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SEQUENTIAL PATTERNS OF BEHAVIOR IN THE BLACK BUCK, *ANTILOPE CERVICAPRA* (LINNAEUS)

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ABSTRACT: Six male and six female black bucks were observed in the Trivandrum Zoo for one year. Sequential patterns of behavior were homogeneous throughout all observation periods. Sequences were longer with more acts occurring during morning hours than evening hours. However, acts were of shorter duration during noon hours. Sexually dimorphic features were reflected in the behavior sequences. The dominant buck was more active and aggressive than other group members. The behavior sequences of the black bucks are explained in terms of a first order Markov chain with five states. Inhibiting and directing behavior patterns are discussed within an ecological, functional framework.

INTRODUCTION

A sequential pattern of behavior is an ordered succession of identified behavioral activities of an animal at any time period. The behavioral sequence of an animal at any time is set up on the basis of various internal and external factors (Baerends, 1985). Investigations of sequential patterns of behavior have considerable relevance in formulating behavioral models and in the prediction of future states of behavior of any animal species.

Various activities of animals do not occur at random, but fall into a homogeneous pattern of sequence (Hinde & Stevenson, 1969). This integration of heterogeneous units into a sequence depends on a variety of factors operating at different levels. McFarland (1969) described how a sequence of behavioral transitions occur by the 'inhibition, disinhibition and reinhibition' processes. A dominant state of behavior permits a disinhibited behavior to appear for a certain time period showing the 'time-sharing' phenomenon.

Chase (1974; 1980; 1982a; 1982b; 1985) developed new theoretical and methodological approaches to the study of sequential analysis of behavior in a few species of animals. However, data on mammals necessary for ethological theory are scanty (Bekoff, 1977; Seyfarth, Cheney & Hinde, 1978) and hence the present investigation studies and analyses the sequential pattern of behavior of the Black Buck, *Antilope cervicapra*.

METHODS

Animals: Black bucks were kept in an open enclosure at the Trivandrum Zoo. In August, 1985, during the initial period of this investigation, this group consisted of 24 females, 21 males, and four fawns. For the present investigation, six male and six female adults were selected at random. These individuals were identified on the basis of their dominance status, determined during the preliminary observation period (see below), the nature of horns, body color and other identification marks seen on different parts of their body. They were designated as M1, M2, M3, M4, M5 and M6 (males) and as F1, F2, F3, F4, F5 and F6 (females).

PROCEDURES

On the basis of the two-week preliminary observation, various observable behaviors of the black buck were identified. These behavioral activities were categorised into the following five states on the basis of functional features.

State 1.   Behavior in relation to olfaction
State 2.   Feeding behavior
State 3.   Behavior in relation to aggression
State 4.   Grooming and licking
State 5.   Reproductive behavior

Direct behavioral observations were made for a period of one year from August, 1985 to July, 1986. Only one animal was observed at a time. Each observation period was two hours. Daily observations were made during 08 00h to 17 00h at random. Data were recorded on an observation chart and analysed by a computer to identify a first order Markov Chain in the sequential pattern of behavior.

Markov Chain analyses: Observations were made on continuous actions to estimate the transition probability matrix as detailed by Basawa and Rao (1982). 'N' transitions (i.e. 'N' sequential acts) of animals performing diverse actions belonging to the five identified states were observed. The data on individual males and females were then subjected separately for analysis using procedures for testing homogenity of behavior among females and males (Bhat, 1972). This provided concurrence for continuing the analysis by combining the observation on all animals of both sexes separately for each 2h observation period from 08 00 to 17 00h. It may be noted that the transition matrix explains the Markov Chain.

The estimated Markov Chain model for the sequential dependence in behavior was subjected to a contingency test for inference purpose.

A further analysis for identifying the specific states that account for temporal dependence was carried out, by breaking down the transition table which was found to be statistically valid (Bishop, Fienbory & Holland, 1975).

The probability matrix of order 5 was estimated for females and males separately for five time periods as given in Table 1.

TABLE 1

Estimated Transition Probabilities from Each Preceding Act to Following Act of Black Bucks (A. cervicapra) for Five Different Time Periods

Time periods (h)	Observed states	Males					Females				
		1	2	3	4	5	1	2	3	4	5
0800–1000	1	.440	.075	.054	.140	.292	.428	.077	.0	.181	.313
	2	.361	.157	.108	.108	.265	.310	.169	.0	.225	.296
	3	.337	.048	.193	.157	.265	.0	.0	.0	.500	.500
	4	.421	.086	.086	.114	.293	.490	.006	.006	.116	.320
	5	.416	.058	.066	.113	.346	.473	.003	.003	.165	.299
1000–1200	1	.416	.117	.070	.117	.280	.401	.092	.003	.155	.350
	2	.427	.115	.135	.146	.177	.392	.108	.0	.176	.324
	3	.326	.109	.207	.076	.283	.0	.0	.0	.0	.0
	4	.552	.048	.057	.057	.286	.443	.078	.0	.104	.374
	5	.427	.073	.070	.089	.341	.424	.098	.0	.148	.329
1200–1400	1	.392	.121	.049	.127	.310	.397	.140	.003	.162	.301
	2	.325	.130	.142	.130	.273	.286	.186	.0	.171	.357
	3	.226	.075	.151	.075	.471	.0	.0	.0	.0	.0
	4	.422	.084	.024	.120	.349	.438	.125	.0	.086	.350
	5	.409	.077	.069	.112	.332	.452	.096	.0	.128	.324
1400–1600	1	.410	.114	.066	.116	.299	.381	.096	.0	.192	.332
	2	.319	.143	.132	.198	.209	.431	.097	.0	.194	.278
	3	.316	.066	.145	.105	.368	.0	.0	.0	.0	.0
	4	.442	.050	.058	.108	.342	.397	.074	.0	.184	.346
	5	.471	.075	.051	.156	.247	.473	.090	.0	.184	.253
1600–1700	1	.392	.091	.072	.091	.354	.447	.096	.0	.128	.329
	2	.292	.083	.167	.167	.292	.351	.108	.0	.162	.378
	3	.299	.029	.239	.119	.313	.303	.0	.0	.0	.0
	4	.228	.044	.074	.162	.500	.317	.067	.0	.2	.417
	5	.433	.055	.080	.092	.340	.438	.071	.0	.130	.361

State 1. Behavior in relation to olfaction   State 4. Grooming and licking
State 2. Feeding behavior   State 5. Reproductive behavior
State 3. Behavior in relation to aggression

To estimate the matrix, it was necessary for the chain to be homogeneous in time. This was also necessary for the practical side of observation. When treating the number of transitions of all females and males together for each state, the results showed evidence towards the homogeneity of behavior (Table 2). Homogeneity was observed in the behavior of all animals during all the observation periods. The combined χ^2 values have been given separately for males and females in Table 3. The analysed data revealed that the sequential behavior of the black bucks could be explained by a first order Markov Chain with five states. In the case of females, the hypothesis of first order Markov Chain could be accepted for the period from 0800 to 1000 h and 1600 to 1700 h only, whereas in the case of males, it could be accepted for the whole observation period from 0800 - 1700 h.

TABLE 2

χ^2 Values for Testing Homogeneity of Behavior of Black Bucks.

Sex	States of Behavior	Time in hours				
		0800–1000	1000–1200	1200–1400	1400–1600	1600–1700
Males	1	18.32	20.24	24.38	13.86	6.57
	2	6.76	7.46	30.13	16.8	17.69
	3	22.37	17.25	25.04	11.31	14.38
	4	15.01	15.91	17.58	17.46	10.29
	5	23.21	15.81	24.44	14.38	10.36
Females	1	7.77	12.41	9.49	12.98	2.46
	2	6.29	15.10	7.51	8.48	8.98
	4	15.01	13.51	18.92	19.21	15.12
	5	10.66	6.59	8.17	16.22	4.33

χ^2 20 df = 31.41 (males)
χ^2 15 df = 23 (females)
States 1–5 as in Table 1.

TABLE 3

Calculated Values of χ^2 for Testing the First Order Markov Chain.

Animals	Time in hours				
	0800–1000	1000–1200	1200–1400	1400–1600	1600–1700
Male	37.16*	48.15*	28.81*	39.59*	42.16*
Female	23.56*	8.85	12.79	8.42	36.01*

* p = .05
** p = .10

RESULTS

The observed behavioral transition and estimate of the transition probabilities revealed that the pattern of transition for an animal over different observation periods was different. However, approximately the same pattern was observed for different individuals in the same observation period. It was further revealed that state 3 (behavior in

TABLE 4

The Relationship of Each State of Behavior in the Sequential Pattern Formation in the Black Buck *

Time (h)	States°	Directing states		Inhibiting states	
		Males	Females	Males	Females*
0800–1000	1	1,4	4	3,5	1
	2	1,2,3	2,4	4,5	1
	3	3	—	1,2,4,5	—
	4	2,3	5	4,5	1,2,4
	5	5	1	2,3,4	2,5
1000–1200	1	2,4	4	1,3,5	1
	2	2,3,4	2	5	1,4,5
	3	2,3	—	1,4	—
	4	1	1,5	2,3,4	2,4
	5	5	2	2,3,4	5
1200–1400	1	1,2,4	2,4	3,5	5
	2	2,3,4	2,4,5	1,5	1
	3	3,5	—	1,2,4	—
	4	1,4,5	1,5	2,3	4
	5	1	1	2,4	2,4
1400–1600	1	2,5	2,5	1,3,4	1
	2	2,3,4	—	1,5	5
	3	3	—	1,2,4,5	—
	4	1,5	5	2,3,4	1,2
	5	1,5	1	2,3,5	5
1600–1700	1	1,2	1,2	3,4	4,5
	2	2,3,4	2,4	1,5	1
	3	3,4	—	1,2,5	—
	4	4,5	4,5	1,2,3	1,2
	5	1	1	2,3,4,5	2,4

* State 3 was not pronounced among females
° States 1–5 as in Table 1.

relation to aggression was not important for the females of the species as there were very few transitions, showing a difference in the behavioral patterns of states with respect to transitions in the states of activities.

Even though all the behaviors were observed throughout the day, the behavioral sequences were of longer duration with more behavioral acts, during morning and evening hours. The sequences hence, were shorter, with fewer behavioral acts, during noon hours. The appearance and disappearance of behavioral phases were in relation to the time of the day.

The sequential pattern of behavior varied according to the sex and dominance status of the individuals. Females spent much of the time in roaming, eating, and resting, while the males very often indulged in several types of aggressive behaviors such as chasing, thrashing and sparring. Variation in the pattern of behavior was also observed in the sub-dominant and dominant animals. The dominant individual was found to be highly active and aggressive.

Discrimination of behavioral states as 'direction' and 'inhibition' are shown in Table 4. By observation of the data in Table 4, each of the states 1, 2, 3, 4 and 5 may be seen to direct and/or inhibit other states, as shown in Table 5.

TABLE 5

The Trends of Directing and Inhibiting Acts of the Five States of Behaviors of the Black Buck.

Sex	States°	Directing Act	Inhibiting Act
Males	1	1,2,4	3,5
	2	2,3	5
	3	3	1,2,4,5
	4	5	4
	5	1	2,3,4
Females*	1	2,4	1,5
	2	2,4	1,5
	4	5	1,2,4
	5	1	2,4,5

° States 1–5 as in Table 1.
* State 3 was not pronounced among females

DISCUSSION

A Markov Chain can be used to denote a sequence of events with the probability of future events depending on past events. A first order Markov Chain model for the sequential behavior of the black buck assumes

that the probability of an act depends on the immediately preceding act only. A Markov Chain would be characterised by the initial distribution and the transition probability matrix. For practical purposes, the initial distribution could be omitted as it corresponds to the probability that the animal was in one of these five states at birth. Since these animals have lived for a number of years, the process may have started long before the study and the initial distribution may be of no consequence.

All animals possess a behavioral repertoire during various social interactions. It would be interesting to examine the relationship among these different acts which consist of one type of act being preceded or followed by another type. For example, 'push' always precedes 'shove' (Fagen & Young, 1978). Behavioral acts of directing and inhibiting tendencies of the states of behavior at any time period can be substantiated on biological bases.

Since various types of olfactory responses of the black bucks were studied and grouped as a single state, it is possible that during olfactory signalling the animals may use various modes of signalling so as to achieve the maximum benefits. Signalling would be more effective if various modes are used even to convey the same message or to convey different messages during the same type of interactions (Mykytowycz, 1970). To some extent, grooming and licking also have the effect of chemical signalling. It may also be possible that this behavior has an inhibitory effect on aggressive tendencies during social interactions as olfactory signals would be used to convey messages of individual status. Among artiodactyles, behavior in relation to olfaction includes scent marking and related acts (Müller-Schwarze, 1983). Since most of the marking was performed by the most dominant individual of the group, others would withdraw from aggressive encounters as it would be easy for them to identify the individual and its status at any particular time. Since they are more responsible to olfactory cues of specific signals at any time, they may be less interested in other behavioral activities, unless induced by some other motives.

Feeding is one of the primary requirements of any animal species. However, in natural habitats, the animal may have to forage and seek out its food. Various behavioral interactions in relation to feeding in natural habitats are exploratory activities, locating the prey or food, responses oriented towards the food, manipulation of the food, and the feeding itself. However, in captive zoo conditions, they are acclimated to the specific feeding time and the daily availability of their ration. There may be considerable limitations in the availability of food items and each individual of the group is prompted to achieve the maximum food within the limited time. In such circumstances, a tendency is developed to go on feeding until satiation is achieved or until the maximum available food is consumed. Hence, feeding in zoo conditions will direct feeding to the maximum level. Since competition for food is very common among the individuals in such conditions, fighting is

very pronounced, especially among species which maintain a social hierarchy. This may not influence the feeding of females in the group to a significant level as fighting is not pronounced among them. Females of the black buck do not maintain a dominance hierarchy.

During aggressive encounters, the dominant male chases the sub-dominants as it has to fight to maintain control over other individuals in the group. Aggression, once it is started, can cease only on the final achievement of the goal or when the aggressive individuals with heavy injuries are isolated. Since other behaviors are interrupted on such occasions, aggression inhibits other states of activities.

Grooming and licking are considered to have prominant roles in communication signalling, in thermoregulation, in getting rid of ectoparasites and or in maintaining social cohesion among individuals of the group. It is also part of reproductive behavior as a prelude to mating behavior. Hence, grooming and licking have relevance in influencing other behavioral activities of the same or other individuals of the group. It inhibits grooming and licking by other animals because it may more often influence the reproductive behavior itself.

Since reproductive and related activities direct olfaction and related behavior, it can be confirmed that in this species olfaction has a significant role to play in the reproductive behavior. Other activities such as behavior in relation to feeding, aggression, grooming and licking are inhibited when mating and related activities progressed. Meier *et al.* (1973) and Dubost & Feer (1981) have described behavioral display during courtship in the black buck.

During noon time the behavioral sequences consisted of activities with a low threshold requiring a lower level of motivational factors or a weeker eliciting stimulus than occurring in the morning and evening hours. This factor was described as non-stationary behavior in probability, i.e., the behavior depends upon the time. The number of time units in which a behavior occurs depends on the temporal pattern of the behavior and on its duration.

It is clear from analyses of the data that certain states of behavior alternate with certain other states of behavior for particular durations. Here, a specific behavioral sequence is formed depending on time. Further, it may be true that the dominant behavior at any time has control over other types of activities as already stated by McFarland (1969); that, not only does the dominant system determine the time of occurence of the disinhibited activity, but it also determines its duration.

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