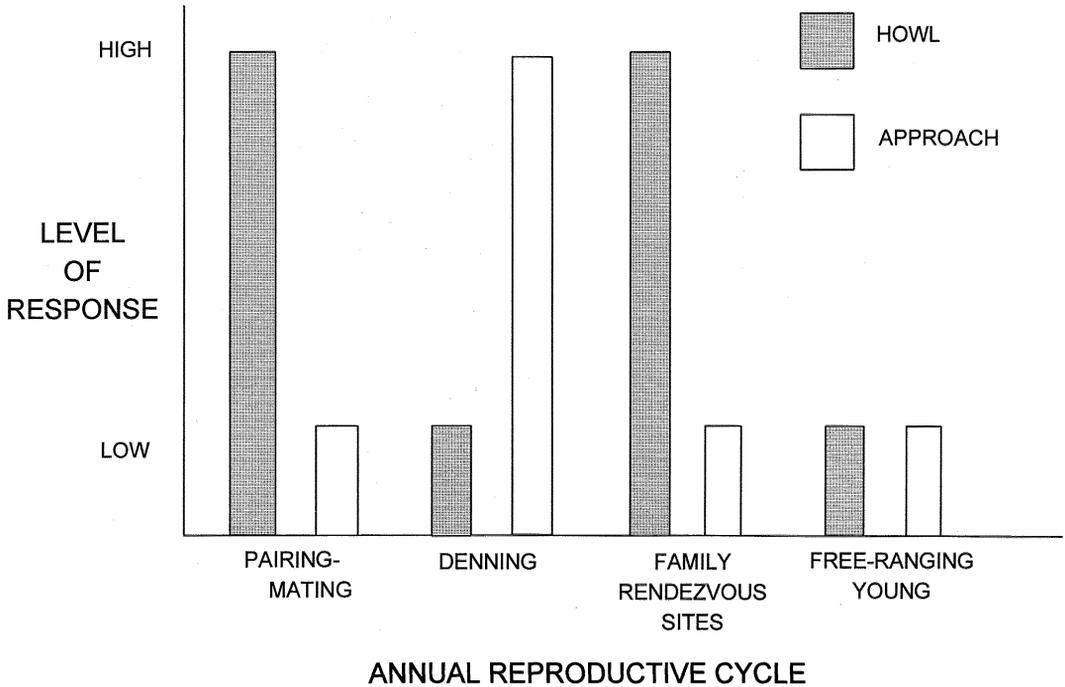


FIG. 1.—Hypothetical relationship between the frequency of elicited howls and approach responses during successive stages of the annual reproductive cycle of *Canis*.

ing influences approach and confrontation. There are three responses that dominant animals can use to defend their territories when intruders are known to be present: howl and warn-off conspecifics; approach and confront; howl followed by approach. Wolves, coyotes, and jackals all approach a source of broadcasted howling (Joslin, 1967). Available evidence suggests that it is territorial, dominant animals that approach (Harrington and Mech, 1979), or territorial groups (R. T. Bowyer, pers. comm.). If howling functions to reduce confrontations and if elicited howling is higher during pairing-mating than during denning, we expect approach and confrontation to be higher during denning than during pairing-mating. This assumes that the incidence of challenges remains the same. If howling, conversely, promotes confrontation, approaches would occur more frequently during mating; and if howling and confrontation are not directly associated,

approaches would occur with equal frequency during both mating and denning.

Objectives of this study were to determine whether there is a seasonal pattern in howl responsiveness by golden jackals (*Canis aureus*) consistent with that for other members of the genus *Canis*, which supports howling as a response of territorial (versus transient) animals, and whether approach responses vary between seasons inversely to howl responses (Fig. 1), supporting the argument that howling functions as a passive means of territorial maintenance.

#### MATERIALS AND METHODS

This study was conducted in central Bangladesh near Sripur (24°11'N, 90°25'E). The area is densely populated and intensively cultivated (Sultana and Jaeger, 1992). Plots of rice and sugarcane are interspersed with small patches of sal (*Shorea robusta*) forest and bamboo (*Bambusa*). Sugarcane is the most important source of day-

time cover for jackals in Bangladesh; where it is abundant, so are jackals. Sugarcane is produced in small plots (<1 ha) and is present throughout the year. The harvest of individual fields is staggered from December until April. Sripur is an upland area, and monsoon flooding (July–September) is confined to old river channels. Golden jackals and jungle cats (*Felis chaus*) are the largest carnivores in this area and both are relatively common. A high density of jackals is suggested by the small size of their territories, which ranged from 1 to 2 km<sup>2</sup> ( $n = 6$ ) in a radiotelemetry study at a separate site in Bangladesh. Patterns of space use were not determined in this study. The annual reproductive pattern of golden jackals in Bangladesh is typical of the genus *Canis* (Bueler, 1973; Poché et al., 1987); pairing and mating in winter (December–February) and denning in spring (March–June).

A trial consisted of three separate 30-s broadcasts played at 30-s intervals. A group-yip howl (Lehner, 1978) by 10 caged jackals was used for broadcasts. Two observers listened for howl responses following each broadcast; at the conclusion of each trial observers shined a searchlight in a 360° arc around their position looking for approaching jackals. A jackal could be identified from as far away as ca. 200 m. The area of sugarcane was sampled in both seasons because an underestimate of the number of approaches by jackals might occur when sugarcane was more widespread and likely to be a greater obstruction to sighting jackals. The number of 1-ha plots randomly sampled for sugarcane was 24 in spring and 20 in winter.

A map (scale = 1:10,000) of the Sripur area was made from Landsat photographs (January 1988) and a 25-km<sup>2</sup> study site demarcated in 1-km<sup>2</sup> grids. Separate trials with broadcasted howling were conducted within randomly selected 1-km<sup>2</sup> blocks. A loudspeaker system (Thunderbird Scare-Away, Reed-Joseph Co., Greenville, MS) mounted on a vehicle was used to broadcast taped howling. The vehicle was positioned as close to the center of each 1-km<sup>2</sup> block as possible. The size of grid squares was based on the maximum distance from which we could hear caged jackals howling (ca. 400 m).

Trials were conducted in the two biological seasons, pairing-mating (winter) and denning (spring). Trials in spring were from 2 April to 27 June 1989 on 1 night/week between 2100–

2300, 0000–0200, and 0300–0500 h. During this period, a total of 108 trials occurred in 11 separate weeks ( $\bar{X} = 9.8$ ,  $SD = 3.28$  trials/night). For winter, 129 trials were conducted from 4 December 1989 to 17 January 1990 by testing 1 night/week for 6 consecutive weeks ( $\bar{X} = 21.5$ ,  $SD = 1.05$  trials/night) throughout the night from 2000–0600 h. Each trial was conducted in a separate 1-km<sup>2</sup> block. A particular block could be used only once each night, and the sequence in which blocks were used was random. The ratio of hours of light to dark each day averaged 13 h 22 min:10 h 49 min for spring ( $n = 86$  days) and 10 h 43 min:13 h 17 min for winter ( $n = 44$  days).

Dependent variables included the type of response and whether it was made by an individual or group (two or more animals). We could not be more specific about the number of jackals howling in a group because more than two animals could not be distinguished with confidence. Three types of responses were recorded; howls, approaches, and combined howl-approaches by the same individual or group. A separate response could have been from either an individual or group. For example, if two jackals were simultaneously howling from the same position, this was recorded as a single howl response by a group. More than one separate response per trial was possible. Independent variables included season (pairing-mating versus denning) and time of night. Independence among variables was tested with the *G*-test. Analysis of three-way contingency tables was based on log-linear models; values of *G* were adjusted using William's correction (Sokal and Rohlf, 1981).

## RESULTS

A total of 237 trials was conducted, of which 52.7% were positive for a response. The relative occurrence of positive trials did not differ between seasons ( $G = 0.63$ , *d.f.* = 1,  $P > 0.50$ ). There was a significant three-way interaction between positive trials, season, and time of night ( $G = 9.600$ , *d.f.* = 2,  $P < 0.01$ ), such that in spring positive trials peaked 0000–0400 h, whereas those in winter were highest 2000–0000 h (Fig. 2). These interactions did not occur when time of night was partitioned differently (2000–2200, 2200–0000, . . . 0400–0600 or 2000–0000, 0000–0200, 0200–

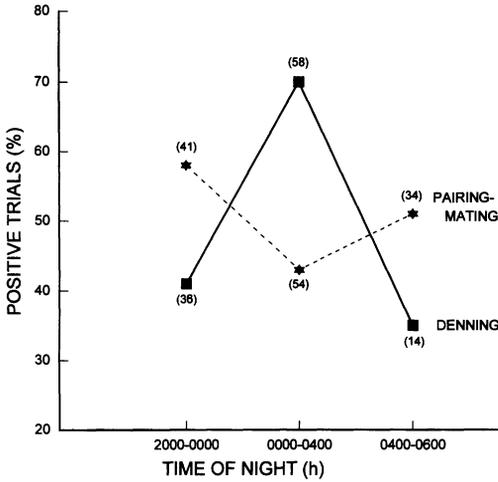


FIG. 2.—Influence of season and time of night on the occurrence of positive trials in which jackals responded to broadcasted howling by howling, approaching, or both. Numbers in parentheses represent subtotals of positive responses. Responses were recorded in Bangladesh during 1989–1990.

0600 h), so as to place less emphasis on the middle-night comparison.

The 125 positive trials included 197 separate responses (Table 1); 129 howls, 42 ap-

proaches, and 26 howl-approaches. There was no three-way interaction among response types, time of night, and season ( $G = 4.494, d.f. = 2, P > 0.10$ ). There was, however, a significant two-way interaction between response type and season for each period of night ( $G = 12.993, d.f. = 3, P < 0.005$ ) such that howling (howls plus howl-approaches) was relatively more frequent during the pairing-mating season and approaching relatively more frequent during denning (Fig. 3). This result is unlikely to have been due to seasonal differences in the amount of vegetative cover obscuring approaching jackals. Sugarcane covered 30% of the area sampled during denning compared with 21% during pairing-mating. In addition, the main rice harvest had been completed before pairing-mating so that sighting approaching jackals should have been easier at this time. The relative occurrence of howl-approaches did not differ between seasons ( $G = 0.278, d.f. = 1, P > 0.50$ ). Overall, howl responses were more frequent than approaches, including in the denning season ( $\chi^2 = 4.263, d.f. = 1, P < 0.05$ ).

TABLE 1.—Number of responses of jackals to broadcasted howling by type, social group, season, and time of night. Social group refers to the number of jackals responding together as a unit (one or two or more). Trials were near Sripur, Bangladesh, during spring 1989 (denning) and winter 1989–1990 (pairing-mating).

Season	Time (h)	Response type and social group						Total
		Howl		Approach		Howl and approach		
		1	≥2	1	≥2	1	≥2	
Pairing-mating	2000–2200	1	7	2	0	2	3	15
	2200–0000	5	17	1	2	1	2	28
	0000–0200	4	10	2	0	0	0	16
	0200–0400	14	4	4	1	1	1	25
	0400–0600	5	15	0	1	2	1	24
Subtotal		29	53	9	4	6	7	108
Denning	2000–2200	4	1	0	1	0	0	6
	2200–0000	6	2	1	3	1	1	14
	0000–0200	9	11	9	5	2	4	40
	0200–0400	7	4	5	1	2	2	21
	0400–0600	1	2	4	0	1	0	8
Subtotal		27	20	19	10	6	7	89
Totals		56	73	28	14	12	14	197

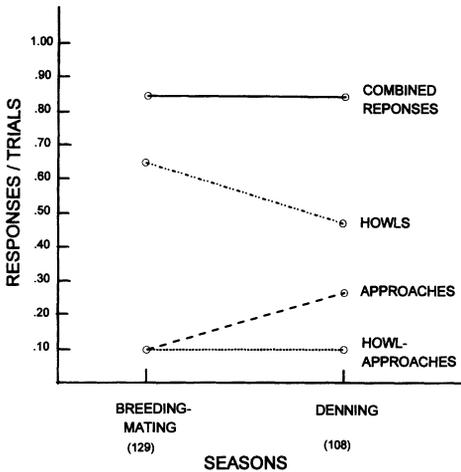


FIG. 3.—Comparative differences among types of response during pairing-mating and denning illustrating the inverse relationship between howling and approaching. Numbers in parentheses represent the number of total trials each season. Trials were conducted in Bangladesh during 1989–1990.

Of the 197 positive responses, 49% were by individuals and 51% by groups of two or more ( $\chi^2 = 0.127$ ,  $d.f. = 1$ ,  $P > 0.90$ ). The four-way interaction among response type, response group, season, and time of night could not be meaningfully analyzed because of low expected values in too many cells. The three-way interaction among response type (howls plus howl-approaches versus approaches), response group, and season was not significant ( $G = 1.698$ ,  $d.f. = 1$ ,  $P > 0.15$ ). The two-way interaction between response type and response group was not significant for either season ( $G = 5.718$ ,  $d.f. = 2$ ,  $P > 0.05$ ). When seasons were combined there was a significant difference ( $G = 6.920$ ,  $d.f. = 1$ ,  $P < 0.01$ ) such that approaches were more common by individuals than groups. In addition, there was a significant three-way interaction among group howls (versus all other responses), season, and time of night ( $G = 8.972$ ,  $d.f. = 1$ ,  $P < 0.005$ ) when times of night were combined into early-late (2000–0000 plus 0400–0600 h) and compared with middle (0000–0400 h) such that group

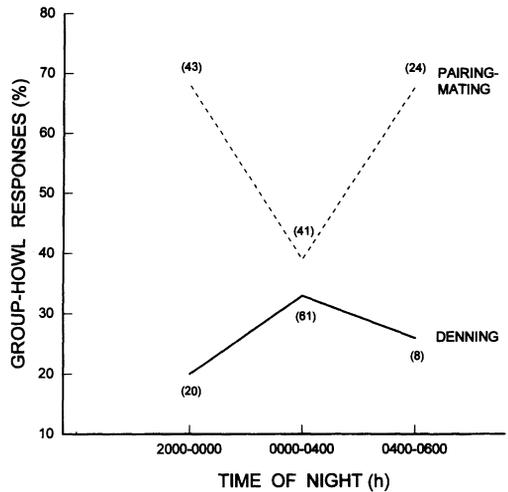


FIG. 4.—Interaction between responses of group-howling, stage of the mating season, and time of night. Numbers in parentheses represent subtotals of positive responses. Trials were conducted in Bangladesh during 1989–1990.

howl responses were highest early and late at night during the pairing-mating season (Fig. 4). Furthermore, during pairing-mating, individual responses (all types) were more common in the middle of the night and group responses were more common early and late ( $G = 11.089$ ,  $d.f. = 1$ ,  $P < 0.001$ ).

#### DISCUSSION

Howl and approach responses, collectively, occurred in a high percentage (52.7%) of the trials, in the same proportion during both the pairing-mating and denning seasons. This level of responsiveness is in general agreement with findings for other canids. Okoniewski and Chambers (1984) reported that howl responses of coyotes occurred in 53% of test sessions during pairing-mating compared with 27% of the sessions for all seasons. Similarly, Harrington and Mech (1979) reported radiocollared wolves howling in 40% of test sessions during pairing-mating compared with 28% overall.

The distribution of positive trials for jackals within the night differed between

seasons. During spring (denning), responsiveness peaked later than during winter (pairing-mating). This may be because of the shorter nights in spring, but it probably also reflects seasonal differences in activity of humans. During winter, farmers retired earlier to their dwellings, whereas in spring it was hot and humid and people tended to remain outdoors relatively late. Jackals seem wary near humans because those flushed from fields of farmers are pursued and sometimes killed.

The seasonal pattern of howl responses by golden jackals in Bangladesh, and of group-howl responses in particular, is consistent with the hypothesis of a territorial function for howling during the pairing-mating and denning seasons. These responses showed the same annual trend reported for other canids, being relatively more frequent during pairing-mating when territories are being established and relatively low during denning when vulnerable young are present. This pattern is consistent with the explanation that it is territorial animals that howl, and that howling functions primarily as a mechanism to advertise territorial occupancy and the location of dominant animals, so that confrontations with neighboring pairs and transients can be reduced (Harrington and Mech, 1979). The annual occurrence of territoriality is coincident with the reproductive season and probably an adaptation to rearing young. If transients howl at the same level as territorial, breeding animals, we would have expected no difference in the level of the howl response between separate stages of the breeding season, unless transients were relatively few in number.

Group-howl responses further support a territorial function for howling because nonterritorial, transient canids do not typically associate in groups (Harrington and Mech, 1979). In our study, howl responses during the pairing-mating season were most frequent by groups (presumably the dominant territorial pair) before midnight (2000–0000 h) and early in the morning (0400–

0600 h). Group howls may carry more authority, in terms of claiming territory ownership, than howls by individuals (Harrington and Mech, 1979). In addition, mates are probably together more during pairing-mating than during denning when females are suckling young while males forage. Early and late-night peaks in howling during pairing-mating are consistent with the findings of Skead (1973), who reported that spontaneous howling of black-backed jackals in southern Africa during the mating season peaked during 1900–2300 and 0400–0700 h. Howling in wolves also peaks bimodally during 2000–0000 and 0400–0600 h (Carbyn, 1975; Harrington and Mech, 1978). Results presented here suggest that during pairing-mating, paired jackals tended to be apart from one another during the middle of the night (0000–0400 h) when howl responses were fewer and together early and late when group howling was more frequent.

The inverse relationship between howl and approach responses reported here corroborates the argument that howling functions as a passive means of territorial maintenance. Approach responses were relatively more frequent during the denning season than during pairing-mating, although howling remained the more common response during both seasons. Approach and howl responses are not directly comparable because howling probably is easier to detect, can be detected over a greater area, and is more likely to occur simultaneously from separate locations. This results in more than one howl response per trial. Therefore, we expected more howl than approach responses. If the relationship between howl and approach responses had not been inverted, but in the same direction, the number of approach responses per trial would have been more frequent during pairing-mating than during denning (Fig. 3). Combined howl-approaches were infrequent and independent of season. Howls and approaches, therefore, did not seem to be used in tandem such that howling preceded the

approach, warning away intruders in time to avoid confrontation. The howl-approach might have represented a howling jackal that was already nearby to the observers prior to onset of the trial. The strategy of territory defense in response to an intruder seems to be to howl, but avoid confrontation (i.e., injury or death—Mech, 1994) during pairing-mating. In contrast, during denning howling is avoided, especially from close to the den site, and defenders approach and confront intruders before they can close in on the den.

Do approaches also occurring during pairing-mating argue against approach functioning for the purpose of confrontation and defense of den sites and young? Possibly approaches represent inquisitiveness rather than defense. Inquisitiveness, does not explain why approach responses were greater during the denning season. Approach and confrontation probably function in the defense of a variety of resources including young (e.g., feeding sites, patches of sugarcane used for daytime cover, and mates). This interpretation may help explain why approaches were more common by individuals than by groups in both seasons. During pairing-mating individuals may be defending against challenges for their mates, whereas during denning one of the pair may be guarding the den site while the other forages. Furthermore, in our study the approach response was independent of time of night, which is consistent with the expectation that a resource should be defended whenever threatened.

What are the alternatives to passive maintenance of the territory as an explanation for the primary function of howling? The results presented here imply that confrontation occurs less during pairing-mating when howling is high and more during denning when howling is low. What would be the value of reducing aggression in only one of the two seasons? One explanation is that howling is high when territories are being established and that the need for territory advertisement diminishes during den-

ning when neighboring pairs (or packs) have learned one another's territory. We argue that the effect of howling extends beyond pairing-mating and reduces trespassing during the subsequent denning period. The increased confrontation during denning in this study was artificially created with our broadcasted howling. Similarly, Harrington and Mech (1978) noted that howling by wolves was infrequent and sporadic during the homesite season (April–August), which seems to argue against its utility for intrapack communication. They concluded, that by this time of year the general location of a wolf pack probably was predictable to neighboring packs as evidenced by the low level of trespassing.

We have discussed the function of howling in terms of maintenance of territory or intergroup communication. Howling is also likely to function for intragroup communication (Harrington and Mech, 1978, 1979), which is supported by evidence from wolves for individually distinct vocalizations (Tooze et al., 1990). The need to regroup probably is greater for large groups such as packs of wolves that cover large areas than it is for jackals in rural Bangladesh. An intragroup function offers an alternative explanation for why howling is low during denning (i.e., because a fixed and predictable den site precludes the need for howling), but one that is not mutually exclusive of territorial maintenance. The intragroup assembly function, does not explain why approaches are higher during denning. In addition, advertisement of territory seems to better explain the predominance of group howling by pairs of golden jackals during pairing-mating.

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