BARKING IN A PRIMITIVE UNGULATE, *MUNTIACUS REEVESI*: FUNCTION AND ADAPTIVENESS

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Muntjacs (*Muntiacus* spp.), or barking deer, are native to Asia and usually occur in dense subtropical or tropical forests from sea level to medium elevations (Walker 1975). These deer have changed little morphologically from ancestral forms (Dubost 1971; Barrette 1977c, 1977d) and exhibit a social structure which is considered primitive in the cervid family by remaining solitary or occurring in small groups (Dubost 1970). Because the communication system mediates the cohesiveness of social units and is an important factor in the evolution of social organization (Wilson 1975), an understanding of auditory communication in muntjacs is necessary for a systematic analysis of communication and social systems in more advanced cervid species. The vocal repertoire of muntjacs has not been given adequate attention due to difficulties in studying the species in their natural environment and because of their secretive habits. Barrette (1975, 1977a, 1977b, 1977c, 1977d) completed an extensive study of the social behavior of *M. reevesi* and *M. muntjak,* but data on auditory communication were scant. Auditory communication is, therefore, the least known mechanism of communication, yet is probably one of the most important mechanisms because the dense vegetation in the natural habitat reduces the effectiveness of visual signals.

Here I examine auditory communication, specifically the vocalization termed barking, in the Reeve's muntjac (*M. reevesi*). Three null hypotheses are tested: (1) Rate of barking bouts does not differ with season or time of day, (2) rate of barking bouts or parameters associated with barking bouts do not vary among individuals, and (3) barking bouts are not elicited by stimuli which may indicate potential danger.

METHODS

Animals and Study Area

A captive population of Reeve's muntjacs was studied from July, 1977, to May, 1978, at the Conservation and Research Center, National Zoological Park, Front

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Royal, Virginia. Two young born during the study, four adult males, and six adult females were marked with colored ear tags for individual recognition. The muntjacs were separated into four different outdoor enclosures, each containing one adult male and at least one adult female. Enclosures ranged from 0.3 to 0.5 ha and were surrounded by 2.5-m chain-link fences. The outside perimeter of the enclosures was bordered by an additional 2.5-m electrified chain-link fence to prevent large terrestrial predators from entering the enclosures. Density of shrubs and trees within the enclosures were kept low by Center personnel to enhance observations of the animals. In addition, Center personnel regularly mowed approximately 85% of the herbaceous vegetation within the enclosures. The unmowed sectors provided resting sites, whereas the mowed sectors furnished a continual source of succulent vegetation upon which the deer readily fed. Also, a source of running water and several types of supplemental feed were supplied to the deer in ample quantity. Each muntjac had access to 1 × 2 m wooden shelters which contained bedding and were heated during inclement weather. A 6-m observational tower was positioned in a central region surrounded by the enclosures.

Recording and Analysis of Barking Bouts

A barking bout was defined as a series of barks produced in succession by one or more muntjacs concurrently within a relatively short time span. Barking bouts elicited by experiments (EBB) were distinguished from those which occurred naturally (NOBB). Seasonal and diurnal variations in the rate of NOBB were determined by observing the muntjacs for a 24-h cycle each week for 10 consecutive weeks during three periods corresponding to the seasons summer, autumn, and winter ($N = 30$ diurnal cycles). Each diurnal cycle was divided into four periods designated as (1) sunrise, 2 h before until 2 h after dawn, (2) sunset, 2 h before until 2 h after dusk, (3) day, the remaining time between sunrise and sunset, and (4) night, the remaining time between sunset and sunrise. Rates of NOBB, expressed as number/hour of observation, among season and diurnal period were analyzed by a two-way analysis of variance (Sokal and Rohlf 1969).

Barking bouts were recorded with a Model 4000 Uher Tape Recorder and a directional Uher microphone. Individual barks were analyzed with a Kay Electric Sound Spectrograph using the wide-band and narrow-band filters. The rate (no./day) of NOBB and five parameters associated with barking bouts (NOBB and EBB) of each muntjac were measured and compared among individuals using single-classification analyses of variance (Sokal and Rohlf 1969). These parameters include duration (s) and dominant frequency (kHz) of barks (after Marler 1973), interbark interval (s) within a bout, rate (no./min) of barks per bout, and total duration (min) of a bout.

In an attempt to determine whether rates of NOBB can be predicted by activity levels or other aspects of muntjac behavior, two types of correlation analyses were performed. First, rates of population and individual NOBB were correlated to population and individual levels of activity, respectively, obtained from other analyses (Yahner 1980a). Second, behavioral profiles were constructed by

randomly observing each adult muntjac from the observational tower for a 10-min sampling period during each of the four diurnal periods (sunrise, day, sunset, and night) every week in summer using the focal-animal method (Altmann 1974; Yahner 1980b); therefore, each adult was observed for 400 min to establish its individual behavioral profile. Observations after dark were aided by floodlights attached to the corners of the tower. All behaviors performed by the focal animal during the sampling period were recorded with 7×35 field glasses and a portable cassette recorder. Duration (s/min) and frequency (no./min) of each behavior during each sampling period were calculated (after Yahner 1978b). Behavioral profiles were derived from summer data because climatic conditions, food availability, and their effects on behavior of muntjacs are probably more similar in this season to those of natural environments inhabited by muntjacs compared to other times of the year in Virginia. Rate of NOBB by individual muntjacs in summer was divided into two components, rate of NOBB which were apparently caused by a disturbance and rate of NOBB which occurred in a subordinate context (see further explanation of these contexts in a later section). Rate of NOBB in these two contexts for the 10 adult muntjacs ($N = 10$ cases) were considered as two dependent variables, and each was regressed on 70 independent variables corresponding to mean duration and mean frequency of 35 behaviors using stepwise multiple regression (BMDO2R, Dixon 1973).

Mean duration of barking bouts and mean rate of barks per bout obtained from eight adult muntjacs ($N = 8$ cases) known to bark during the study were also considered as dependent variables. These were regressed on the 70 independent variables using stepwise multiple regression. Terminology and description of behaviors are taken from Barrette (1977d).

Experiments

The experiments, or presentations of stimuli which could indicate a potential source of danger to the deer, were designed to determine the types of stimuli to which muntjacs vocalize. These consisted of 28 different stimuli, including both stationary and moving models of terestrial and aerial visual stimuli, plus olfactory stimuli, auditory stimuli, and combinations of different types of stimuli (table 1).

Presentation of stimuli 1–27 comprised stage 1 of the experiments. Responses (table 2) of the muntjacs to each stimulus were noted for a 2-min period subsequent to detection of the stimulus. Each stimulus was presented at least twice to each adult muntjac during the study. At least 2 days elapsed before successive presentation of the same stimulus to a particular muntjac.

Stage 2 of the experiments consisted of presenting stimulus 28, followed by later presentations of stimuli 2, 16, 21, and 27. The purpose of this aspect of the experiments was to resolve how muntjacs react to a stimulus which is known to be associated with attack and chase. In a sense, stimulus 28 represented a "fabricated" predator which hunts by initially stalking the deer and then attacks when spotted by its prey. Responses to stimuli in stage 2 were recorded as in stage 1.

TABLE 1

STIMULI PRESENTED TO MUNTJACS

Type	Description
Visual terrestrial stimuli	
1. Raptor 1	Museum skin of horned owl (*Bubo virginianus*) attached to a 2-m pole, presented in stationary position
2. Canid	Mounted red fox (*Vulpes fulva*); presented in stationary position in unmowed sectors, or moving at 1 m/s or 3 m/s near ground level via motorized pulley system
3. Domestic dog	Large dog (*Canis familiaris*) walked on leash by a human immediately outside and within enclosures
4. Distant object	Human moving slowly and quietly in a crouched position in tall vegetation approximately 20 m beyond perimeter of enclosures
5. Felid	2 × 2 m leopard skin (commercial fabric) draped over stationary red fox (see canid above) in unmowed sectors
6. Branch	Visual and auditory disturbance created by moving 1-m segments of tree branches in unmowed sectors; movement achieved by pulling on bailing twine suspended from tower to immovable objects in enclosures to which the branches were attached
7. Camel pelage	1 × 1 m mass of molted camel pelage draped over branch (see above) in unmowed sectors
8. Shirt	Checked flannel shirt draped over branch (see above) in unmowed sectors
9. Handkerchief	White handkerchief tied to branch (see above) in unmowed sectors to simulate tail-flagging of deer
Visual aerial models	Each projected across the enclosures at 3 m/s along clothes line suspended at ht of 2.5 m to simulate an aerial predator swooping into the enclosures as if to attack via motorized pulley system
10. Small circle	2-dimensional, .05-m^2 circle
11. Large circle	2-dimensional, .13-m^2 circle
12. Small hawk	2-dimensional, .05-m^2 silhouette of flying hawk
13. Large hawk	2-dimensional, .13-m^2 silhouette of flying hawk
14. Raptor 2	Museum skin of red-shouldered hawk (*Buteo lineatus*) mounted with wings outstretched in a flying position
Olfactory stimuli	
15. Canid urine	urine of bush dog (*Speothos venaticus*)
16. Canid musk	musk of coyote (*Canis latrans;* Pete Richard, Inc.)
17. Felid feces	feces of tiger (*Panthera tigris*)
18. Control	after-shave lotion (commercial brand)
Auditory stimuli	
19. Thumping noise	Disturbance produced by hidden observer rapidly hitting the ground with a metal pipe outside enclosures to simulate thumping of muntjac's hindfeet in flight
20. Clanging noise	Disturbance produced by hidden observer gently hitting the fence of enclosures with a metal pipe to simulate a large predator attempting to enter enclosures
21. Rustling noise	Disturbance produced by hidden observer rustling leaf litter and vegetation outside or within the enclosures
22. Familiar playback	2-min amplified recording of barking bouts given by known conspecifics
23. Unfamiliar playback	2-min amplified recording of barking bouts given by unknown conspecifics (obtained from British Library of Wildlife Sounds)

(continued)

TABLE 1 (*Continued*)

Type	Description
Combinations of stimuli	
24. Comb 1	Stimuli 2 and 16 (presented simultaneously
25. Comb 2	Stimuli 2 and 21 presented simultaneously
26. Comb 3	Stimuli 16 and 21 presented simultaneously
27. Comb 4	Stimuli 2, 16, and 21 presented simultaneously
28. Comb 5	Stimuli 27 presented, then muntjacs immediately chased for 2 min by a human in a crouched position and disguised in a drooping raincoat to obscure the human form

TABLE 2

RESPONSES GIVEN BY MUNTJACS

Type (Symbol)	Description
1. No response (NR)	Completely ignore stimulus and continue ongoing activity; briefly look at stimulus, then resume ongoing activity; or continue ongoing activity, but intermittently look at stimulus
2. Approach slowly & investigate (AI)	Walk slowly and cautiously toward stimulus, while occasionally sniffing the air and moving the head as if to better perceive the stimulus
3. Investigate from a distance (ID)	Look at stimulus from a distance while in a stationary position for a prolonged period; no attempt to approach and investigate
4. Avoid (A)	Move slowly and cautiously away from the stimulus, while occasionally stopping and looking at the stimulus
5. Run & investigate (RI)	Run a short distance, then look at stimulus from a stationary position
6. Bark (B)	Remain in a stationary position or run a short distance, then look at stimulus and bark from a stationary position
7. Yap (Y)	Run, usually with tail in a vertical position, while yapping
8. Run (R)	Run, usually with tail in a vertical position, to a far corner of the enclosure and then remain stationary as if to hide from the stimulus

RESULTS

Temporal Occurrences of Barking Bouts

Naturally occurring barking bouts (NOBB, $N = 21$) involving one or more muntjacs were heard at a rate of 0.7 bouts/24-h cycle. Mean rates of NOBB in autumn and winter were comparable ($P > .05$; Student-Newman-Keuls test), but both were less than the summer rate ($P < .05$; table 3). Although no significant differences were found in rates of NOBB among diurnal periods ($.10 < P < .25$), few bouts occurred during the day (table 3). Bouts were usually heard at night, sunrise, or sunset.

TABLE 3

Mean Rate (No./h) and Percent of Total Naturally-Occurring Barking
Bouts (N = 21) Given by Ten Adult Muntjacs during
Each Season and Diurnal Period

| | Season | | | Total Rate | Total Rate |
Diurnal Period	Summer	Autumn	Winter	(no./h)	(%)
Sunrise	.13*	0	.03	.040	34.5
Day	.01	0	0	.003	2.6
Sunset	.10	0	0	.033	28.4
Night	.08	.03	.01	.040	34.5
Total Rate (no./h)	.080	.008	.010		
Total Rate (%)	82.1	7.7	10.2		

Note.—Diurnal periods explained in text.
* Two-way analysis of variance. Rates significant among seasons (F = 5.1; df = 2, 114; P < .01).
Rate not significant either among diurnal periods (F = 0.9; df = 3, 114; P > .25) or with season ×
diurnal period (F = 1.0; df = 6, 108; P > .25).

The contexts of 10 of the 21 NOBB were unknown. In these instances the vocal animals typically faced in the direction of the vegetation which surrounded the outside perimeters of the enclosures. Eleven of the 21 NOBB were given by a subordinate female (F5) after being attacked and bitten by a dominant female (F4; see Yahner 1978a). As a result of these attacks F5 was moved to a previously uninhabited enclosure in late summer; she was never heard barking again during the study. When these 11 instances of NOBB are omitted from a seasonal analysis of rates, rate in summer (60%) still exceeded those in autumn (20%) and winter (20%; P < .05; single-classification analysis of variance).

Rate of NOBB was not related to percent time spent active (i.e., not resting). Mean activity levels of the population (N = 10 adults) during each season-diurnal period and mean activity of individual adult muntjacs during each season (Yahner 1980a) did not correlate, respectively, to mean population rate of NOBB (r = .5; df = 10; P > .05) or to mean individual rate of NOBB (r's = .49 to −.26; df = 8; P's > .05).

*Participation and Individual
Differences in Barking Bouts*

In addition to the NOBB, barking bouts resulting from the experiments (EBB) were elicited on seven occasions. In 23 (82.2%) of the 28 barking bouts (NOBB + EBB), only one individual vocalized; in two (7.1%), two individuals emitted barking bouts simultaneously; and in three (10.7%), three to five individuals barked concurrently. The frequency of barking bouts in which only one muntjac barked versus that in which two or more muntjacs barked at the same time were significantly different (P < .001; goodness-of-fit test). Responses by nonvocal muntjacs to barking bouts of a conspecific(s) ranged from apparent disinterest to infrequently looking in the direction of the vocal animal(s) while remaining in a

stationary position for approximately 2 min or less, followed by resumption of normal activity.

Mean rates of NOBB were similar between adult males (0.08/day) and adult females (0.10/day; $P > .25$; single-classification analysis of variance). Rate of NOBB varied from 0.03 to 0.33 per day among eight animals (hereafter called barkers); two adult muntjacs never barked during the study (table 4). Based on the total frequency in which each muntjac barked during NOBB ($N = 28$ instances; see table 4), one of the adult muntjacs could be expected to participate in a NOBB once every 11 days during the year. The two young animals never barked.

Individual barking bouts ranged from a single bark ($N =$ two instances) to 15.4 min in duration. Mean duration of barking bouts varied among barkers (table 4), but significant differences in duration existed only between M3 and F5 ($P < .05$, Student-Newman-Keuls test). Mean rate of barks per bout and mean interbark interval differed appreciably among barkers but were not statistically different (table 4).

Considerable overlap occurred among barkers in both mean duration and mean dominant frequency of barks (table 4). Mean duration of F5's barks was comparable to those of F1 and M2 ($P > .05$), but it was less than those of the remaining five barkers ($P < .05$). Moreover, barks given by F1 and M2 were similar in duration to those of others ($P > .05$).

Three muntjacs, M1, F3, and M3, produced barks which emphasized approximately the same mean dominant frequency ($P > .05$). However, of these three individuals, only the barks of M1 were different in mean dominant frequency from those of F1 ($P < .05$). Further, mean dominant frequency of barks given by F5 and F2 were equal ($P > .05$) but were unlike those of the previous four muntjacs ($P < .05$). Mean dominant frequency of barks given by F4 and M2 varied ($P < .05$), and these were higher than those of the other barkers ($P < .05$).

Although mean duration and mean dominant frequency of barks were similar among certain muntjacs, other features of barks were characteristic to given individuals. For example, virtually all energy in the bark of F1 appeared to be concentrated within a narrow frequency band, presumably the fundamental (fig. 1D). In the barks of F2 (fig. 1E) and F3 (fig. 1F), a portion of the energy was seemingly distributed in other harmonic bands beyond the fundamental. In contrast, the energy in the barks of M3 was scattered over a wide area, and different harmonic bands were not discernible (fig. 1C). Because all barks were recorded within a distance of 20–50 m, these variations in energy concentrations were not likely to be a result of fading of different frequencies over distance (see Marler and Isaac 1960). Instead, these differences probably occurred because of actual variations in sound production among individuals. In addition, harmonic bands in the barks of M2 (fig. 1B) and F5 (fig. 1H) consistently arched up and down, indicating that perhaps the frequency of the bark increased and decreased due to the manner in which these two animals opened and closed their mouth while vocalizing (see Davis 1964).

Several parameters associated with barking bouts could be predicted on the basis of the behavioral profiles of individual muntjacs (table 5). First, rates of NOBB in response to disturbances in the environment were higher in animals

TABLE 4

COMPARISON OF RATES OF NOBB AND MEANS OF FIVE PARAMETERS ASSOCIATED WITH TOTAL BARKING BOUTS (NOBB + EBB) AMONG TEN ADULT MUNTJACS OF BOTH SEXES

Individual (sex)	No. of NOBB	Rate of NOBB (no./day)	Mean duration of barking bout (min)	Mean rate (no./min) of barks per bout	Mean inter-bark interval (s)	Mean duration of bark (s)	Mean dominant frequency of bark (kHz)
Barkers							
101615(M1)	4	.13	2.6	4.1	20.5	.51	.67
101616(M2)	2	.07	1.5	4.8	19.3	.37	1.12
35417 (M3)	3	.10	7.6	8.4	8.4	.50	.71
M01215(F1)	2	.07	4.9	8.5	9.0	.34	.79
101741(F2)	3	.10	1.6	7.2	10.6	.41	.93
101432(F3)	2	.07	6.5	4.8	13.3	.49	.70
M01266(F4)	1	.03	6.2	6.8	9.5	.46	1.04
101479(F5)	11	.33	1.3	9.9	9.2	.27	.90
Univariate F-ratio ......:.			2.4	1.6	2.0	54.7	45.5
Degrees of freedom			7, 27	7, 27	7, 27	7, 96	7, 96
Level of significance			$P < .05$	$P > .10$	$P > .05$	$P < .001$	$P < .001$
Nonbarkers							
M01265(M4)	0	0					
M00510(F6)	0	0					

NOTE.—Univariate F-ratios, df, and levels of significance based on single classification analysis of variance. NOBB = naturally occurring barking bouts; EBB = barking bouts elicited by experiments. M1 = adult male one, F1 = adult female one, etc.
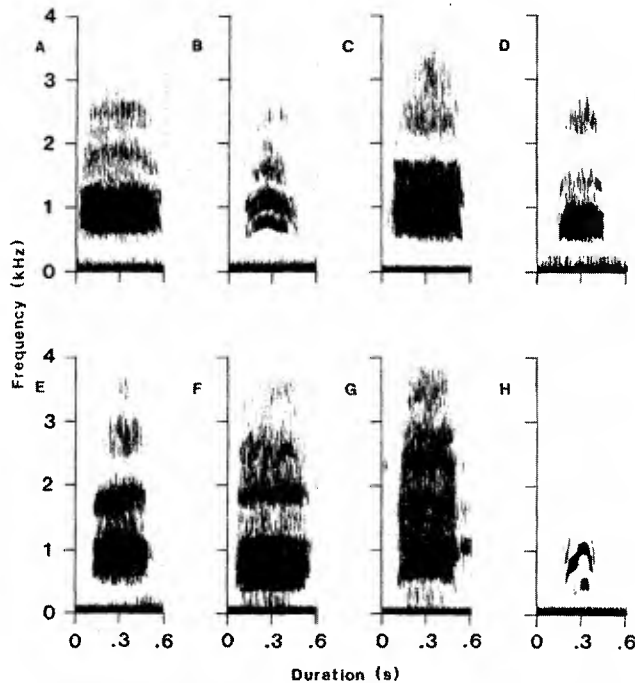
FIG. 1.—Sonographs of representative barks given by eight adult muntjacs: *A*, 101615(M1); *B*, 101616(M2); *C*, 35417(M3); *D*, M01215(F1); *E*, 101741(F2); *F*, 101432(F3); *G*, M01266(F4); *H*, 101479(F5). Wide-band setting.

TABLE 5

STEPWISE MULTIPLE REGRESSION OF FOUR PARAMETERS ASSOCIATED WITH
BARKING BOUTS (Dependent Variables) AND DURATION AND
FREQUENCY OF THIRTY-FIVE BEHAVIORS (Independent Variables)

Dependent Variable	R	Multiple Regression Equation: $y = b_0 + b_1x_1 + b_2x_2 \ldots$
Rate of NOBB (no./day) caused by a disturbance	.76	$Y = .71 + .13$ (frequency graze) + .08 (frequency walk) − 14.62 (frequency sniff head)
Rate of NOBB (no./day) given in a subordinate context	.99	$Y = 0 + 1.10$ (frequency lying down flat)
Mean duration (min) of barking bout (NOBB + EBB)	.72	$Y = 6.39 + 110.06$ (frequency sniff head) + .26 (frequency lick head) − 11.22 (duration sniff body) − 4.01 (duration head low and crouch)
Mean rate of barks (no./min) per bout (NOBB + EBB)	.62	$Y = 4.46 + 14.33$ (frequency lying down flat) − .09 (frequency graze)

NOTE.—NOBB = naturally occurring barking bouts; EBB = barking bouts elicited by experiments; R = multiple regression coefficient. Descriptions of most behaviors in table given by Barrette (1977*d*).

which frequently walk and graze, suggesting that individuals which traverse greater distances in their daily activities are more likely to encounter stimuli which elicit barking bouts. Second, rates of NOBB were higher in individuals which often exhibited the submissive behavior, termed lying down flat (see Barrette 1977d), when approached by a dominant individual. While lying down flat female F5 frequently emitted a whine (fig. 2) as male M3, a dominant muntjac, licked and attempted to scent mark her body. Third, contact-promoting behaviors, such as sniffing head, licking head, and sniffing body, were less often performed by barkers who vocalized for long periods during barking bouts. In other words, the more social a muntjac, the less likely it barked for extended periods. Fourth, rate of barks per bout were greatest in animals which either displayed submissive behavior (lying down flat) or frequently moved while searching for and consuming food (grazing).

Experimental Presentation of Stimuli

Initial and subsequent responses, stage 1.—Responses of muntjacs often varied both between initial and subsequent presentations of the same stimulus and among different stimuli (table 6). Muntjacs consistently showed little interest in either stationary and moving aerial models (stimuli 1 and 10–14) or in olfactory stimuli (15–18) at initial and subsequent exposures. The deer investigated and sometimes barked at large, conspicuous stimuli (2 and 5) when sighted for the first time, but these were generally ignored on subsequent occasions. Muntjacs also infrequently barked upon seeing other types of terrestrial stimuli (such as 7, 8, and 27), but the predominant response to stimuli 7–9 and 24–27 was to investigate at close range or from a distance regardless of previous exposure. Stimuli 3 and 6 always evoked some type of response involving flight; barks or yaps (see Barrette 1977c) were sometimes given when fleeing from stimulus 6. Auditory stimuli (4 and 19–21) attracted the attention of muntjacs, but the deer never fled or vocalized in response to these disturbances. A muntjac barked on one occasion subsequent to hearing a playback of a known conspecific; however, playbacks (stimuli 22–23) were typically ignored. The frequency in which playbacks initiated barking bouts (1.3%) was considerably less than the frequency in which terrestrial models (stimuli 2, 5–8, 27) elicited barking bouts (8.0%; $P < .05$, Fisher's exact test).

Responses to known danger, stage 2.—When exposed to stimulus 28, the deer consistently fled with the tail held in an upright position; yaps were elicited on one occasion (table 6). Subsequent to exposures to this stimulus, responses to select stimuli (2, 16, or 21) presented separately or in combination (stimuli 27) evoked very different responses (table 7) than those given by the deer prior to stage 2 of the experiments (table 6). Rather than ignoring, investigating, or barking at stimuli 2, 16, 21, or 27, the deer now avoided, investigated from a distant position, or fled to far corners of the enclosures when either of these stimuli were detected. In short, they appeared to associate each of the components of stimulus 28 (stimuli 2, 16, 21, or 27) with a predator that hunts by first stalking its prey and then attacking and persistently chasing its prey after being detected regardless of the prey's
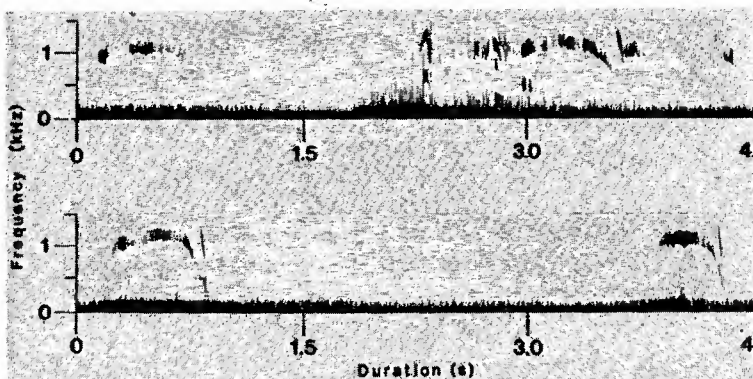
FIG. 2.—Sonographs of representative whines given by 101479(F5) when courted by 35417(M3). Wide-band setting.

TABLE 6

RESPONSE GIVEN BY TEN ADULT MUNTJACS AT INITIAL AND SUBSEQUENT
PRESENTATIONS OF TWENTY-EIGHT STIMULI DURING STAGE 1

	RESPONSE (%)		
Stimulus	Initial Presentation	Subsequent Presentation	Level of Significance
1	NR (100)	NR (100)	NS
2	AI (60)*	AI (52), NR (30)	.05
3	R (60)	R (53), RI (34)	NS
4	ID (100)	ID (100)	NS
5	AI (100)	NR (75), AI (25)	.05
6	RI (70)*	RI (45)†	NS
7	AI (50)*	AI (43), ID (43)	NS
8	AI (50), ID (30)*	AI (50), ID (33)	NS
9	ID (40), A (40)	ID (42), RI (25)	.001
10	NR (80)	NR (81)	NS
11	NR (50), ID (30)	NR (67)	NS
12	NR (70)	NR (85)	NS
13	NR (70)	NR (75)	NS
14	NR (50), R (30)	NR (70)	NS
15–18	NR (100)	NR (100)	NS
19–21	ID (100)	ID (100)	NS
22	NR (70)*	NR (87)	NS
23	NR (90)	NR (83)	NS
24	AI (50), R (40)	AI (55), R (28)	NS
25	AI (40), ID (40)	ID (50), AI (32)	NS
26	AI (60)	AI (43), ID (30)	NS
27	ID (40), R (30)*	ID (56), R (34)	NS
28	R (100)	R (100)†	NS

NOTE.—No. of stimuli correspond to those given in table 1. Descriptions and symbols for stimuli correspond to those given in table 2. Responses occurring ⩾ 25% of the time at initial or subsequent presentations are included in table. Level of significance based on $R \times C$ Contingency tests where frequency of responses are compared between initial and subsequent exposures: NS = not significant; .05 = $P < .05$; .001 = $P < .001$.

* A barking bout given at least once to this stimulus.

† Yapping given at least once to this stimulus.

TABLE 7

MAJOR RESPONSES GIVEN BY TEN ADULT MUNTJACS TO FOUR
TYPES OF STIMULI COMPRISING STIMULUS
TWENTY-EIGHT DURING STAGE 2

Stimulus	Major Response
2	Avoid (A) or Investigate from a Distance (ID)
16	Avoid (A)
21	Investigate from a Distance (ID)
27	Run (R) or Avoid (A)

NOTE.—No. of stimuli correspond to those given in table 1. Descriptions and symbols of responses correspond to those given in table 2. Inclusion of responses in table based on a percent occurrence ⩾ 50%.

response to it (see later section describing the hunting strategies of natural predators).

DISCUSSION

Temporal Timing of Barking Bouts

The timing of barking bouts appears to be related to (1) environmental conditions, imposed by seasonal (in temperate climates) and diurnal cycles, which reduce visibility; and (2) the frequency of certain types of subordinate-dominant encounters. First, seasonal rates of barking bouts coincided with vegetative growth. Maximal rates occurred in summer (table 3) when tall herbaceous growth (> 1 m) was present in areas adjacent to outside perimeters of the muntjac enclosures. In contrast, rates declined in autumn and winter when herbaceous cover was reduced due to change in season. Second, regardless of season, bouts most often occurred at sunset, night, or sunrise (table 3). These results suggest that incidences of barking bouts are associated in part with a reduction in the ability of muntjacs to discern or perceive the exact cause of a nearby disturbance solely by visual means due to vegetative obstructions or poor light. In natural habitat free-ranging muntjacs sometimes cannot see more than 1 m distant because of dense vegetation (Dansie 1970), and barking bouts most often occur at dawn and dusk (Wood 1931; Barrette 1977c) or at night (Powell 1964).

Eleven of the 17 barking bouts recorded in summer were given by F5 subsequent to being chased and bitten by F4; F5 had a history of subordination and was relatively immobile because of hoof injuries from frostbite during the previous winter (see Yahner 1978a). That barking bouts occur in a subordinate context during actual or potential aggressive encounters is supported by field and other captive studies (Barrette 1977d). For example, water is a limiting resource to muntjacs in the wild, and often subordinate animals emit barking bouts when approaching a dominant conspecific present at a waterhole. Barrette (1977d) suggested that subordinate muntjacs bark occasionally during these circumstances as if to "pretend" to have detected a source of danger, thereby diverting the dominant's attention away from himself or the desired resource. A water source

was not limited in my study, but the ability of the immobile subordinate female to escape aggressive interactions directed at her by the dominant female was restricted and in a sense "limited."

Possible Functions of Barking

Reproductive function.—Rutting calls are common and quite diverse among species of ungulates (Espmark 1964; De Vos et al. 1967). Although the bark of muntjacs has been proposed to be a mechanism of communication during the mating season (Powell 1964; Soper 1969; Hoogerwerf 1970) or to be used by rival males when challenging one another during the rut (Wood 1931), evidence for the use of barks in these two contexts is lacking (Barrette 1977c; personal observation). Males, however, frequently emit a sound similar to a soft "buzz" when courting a female (Dansie 1970; Barrette 1977d; personal observation). This sound probably functions as appeasement to permit and maintain close proximity between prospective sexual partners, which are normally solitary and widely dispersed (Barrette 1977d). Another vocalization heard during courtship is one given by the female while lying down flat and head weaving (see Barrette 1977d), which I term a whine (fig. 2). Whining is perhaps a submissive vocalization that could be similar in function to the infant whine of many viverrids (Wemmer 1977).

Long-distance or advertisement function.—Based on the physical structure of muntjac barks, the social organization of these deer, and their dependency on other systems of communication, barks of muntjac probably do not function as a primary source of long-distance or advertisement signals. First, little or no energy in the barks of muntjacs is concentrated in the 1.6 to 2.5 kHz range; neither is energy contained within a narrow frequency band (table 4; fig. 1). Thus, the barks of muntjacs probably do not pass vegetative barriers in the forest as readily as those which are higher in frequency and are not spread out over a wide frequency band (after Konishi 1970; Morton 1975; Waser and Waser 1977). Second, muntjacs, although solitary, are not territorial (Barrette 1977d). Long-range communication or advertisement of presence and identity as a means of maintaining patterns of dispersion are carried out via olfactory mechanisms rather than by the use of acoustic signals (Eisenberg and Lockhart 1972; Barrette 1977b). Results from the playback experiments support the secondary or perhaps nonexistent role of acoustic mechanisms for these purposes; responses to familiar and unfamiliar barks are virtually identical (table 6). In contrast, many solitary, territorial passerines utilize sounds to advertise themselves and their position in the habitat. The reaction of a resident passerine to a song of a known neighbor is less intense than that to a stranger's, indicating that individual recognition exists (Emlen 1971; Wiley and Wiley 1977). This is not meant to imply that no individual recognition of barks of different muntjacs occurs because of the lack of a differential response to familiar versus unfamiliar vocalizations. Those characteristics functioning as a means of recognition, if they exist, will appear consistently in the sounds of each individual (Marler and Isaac 1960). Some measurable parameters associated with barking were similar, whereas considerable overlap occurred in other parameters among individuals (table 4; fig. 1). Thus, individual recognition using an interac-

tion of several features of the barking bout, i.e., the "Gestalt," may occur as a means by which muntjacs can distinguish barks of neighbors from those of strangers (after Espmark 1975).

Anti-predator function.—Alarm or warning signals are common in ungulates. Axis deer (*Axis axis*), hog deer (*A. porcinus*), barasingha (*Cervus duvauceli*), elk (*Cervus elaphus*), and sambar (*Cervus unicolor*) bark; white-tailed deer (*Odocoileus virginianus*) snort; and reindeer (*Rangifer tarandus*) grunt in the presence of danger (Schaller 1967; Fuchs 1968; Eisenberg and Lockhart 1972; Ericson 1975; Hirth and McCullough 1977). Muntjacs yap and/or bark when frightened or excited by potential danger (Wood 1931; Powell 1964; Dubost 1971; Jayewardene 1976; Barrette 1977*c*, 1977*d*).

Axis deer and barasingha are among several species which become alert at the barks of a sympatric species of ungulate (Schaller 1967). Interspecific communication in these ungulates may have been selected for in the same manner as alarm calls among coexisting primates (*Cercopithecus* spp.; see Marler 1973). These ungulates form herds and live together in open and secondary forests (Schaller 1967). However, axis deer, for example, take little notice of the barks given by the solitary, forest-dwelling muntjac (Eisenberg and Lockhart 1972). Because muntjacs rarely became alert or vocalized in response to the barks of conspecifics (table 6), muntjacs in captivity, and perhaps in the wild, presumably do not readily associate the barks of another muntjac with immediate danger. Further, free-ranging muntjacs probably do not respond to vocalizations of other species, but field evidence to support this assumption is not reported to my knowledge.

When startled by a disturbance at close range, muntjacs sometimes emit yaps and expose their rump patch while fleeing. These auditory and visual signals could combine to surprise a potential predator and thus increase the chance of escape (after Guthrie 1971; Driver and Humphries 1969). Barks, in contrast, are given when a disturbance is detected at a greater distance (Barrette 1977*c*). In my study, yaps occurred in response to a startling disturbance created less than 5 m from the deer (table 6), whereas barks were given when the deer were 10 m or more from the disturbance. Thus, the use of the yap and the bark may depend on the closeness of the potential danger and hence on the degree of alarm. The occurrence of various types of alarm notes which occur in the gray catbird, *Dumatella carolinensis,* are also contingent on the distance of the bird from a prospective enemy (Collias 1960).

Passerine birds and marmosets (*Sagiurnus fuscicollis*) use a high-frequency (within the 2–5 kHz range) alarm signal described as a drawn-out "seeet" call which begins and ends abruptly. Such calls are difficult to localize because they are too high in frequency to permit binaural comparisons of phase differences; thus, they are effective warning devices against most terrestrial predators (Marler 1955; Vencl 1977). Compared to these high-frequency, pure-tone-like "seeet" calls, both the signals used for long-distance communication (see Morton 1975) and barks of muntjacs (table 4; fig. 1) are presumably more easily localized. If so, rather than confusing or perhaps surprising a potential predator, barks of muntjacs apparently make the caller more conspicuous to the predator. The relationship

between the physical structure of a muntjac bark and its presumptive use in an alarming context is, therefore, in marked contrast to that of arboreal primates and passerines.

The Adaptiveness of Barking,
or Why Be Conspicuous?

In order to both explain the relationship between the physical structure and the function of muntjacs barks and give insight into the adaptive consequences of barking in the presence of potential danger, the responses of muntjacs to different types of stimuli, the vegetative structure of natural habitat, and the hunting strategy of important predators in the wild must be considered simultaneously. Barking bouts were typically elicited by stationary or slightly moving terrestrial stimuli which were either novel or somewhat inconspicuous because of their location in tall herbaceous vegetation (table 6). After initial exposure to stimuli which elicited barking, muntjacs generally ignored and rapidly habituated to these because the stimuli remained at the same location and could be approached and investigated after barking with no danger to the deer. In other words, the deer presumably "sensed" them to be harmless objects in their environment. However, when certain stimuli which previously accompanied immediate danger (stimuli 2, 16, 21, or 27 after presentations of stimulus 28) were present within the enclosures, the deer did not bark but fled or exhibited some form of avoidance behavior (table 7). Based on these responses and the fact that olfactory and auditory stimuli (excluding playbacks) never elicited barking bouts during experiments (table 6), I contend that many NOBB (table 3) were probably initiated by visual, inconspicuous (at least to me) disturbances beyond the perimeters of the enclosures. Perhaps some of the disturbances could have been caused by mammals hunting or moving slowly in the adjacent vegetation, such as domestic cats (*Felis domesticus*) or raccoons (*Procyon lotor*), which were abundant in the area. Thus, stimuli to which muntjacs bark have some properties in common (table 8). These stimuli may provide an intrinsic contrast with background stimulation or with immediately preceding stimulation, or "stimulus contrast," such that they are capable of arousing intense or prolonged attention in the deer (after Andrew 1962, 1964). Moreover, prior to or while barking, muntjacs often moved their heads as if to better assess the identity of the stimulus while either facing the stimulus in a stationary position or walking slowly and cautiously toward the stimulus (Dubost 1971; Barrette 1977c; personal observation).

Most disturbances or stimuli encountered by muntjacs in the wild, including predators, are probably difficult to discern and provide "stimulus contrast" because of dense vegetation. Tigers (*Panthera tigris*) and leopards (*Panthera pardus*) are among the major predators of muntjacs; because both species are solitary hunters and occasionally hunt prey which are widely dispersed and time consuming to find in the forest, they rely heavily on concealment in order to approach and surprise their victims (see Schaller 1967; Eisenberg and Lockhart 1972). The tiger, for example, is successful in killing its prey in only about one of 20 attempted

TABLE 8

CHARACTERISTICS OF VISUAL TERRESTRIAL MODELS WHICH ELICITED
BARKING BOUTS IN ADULT MUNTJACS DURING STAGE 1

1. Novel or inconspicuous due to their position in tall (>1 m) vegetation
2. Persistent in time such that they arouse prolonged and intense interest
3. Motionless or moving slightly on occasion

stalks. Most stalks occur within approximately 10–25 m of the prey prior to attack; but if the prey is alerted by its presence, an attack from even 15 m or less may be unsuccessful. The alarm bark of muntjacs, directed at a hidden tiger, is apparently a sufficient indication to the cat that additional stalking is futile, because the tiger immediately hunts elsewhere subsequent to barking by a vocal muntjac which was intended as its victim (see Schaller 1967). Provided that an alarm call discourages further stalking of a muntjac by eliminating the tiger's element of surprise, then barking by a muntjac is an adaptive response to "suspicious-looking" objects in their habitat, maximizing individual survival. Sherman (1977) has suggested that the alarm call given by Belding's ground squirrels (Spermophilus beldingi) may function in a similar fashion to deter predation by coyotes (Canis latrans).

Being a small, solitary, cursorial species in a dense rainforest environment, muntjacs have the option to remain cryptic or inconspicuous when danger is present (after Eisenberg and McKay 1974). Other small ungulates, which are similar in social organization and occupy habitat with comparable vegetative structure, such as the mouse deer (Tragulus napu), rely largely on cryptic appearance and behavior to avoid and escape predators (Ralls et al. 1975). Because not all muntjacs bark, or at least some bark less than others (table 4), and tendencies to bark may depend in part on individual behavioral profiles (table 5), free-ranging muntjacs probably respond in several different ways to potential danger (table 2; see Smythe 1970 for review). Barking appears, however, to have a selective advantage over types of responses. If a hidden tiger is simply ignored, the muntjac would obviously become easy prey. A stalking, hidden tiger probably knows the exact whereabouts of its prey in most cases, so freezing is not adaptive unless the prey detects the predator before a stalk is initiated. A muntjac who opts to move quietly or run out of sensory contact with a hidden predator in a visually-obstructed environment could rapidly lose sight of the predator; unless the predator has not detected the prey, the muntjac could be stalked and attacked at another time in the near future by the same predator or by another predator located in the muntjac's route of escape.

Although barking by muntjacs may discourage pursuit and attack by the tiger and perhaps other large predators, such as the leopard, this consequence of barking could simply be an adaptive by-product of a muntjac's tendency to direct its attention at most or all novel, inconspicuous, motionless, or nearly-motionless stimuli, or disturbances created by such stimuli in its environment. For example, suppose a muntjac detected a motionless or slowly moving object in the nearby vegetation which represented either an inanimate object never previously en-

countered in its daily travels or an animal of another species resting quietly that is not a potential threat. Because the vegetation obscured the identity of the object and aroused the attention of the deer, the muntjac barked in response to it. After barking, the object neither moved nor attacked; thus, the muntjac has learned that the object is harmless and can be "ignored" in the future. The result of this learning process is a reduction in wasted time and energy during subsequent exposures to these types of stimuli, such that time-energy budgets will be less interrupted and can be allocated toward other activities which maximize survival and reproductive fitness. Habituation to terrestrial models, such as stimulus 2, which initially elicited barking in some deer in stage 1 of my experiments (table 6), are examples of this. On the other hand, if the inconspicuous or novel object or the disturbance created by it is a hidden tiger prepared to attack, a healthy muntjac aware of the predator has a good chance of escaping, should an attack ensue, because of the muntjac's elusive manner of flight in the dense forest (see Barrette 1977d). By barking, thereby "forcing" the hidden cat to make the next move and perhaps hunt elsewhere, the prey can expend a greater proportion of its time-energy budget engaged in other activities (after Smythe 1970). Suppose that a muntjac barks at a different species of predator hiding in vegetation which is not deterred by vocalizations. Given that the predator is sufficiently smaller in body size than the tiger, the muntjac stands a good chance of defending itself with its canines if flight is not permissible when attacked. The canines, which are used as an offensive weapon during intraspecific fights (see Barrette 1977a), have been used to kill attacking dogs, Canis familiaris (Dansie 1970; Hoogerwerf 1970).

Evolution of Barking

Kin selection (Hamilton 1964; Maynard Smith 1965) and individual selection (Trivers 1971) have been invoked as two explanations for the evolution of alarm calls. If members of a group are closely related, altruistic calling may evolve through kin selection (Hamilton 1964). Females are more likely to emit calls than males when the role of males in the rearing of the young is negligible (Dunford 1977). For example, snorting in white-tailed deer occurs more often in related than in nonrelated groups of animals and is most prevalent in mother-young groups, suggesting that this alarm signal has evolved via kin selection (Hirth and McCullough 1977).

Rate of barking in muntjac, however, does not vary with sex class (see table 4) even though mother and young may associate together for several months without paternal assistance in the rearing of the fawns (Dansie 1970; Barrette 1977d; personal observation). Further, muntjacs do not form social groups but are nearly always found alone (Seidensticker 1976; Barrette 1977c). This suggests that barking in muntjacs has probably evolved through individual selection, because it is not sex-class specific and is not necessarily given in the presence of close kin. Assuming that barking reduces the effectiveness or likelihood of a predator initiating an attack or prevents a predator from developing a preference for hunting that species within the home range of the caller, then auditory signals in muntjacs can evolve at the individual level (after Trivers 1971; Charnov and Krebs

1975). Barking in muntjacs can be envisioned as a mechanism to keep a predator in touch with the caller until it shows disinterest and hunts elsewhere (after Smythe 1977). The overall effect is a direct benefit to the vocal muntjac by maximizing individual survival.

Had calls of muntjacs evolved to warn conspecifics, then a single bark followed by flight to safety would seem to be a sufficient warning device to inform conspecifics of the approximate location of a predator (after Smythe 1977). Yet barks are given repeatedly (table 4), flight by the vocal animal does not accompany barking, and participation by more than one muntjac in a barking bout (both NOBB and EBB) seems to occur only when it appears that all vocal animals sight the same stimulus. Detection of the same stimulus in the wild by more than one muntjac is probably unlikely in most circumstances due to the dense vegetation and the solitary social structure. However, this does not rule out the possibility that, on occasion, the barking of a conspecific is enough of a distraction to divert the attention of a nearby silent muntjac to the direction of the call, thereby enabling the silent muntjac to respond quickly and appropriately should the stimulus causing the barking be a predator which later moves in its direction. Barrette's (1977d) suggestion that barks by a subordinate muntjac in the presence of a dominant individual at a desired resource may distract the attention of the dominant may support the possibility that a muntjac heeds the bark of a conspecific.

Anxiety: An Underlying Factor

Barking bouts in muntjacs occur primarily during subordinate-dominant encounters and when a source of potential danger is detected. Multiple use of the same auditory signal in quite different situations is reported in several other species (see Smith 1963; Fourie 1977). Perhaps the use of the bark by muntjacs in these two seemingly unrelated contexts can be linked by a single underlying factor using the following argument. Anxiety can be defined as a state of distress caused by apprehension of danger or misfortune. When certain muntjacs detect possible danger or encounter a dominant individual, not only is their attention directed to it, but an internal state of distress may result as a consequence of the anticipation of an ensuing attack by a predator or by a conspecific. Barking may hence be an external expression of a motivational state which occurs more readily in individuals characterized by specific behavioral profiles (table 5).

If anxiety is an underlying factor in the causation of barking in muntjacs regardless of the context, then this auditory signal, traditionally considered as an alarm call, would be better termed a distress signal. However, the present "distress call" differs in context, function, and evolution from that of crocodilians (see Staton 1978).

SUMMARY

Barking bouts by muntjacs are given most often when visibility is reduced due to environmental conditions. Some individuals bark more readily than others, and

various parameters associated with barking bouts overlap considerably among individuals. Barking in muntjacs probably does not function in the contexts of food procurement, reproduction, or maintenance and monitoring of individual movements. Rather, barking occurs primarily in two major contexts: during certain social encounters and when novel or inconspicuous stimuli, such as a hidden predator, are detected in the environment.

Barking appears to have evolved via individual selection. Although the physical properties of barking bouts are such that they may make a muntjac more conspicuous and easily localized, this response to potential danger may act to deter predation.

The underlying causal factor linking the two major contexts in which barks are given may be an internal state of anxiety. Anxiety, and hence barking, occurs more often in muntjacs which are characterized by specific behavioral profiles. Barking is proposed to be better termed a distress call than an alarm call.

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