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Sequential Pattern of Behavior in the Common Palm Civet, *Paradoxurus hermaphroditus* (Pallas)

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Animals possess a behavioral repertoire, which forms the basis of activity patterns. In the present investigation, the behavioral sequences of seven palm civets were observed in captivity during 18:00-06:00 h. The transitions from one behavioral state to another were revealed using a contingency table representing the six behavioral states *viz*., resting, feeding, comfort behavior, social behavior, sniffing behavior and locomotion. The behavior sequences were elucidated using a first order Markov chain model. The hypothesis for the first order Markov chain model against a zero order chain is sustaining in palm civets and the probability of the animal being in a particular state depends on the immediately preceding act and all other past history is immaterial.

The common palm civet, *Paradoxurus hermaphroditus* (Pallas; Family: Viverridae, Order: Carnivora) or toddy cat as is commonly called, is one of the least studied mammals due to its strictly nocturnal and highly secretive nature. Three species of *Paradoxurus* have been recognized. They include *P. jerdoni* of South India (Ganesh, 1997), *P. zeylonensis* of Sri Lanka, and *P. hermaphroditus*, the distribution of which ranges from Sri Lanka and India through China, South East Asia, and Philippines (Anderson & Sclater, 1981; Nor, 1996).

The common palm civets are very good seed-dispersal agents (Bartels, 1964; Ganesh, Ganesan & Soubadra-Devy, 1998; Joshi, Smith & Cuthbert, 1995). The coffee beans expelled through the feces of the palm civets yields a world-renowned coffee (Shiroff). They also feed on small animals like insects, grubs, worms, centipedes, millipedes, lizards, mice, rats, and shrews (Krishnakumar & Balakrishnan, 2003; Rabinowitz, 1991). They are fond of palm juice or toddy and hence the name toddy cat. They are gregarious, with a group size of 5-8 individuals, and live in a wide variety of habitats ranging from wilderness to the vicinity of human settlements. They seek refuge in the wooden attic of tiled houses and create havoc at night.

The palm civets are frugivorous and are considered as very serious pests of fruit crops like cocoa, pineapple, coffee pods, and papaya (Lee, 1996; Veenaku-mari, Mohanraj, & Ranganath, 1996). They wake up at dusk, move to the fields, feed on the ripest of fruits and are back at the attic, their safe and secluded resting spot without any human or animal interference, and thus create disturbance for

humans. Locals report them to be extremely active following a fixed chain of activities except for brief spells of rest. Little is known about the behavior patterns of the palm civet. Although Wemmer (1977) has briefly described some behaviors, they have not been studied in detail. The meaning of the behavior depends on the sequence of individual behavioral acts and not merely on their frequency (Pisula, 1994). A sequential analysis can potentially suggest the causes of their behavior (Slater, 1973). Chase (1974, 1980, 1982a, 1982b, 1985) developed new theoretical methodologies for the study of the sequential properties of behavior in a few species. However, data on mammals is scanty (Bekoff, 1977), more so with viverrids. The present study is an effort to determine whether the palm civets follow a fixed chain of activities, and whether there is any relation between the occurrence of certain behavioral acts and the time of the day. Seasonal differences have not been analyzed because the study was conducted in the southernmost part of India, where the climate is more or less uniform throughout the year with temperatures ranging from 28 to 33°C.

Method

Subjects

The present study was carried out on seven palm civets (three males and four females), which were trapped in and around Trivandrum, India. All the palm civets were approximately 1-2 years old.

The animals were maintained in an open area enclosure of size 3.5 x 3 x 2 m with a fence made of galvanized iron pipes and 25 x 25 mm link mesh. The enclosure also had a door of size 2 x 1 m. The flooring was done with cement. The enclosure also contained one mango and one coconut tree, which were entwined with pepper vines. The bases of the trees were not covered with cement. A 15 W bulb was fitted in the enclosure for nocturnal observation.

The animals were fed once a day at 19:30 h with rice, eggs, and bananas. Occasionally they were also supplied with fish, rats, cockroaches and fruits like pineapple, jackfruit, and papaya based on their availability. Water was supplied ad libitum.

Procedure

Direct behavioral observations were made on the seven animals. They were labeled as M1, M2, M3, F1, F2, F3, and F4. M1 was identified as the dominant male, M2 and M3 as the subdominant males, F1 as the dominant female and F2, F3, and F4 as the subdominant females. This classification was done based on previous studies (Krishnakumar, 2001) on the agonistic behavior of these animals.

The animals were observed using the focal animal sampling method (Altmann, 1974) in three unit observation periods (18:00-22:00 h, 22:00-02:00 h, and 02:00-06:00 h) to maintain stationarity in the data. Two observers were involved in the recording of the data and observer reliability was periodically checked by percentage agreement. Though 95% reliability was considered suitable, reliability usually ranged between 98 to 100%. Observations were made between April 1997 and March 1999. The frequency and transition of behavioral elements was recorded with paper and pencil. Data collected during 2,940 h were used for the analysis.

The analysis involved the use of a transition probability matrix. The transition probabilities were calculated from their corresponding frequencies. Assuming that any behavior may in principle follow any other behavior, transition frequency was displayed in the form of a contingency table (Lehner, 1996). The transition between identical acts was taken as zero (Slater & Olasson, 1972).

On the basis of a one-month preliminary observation period, 52 behavioral acts were identified in the palm civets. The same behavioral act may play a different role in different contexts, but this was taken into account during the grouping of behaviors. There was no overlapping of behaviors

except in the case of exploration where sniffing was combined with locomotion and this has been grouped under locomotion. These behavioral acts were initially categorized into 11 behavioral states on the basis of their functional features: resting, feeding, comfort behavior, socialization, reproductive behavior, vocalization, agonistic behavior, scent marking, play, sniffing behavior, and locomotion. Of these, socialization, reproductive behavior, vocalization, agonistic behavior, scent marking, and play were later grouped together as social behavior because the expected frequencies of these behaviors in the Markov chain analysis deviated from the normal (Fagen & Young, 1978).

Thus, in the present analysis, a transition probability matrix of order six representing the six behavioral states (resting, feeding, comfort behavior, social behavior, sniffing behavior, and locomotion) was estimated for the dominant and subdominant animals of both sexes for all the three time periods.

The following definitions of the behavioral states were used.

Resting. The period of inactivity was considered as resting irrespective of whether the animal kept its eyes open or closed. The animal breathed at a lower pace and suspended all its other activities.

Feeding. Catching insects, digging the ground for worms, grubs, larvae etc., eating and drinking water have been grouped under feeding. At times the animal was involved in active hunting or foraging. All the activities involved in obtaining, handling and ingestion of food were considered as feeding.

Comfort Behavior. The behaviors that enhanced the animals' comfort and body care have been designated as comfort behavior. Licking, nibbling, scratching, head wiping, stretching, yawning, shaking, panting, head and neck rubbing, substrate clawing, anal dragging and flank wiping have been grouped under comfort behavior.

Social Behavior. Vocal communication, acts related to agonistic behavior, scent marking, allogrooming, play and reproductive behavior were considered as social behavior. Sniffing during allogrooming and reproductive behavior has been grouped under social behavior.

Sniffing Behavior. Sniffing was referred to the process whereby, the animal perceived the environmental stimuli through olfaction. Sniffing air, ground, food and other objects in the enclosure were recorded as sniffing.

Locomotion. Locomotion was referred to as a voluntary movement with the ability to displace the whole body. Trotting, walking, climbing, jumping, running, galloping and exploration have been recorded as locomotion.

The transition table of the animals for each unit observation period was subjected to a χ^2 contingency test for testing the first order Markov chain. The animals observed were assumed to be in a steady state, in which the behavioral sequence was stationary and the probable structure of events remained constant through time (Slater, 1973). The specific states that account for temporal dependence were identified, by breaking down the transition table, which was found to be statistically valid (Bishop, Fienbory, & Holland, 1975).

Results

The sequential pattern of behavior varied according to the sexual and social status of the individual concerned. The dominants of both sexes were more active than the subdominants and were found to indulge in resting minimally (Table 1). Feeding was more pronounced in females than in males but comfort behavior was more pronounced in males than in females. In the dominant male and in the subdominant females there were higher instances of social behavior. In the dominant male it was contributed by scent marking and in the subdominant females by play behavior. Sniffing was higher among the subdominants than among the domi-

nants and trotting was higher among the dominants than the subdominants. The dominant male was found to be highly active and aggressive.

Behavioral Transitions

The observed behavioral transitions (Table 2) and the estimated transition probabilities revealed that the pattern of transitions from one act to another for an animal over the different time periods was different. Even though most of the behaviors were observed throughout the day, the behavioral sequences were of longer duration with more behavioral acts during the first time period (18:00-22:00 h) in all the animals observed. The sequences hence, were shorter during 22:00-02:00 h and during 02:00-06:00 h. The appearance and disappearance of behavioral phases were in relation to the time of the day (Figure 1).

Table 1
Analysis of the Frequency Distribution of Behavior.

Behavioral state	Time period (h)	Mean ± Standard Deviation			
		DM	SM*	DF	SF*
Resting	18:00-22:00	30.40±7.54	50.40±7.78	45.04±1.45	48.22±12.65
	22:00-02:00	19.40±12.57	31.00±1.27	18.23±11.42	33.00±10.47
	02:00-06:00	20.40±10.70	30.19±4.90	22.42±2.58	30.53±12.22
Feeding	18:00-22:00	15.60±9.58	17.58±10.25	20.28±8.09	24.27±0.07
	22:00-02:00	8.60±8.26	12.14±9.10	18.10±1.05	18.28±5.05
	02:00-06:00	4.20±2.17	4.20±01.17	5.56±1.28	6.25±2.51
Comfort behavior	18:00-22:00	68.80±14.03	45.28±14.03	37.85±1.63	28.29±10.43
	22:00-02:00	54.40±21.47	28.58±21.47	18.28±13.25	19.18±11.49
	02:00-06:00	45.00±18.07	34.00±1.24	17.70±11.29	20.63±2.85
Social behavior	18:00-22:00	36.00±1.79	18.00±10.79	16.50±12.19	30.27±9.12
	22:00-02:00	43.40±11.76	13.08±11.76	20.52±8.53	27.44±5.38
	02:00-06:00	48.00±10.15	14.24±4.52	17.38±21.09	23.42±2.28
Sniffing behavior	18:00-22:00	35.40±12.69	57.52±23.69	32.43±20.42	51.43±14.49
	22:00-02:00	25.00±12.46	58.00±4.22	23.75±12.51	52.57±13.53
	02:00-06:00	28.00±13.34	52.06±1.26	25.27±2.56	58.88±10.25
Locomotion	18:00-22:00	123.60±28.34	49.53±32.34	85.15±30.04	41.67±34.28
	22:00-02:00	152.40±30.75	51.40±31.12	78.14±29.85	31.25±22.58
	02:00-06:00	127.60±32.14	55.49±28.34	77.10±40.14	38.79±29.67

Note. DM: Dominant male; SM: Subdominant males; DF: Dominant female; SF: subdominant females. Mean values for subdominants ± Standard Deviation.

Table 2
Mean Transitions Observed During a Day.

Time period (h)	Mean transitions observed during a day			
	Males		Females	
	Dominant	Subdominants*	Dominant	Subdominants*
18:00-22:00	373.04±40.25	202.36±25.34	235.15±42.34	190.27±40.42
22:00-02:00	347.42±23.63	163.59±40.49	176.52±41.24	170.43±51.09
02:00-06:00	277.17±22.47	151.89±33.58	167.27±32.54	148.45±21.22

Note. * Mean values for subdominants ± Standard Deviation

The mean transition values in the dominant male were significantly higher during 18:00-22:00 h, $\chi^2(2) = 50.86$; $p < 0.001$, during 22:00-02:00 h, $\chi^2(2) = 66.38$; $p < 0.001$, and during 02:00-06:00 h, $\chi^2(2) = 37.10$; $p < 0.001$, than in the subdominant males. Thus, the behavioral sequences were longer in the dominant male than in the subdominant males. But in the case of females, there was no significant difference in the length of the behavioral sequences during any time period. The mean transition values in the males were significantly higher during 18:00-22:00 h, $\chi^2(6) = 58.06$; $p < 0.001$, during 22:00-02:00 h, $\chi^2(6) = 95.50$; $p < 0.001$, and during 02:00-06:00 h, $\chi^2(6) = 27.80$; $p < 0.001$, than in females. Thus, the behavioral sequences were longer in males than in females.
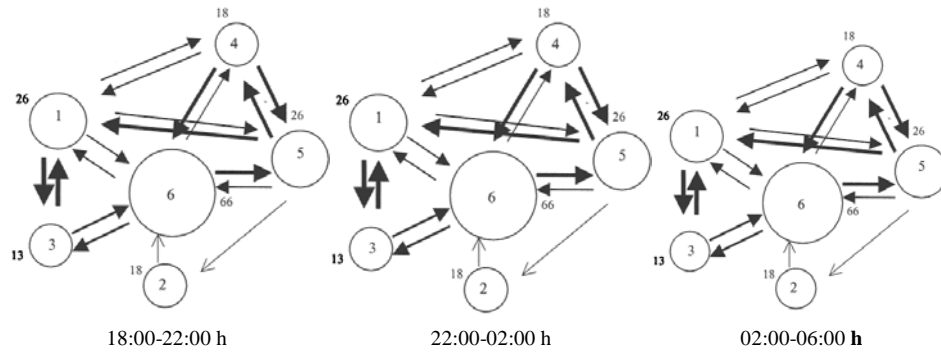

| 18:00-22:00 h | 22:00-02:00 h | 02:00-06:00 h |

Figure 1. Kinematic graphs showing the transition of behavioral acts during the three time periods. The size of the circle indicates mean frequency of behaviors and the width of the arrows shows mean transition probabilities. The numbers inside the circles show the behavioral states. 1: resting; 2: feeding; 3: comfort behavior; 4: social behavior; 5: sniffing behavior; 6: locomotion

Markov Chain Model

The calculated χ^2 values from the transition tables for testing the first order Markov chain model during the different time periods are shown in Table 3. These are significant at 25 degrees of freedom. Thus, the hypothesis of a first order Markov chain was supported in the behavior pattern exhibited by palm civets during the three time periods.

Table 3
Calculated χ^2 Values for Testing the First-Order Markov Chain Model.

Time period (h)	Males		Females	
	Dominant	Subdominants*	Dominant	Subdominants*
18:00-22:00	90.62*	81.57*	95.43*	45.70**
22:00-02:00	127.17*	63.85*	117.91*	43.49***
02:00-06:00	130.49*	68.24*	79.91*	59.92*

Note. * Mean values for subdominants ± Standard Deviation, * Significant at 0.1% level, $\chi^2_{0.001, 25} = 52.62$, ** Significant at 1% level, $\chi^2_{0.01, 25} = 44.31$, ***Significant at 5% level, $\chi^2_{0.05, 25} = 37.65$

Table 4
Relationship of each Behavioral State in the Sequential Pattern of Behavior.

Time period (h)	State	Directing states				Inhibiting states			
		DM	SM*	DF	SF*	DM	SM*	DF	SF*
	1	3,6	3,5,6	3,6	3,6	2,4,5	2,4	2,4,5	2,4,5
	2	6	6	6	1,5,6	1,3,4,5	1,3,4,5	1,3,4,5	3,4
18:00-22:00	3	1,6	1	1	1,6	2,4,5	2,4,5,6	2,4,5,6	2,4,5
	4	3,6	3,6	6	1,6	1,2,5	1,2,5	1,2,3,5	2,3,5
	5	2,4,6	1,2,3,6	2,4,6	2,6	1,3	4	1,3	1,3
	6	1,2,3,4	3,4,5	2,4,5	1,3,4,5	-	-	3	2
	1	3,6	3,6	3,6	3	2,4,5	4,5	2,4,5	2,4
	2	6	1	6	6	1,3,4,5	3,4,5	1,3,4,5	3,4,5
22:00-02:00	3	1,6	4,6	1,6	1,6	2,4,5	1,2	2,4	2,4,5
	4	6	3,6	3,6	6	1,2,3,5	1,2,5	1,2,5	2,5
	5	2,6	2,6	2,6	2,4,5	1,3,4	3,4	1,3,4	3
	6	1,2,3,4,5	4,5	1,4,5	2,3,4,5	-	-	2,3	1
	1	6	2,3,6	3,6	2,3,6	2,4,5	4,5	2,4,5	5
	2	3,6	1,6	6	6	1,4,5	3,4,5	1,3,4,5	1,3,4,5
02:00-06:00	3	6	1,6	1,6	1,6	1,2,4,5	2,4,5	2,4,5	2,4,5
	4	6	1,3,6	6	6	1,2,3,5	2,5	1,2,3,5	1,2,3,5
	5	2,6	2,6	2,6	2,6	1,3,4	1,3,4	1,3,4	1
	6	1,2,3,4,5	3,4,5	1,3,4,5	1,3,4,5	-	2	-	2

Note. 1: Resting behavior; 2: Feeding behavior; 3: Comfort behavior; 4: Social behavior; 5: Sniffing behavior & 6: Locomotion. DM: Dominant male; SM: Subdominant males; DF: Dominant female; SF: Subdominant females. * Mean values for subdominants ± Standard Deviation

Table 5
Trends of Directing and Inhibiting Acts of the Six Behavioral States.

Animal	Behavioral states*	Directing act	Inhibiting act
Dominant male	1	3,6	2,4,5
	2	6	1,3,4,5
	3	1,6	2,4,5
	4	6	1,2,3,5
	5	2,6	1,3,4
	6	1,2,3,4,5	-
Subdominant males*	1	3,6	2,4,5
	2	1,6	3,4,5
	3	1,6	3,4,5
	4	3,6	1,2,5
	5	2,6	1,3,4
	6	3,4,5	1,2
Dominant female	1	3,6	2,4,5
	2	6	1,3,4,5
	3	1,6	2,4,5
	4	6	1,2,3,5
	5	2,6	1,3,4
	6	1,4,5	2,3
Subdominant females*	1	3,6	2,4,5
	2	6	1,3,4,5
	3	1,6	2,4,5
	4	6	1,2,3,5
	5	2,6	1,3,4
	6	1,3,4,5	2

Note. * States 1-6 as in Table 4. *Mean values for subdominants ± Standard Deviation

Temporal Dependence Among the Behavioral States

Discrimination of the behavioral states as "directing" and "inhibiting" are shown in Table 4. By observation of the data in Table 4, it is seen that each of behavioral state in the different groups of palm civets during each time period either direct *viz.*, lead to or inhibit other behavioral states (Table 5). Behavioral states, which are directing do not inhibit and vice versa. It is seen in the dominant male that locomotion directed all other behavioral states and 'inhibited' none during all the three time periods.

Discussion

Certain pairs of behaviors are more likely to occur in one order than in another. Behavioral acts may be closely associated because of common causal factors or because one act would generate or inhibit another. The stimulus releasing a pattern of behavior is likely to last for sometime, producing repetitions of the same response, to attain a particular physical or mechanical effect or to emphasize the purpose of the signal (Lovari & Locati, 1991). The change over from one behavioral state to the next depends in part on the response produced by an external stimulus and also on the detrimental effects consequent upon the performance.

In the present study, the dominant animals showed higher number of transitions than the subdominant ones. Also the activity levels of the dominants were higher than those of the subdominants (Krishnakumar, 2001).

The behavior patterns of the palm civets follow the first order Markov chain model during the three time periods. A similar result was reported earlier in black bucks (Jayarani, Kalyanaraman, & Balakrishnan, 1988). The modeling of the behavior patterns using a first order Markov chain assumes that the probability of occurrence of a given act depends on the immediately preceding act and all other past history is immaterial (Martin & Bateson, 1993).

Resting, drinking, comfort behavior, and exploration are considered as alternative activities (Barnett et al., 1978). The palm civets were found to indulge in comfort behavior or locomotion after any of the six behavioral acts. Comfort behavior, which comprises of acts like licking, nibbling, scratching, and face wiping, has a prominent role in thermoregulation and in the control of ectoparasites. It is also aimed at maintaining social cohesion among individuals in a group (Manning & Dawkins, 1995). Grooming was once classified as a displacement activity (McFarland, 1969), which occurs in several situations (e.g., physical thwarting of appetitive behavior, thwarting of consummatory behavior by the removal of its object or goal and simultaneous activation of incompatible tendencies; McFarland, 1999). Grooming is common especially during exploration (Pisula, 1994). Feeding and locomotion are among the primary requirements of any animal. In natural habitats, the animals may have to move long distances to meet their dietary requirements. The occurrence of an act like feeding, not only inhibits further feeding (Booth, 1976), but also releases alternative activity and is similar to disinhibition (McFarland, 1969). The causal factors of the first act may be assumed to have declined so that exploratory behavior was no longer inhibited.

Thus the data on palm civets reveal three major findings: the dominant animals had higher number of transitions than the subdominant ones, the probability of the animal performing comfort behavior or locomotion after any other behavioral act was higher, and the behavioral patterns of the palm civets followed the first order Markov chain model. These findings could be used in the pest management of the common palm civet.

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