ON THE TIME-BUDGET OF DIFFERENT LIFE-HISTORY STAGES OF CHITAL (*AXIS AXIS*)

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(*With two plates, four sketches and five text-figures*)

INTRODUCTION

Any animal has to undertake a variety of activities in order to survive, grow and reproduce. A male baya weaver-bird in the breeding season, for example, has to collect nesting material, weave his nest, defend the nesting area against intruding males, display to the attendant females, feed, drink, sleep and so on. Each of these activities has a certain benefit and a certain cost attached to it. Reducing the time spent in feeding may enable a male to complete the nest more quickly and display more towards intruding males and receptive females. However, he may at the same time be exposed to a greater risk of mortality through physical exhaustion. Shifting the emphasis from threatening intruding males to collection of nest material, may allow him to construct the nest more quickly, while at the same

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time render him more susceptible to the usurpation of his territory. Obviously all these trade-offs have to be balanced for an appropriate decision regarding the proportion of time to be allocated to each activity. The calculation of such trade-offs and hence the appropriate time-budget will depend on the criterion that the animal wants to maximise. We do not of course imply that the animals consciously choose a criterion and then allocate their time amongst various activities through appropriate calculations of cost and benefit attached to each activity. Rather, we make the assumption that the criterion is genetic fitness, and that the natural selection has moulded the time-budget of any animal so as to maximise its genetic fitness.

A study of such time-budgets can be expected to throw much light on how the behaviour of any organism is structured in relation to its ecology. Fagen (1974), for example, has shown that natural selection should favour the allocation of a larger

fraction of time towards play activity in the juvenile phases of the life-history. MacFarland (1977) makes a much finer analysis and shows how natural selection moulds the proportion of time devoted to and sequence of the various components of a male newt's courtship display. The whole study of time-budget is, however, in a primitive stage, and very few good time-budgets are as yet available (Wilson 1975). Here we analyse the time-budget of spotted deer or chital (*Axis axis*), a highly social deer species of the oriental region, with particular emphasis on the variation in the time-budget at different stages of the animal's life-history.

MATERIAL AND METHODS

The Environment :

The observations reported here were carried out on a herd of chital in the vicinity of the lodges at Bandipur Tiger Reserve in Karnataka (11°39'N and 76°37'E). This herd inhabits a very open, dry deciduous forest interspersed with extensive grassy glades. The tree canopy is dominated by *Anogeissus latifolia*, and the shrub layer by *Lantana camara.* The herb layer is predominantly made up of grasses, although there are extensive patches of *Eupatorium* in places. The mean annual temperature of Bandipur is 20°C, and the mean annual precipitation 1000 mm. The dry season when forest fires occur runs from January to March, when the deer consume considerable browse and fruit. Good rains at the onset of south-west monsoon occur in April-May, followed by a relatively dry spell in June. There is a second peak of rainfall in October corresponding to the north-east monsoon, though the rains continue all the way from July to November. The deer largely consume grasses in this wet period.

The Animal :

The chital, with its coat adorned by white spots, is one of the most handsome deer in the world. It is a medium-sized animal, with adult females weighing around 35-45 and males upto 60 kilograms. The large males grow antlers upto 90 cm in length. This animal's attractiveness is greatly enhanced by its social habits, herds of over a hundred animals not being uncommon in the early monsoon season. After September the herds break up into much smaller units, even as small as two or three animals in the dry season in January-March. The rutting season of the deer coincides with the south-west monsoon. This is when a majority of males are in the hard antler stage, and large bisexual herds are formed. Antlers are shed from September to November, and outside of the rutting season the males tend to form small bachelor herds. The males' antlers are largely in velvet in the dry season from December-March, which is the hardest season for the animals ; but also happens to be the period when most fawns are dropped (Schaller 1967, Sharatchandra and Gadgil 1975).

Chital is the commonest of the resident larger herbivores of Bandipur Tiger Reserve, a population of about 800 inhabiting an area of 20 square kilometres in the vicinity of lodges in the tourist zone. This population is organized rather loosely in herds which do change considerably in strength and composition over the year. One of these herds spends the night on the lodge grounds and forages during the day-time in the forest to the north of the lodge towards Bolugudda hillock. Its strength over the year varies from 80 in the monsoon season, to around 30 in the driest period. Most of the observations presented here are based on the animals of this particular herd.

The Observations :

We have computed the time-budget of chital on the basis of a recording of behavioural sequences of individual animals. The method followed was to focus randomly on an animal without any bias in respect of an animal indulging in a more conspicuous activity. Having focused on an

animal, a record was maintained of the date, time of day, the stage in life-history of the animal, and the number of seconds spent on each activity till the animal went out of sight. The time spent on each activity was recorded with the help of a stop-watch accurate to 0.1 seconds. As soon as the focal animal went out of sight, another animal was picked up, again at random and its behavioural sequence recorded and so on. Over 6500 such behavioural sequences have been recorded over a period of twelve months from October 1975 to September 1976. The observations were restricted to day time from 0530 to 1900 hours. These behavioural sequences were subsequently coded and punched on computer cards. This data was utilized to calculate the time-budget of each life-history stage, and for each season after due corrections for the bias introduced by the fact that observations were concentrated to the dawn and dusk hours when the animals are most active. Here we present the data on the time-budgets of the various life-history stages for the year as a whole.

The Life-History Stages :

While maintaining the field observations, chital were classified into one of the following four major categories and twelve sub-categories :

(1) Juveniles : Immature animals below the age of a year. These were further classified into babies upto the age of 3 months and fawns beyond the age of 3 months (Plate I).

(2) Adult females : These were not classified any further (Plates I, II).

(3) Adult males in velvet : This category included the five sub-categories of shed antlers, and velvet antlered males with antlers less than 25 cm, between 25-50 cm, between 50-75 cm and over 75 cm in length. No particular significance attaches to the antler sizes though as the antlers in velvet continue to grow till the velvet is shed and do not necessarily reflect the ultimate size reached.

(4) Adult males with hard antlers : It is the adult males in hard antlers that are active in social displays, agonistic and sexual activities, and therefore of greatest interest. The yearling males have the so-called spike antlers less than 25 cm in length. Older males have antlers which appear to grow in size with body size. They have been classified in three more categories : antlers between 25 to 50 cm, between 50 to 75 cm and over 75 cm in length (Plate II).

The Activities :

On the basis of our earlier observations at Bandipur from May 1974 to September 1975, we divided the activity pattern of chital into the following 8 major categories, with 29 sub-categories :

(1) Locomotion : Subdivided into (a) walking, (b) running and (c) trotting.

(2) Anti-predatory behaviour : Chital is the major prey species of the three predators of Bandipur—wild dog, panther and tiger, and the deer spends a significant fraction of its time in antipredatory behaviour. The three sub-categories we use are (a) standing, scanning for anything suspicious, (b) an alert posture with the neck outstretched pointing in the direction of the disturbance and (c) giving alarm signals which include tail raising, alarm calls, stamping the ground with forefoot, and when actually confronted with a predator stotting and bunching into a tight herd.

(3) Grooming behaviour includes (a) licking itself (sketch 1), (b) scratching itself, (c) being licked and (d) licking another deer. The last two categories involve mother licking her fawn, and a fawn licking its mother.

(4) The trophic behaviour which dominates at all seasons includes—(a) scanning for fallen fruit, (b) pushing in competition for food items, (c) drinking, (d) feeding, (e) standing and chewing, (f) ruminating, (g) drinking mother's milk, (h) nursing a baby (Plate I).

(5) Fighting, which includes pushing and

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thrashing with forelegs amongst females (Plate I) and shed antlered males, and sparring with antlers in hard-antelered males (Sketch 2). Butting to initiate a fight is also included.

(6) Play, includes the seemingly non-functional vigorous physical activity of the juveniles and yearling males with spike antlers.

(7) Displays : The males, almost exclusively those in hard antlers, indulge in a variety of displays : (a) preaching, includes thrashing the vegetation with forelegs while rearing up, (b) rubbing forehead and preorbital glands on vegetation (Sketch 3), (c) rubbing antlers on vegetation, (d) hitting antlers vigorously, generally on a bush,

(e) giving rut calls. These displays involve a single individual. In (f) dominance display, a male approaches another sideways with head held high and to a side (Plate II). The responding male may ignore the challenge, continuing to feed, or whatever else he was doing, join in a sparring bout or respond with a (g) submissive display which involves moving off with a lowered head.

(8) Sexual behaviour includes (a) male sniffing at the female's vagina (Sketch 4) and (b) mounting another individual. Mounting may involve female-female as well as juvenile-female mountings also, (c) the very rare behaviour of a female soliciting (Plate II).
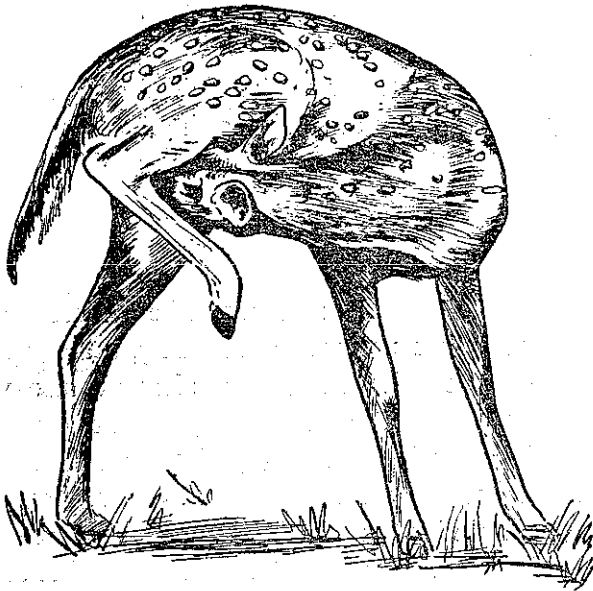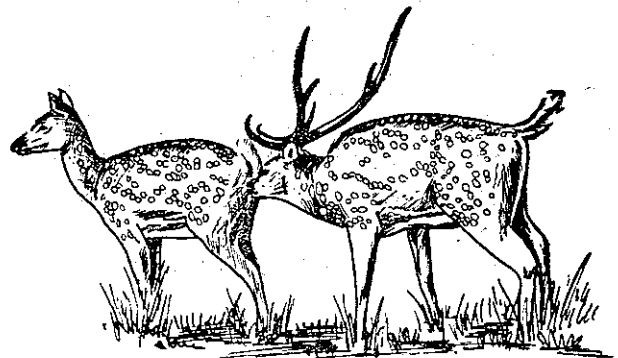

Sketch 1. Grooming : Chital doe cleaning by licking its underparts (after a photograph)
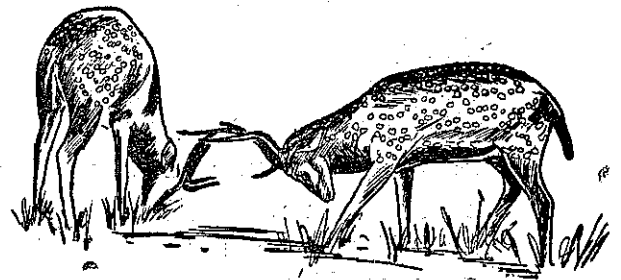
Sketch 2. Sparring match : The males generally spar with other males of the same size class (after a photograph)
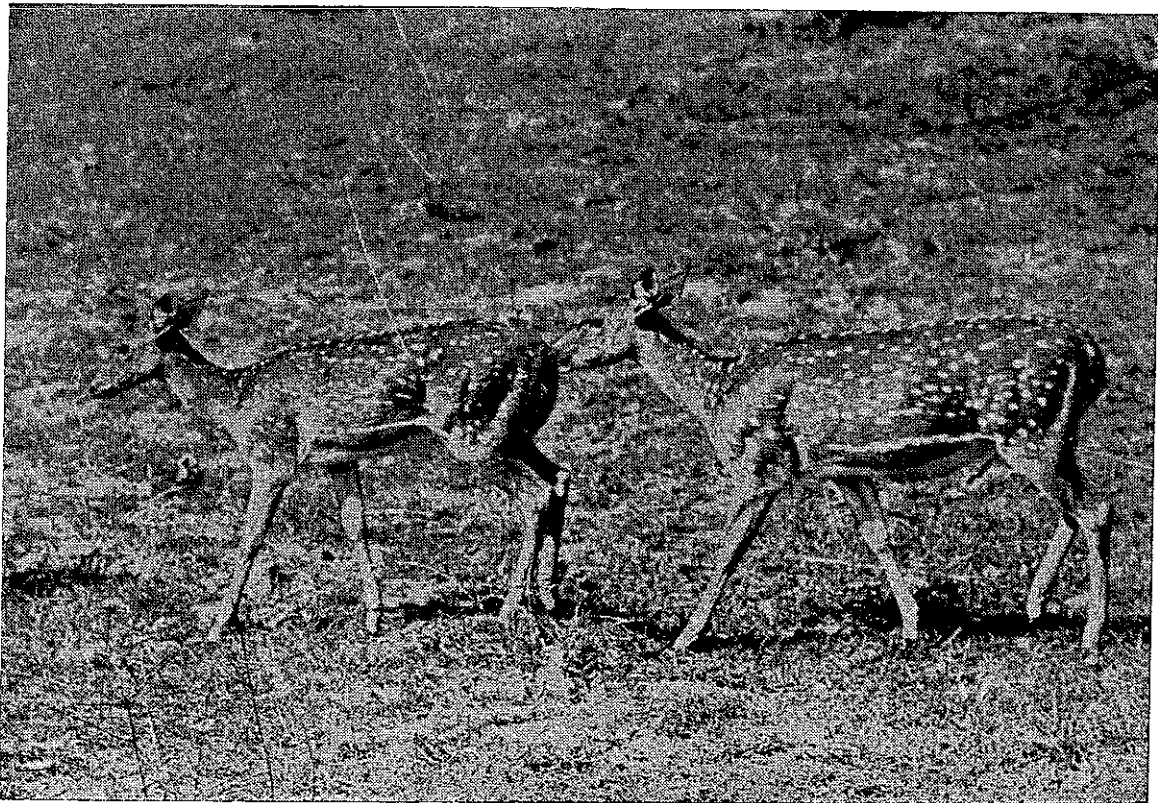

Sketch 3. A chital stag sniffing, after rubbing the preorbital gland on a tree trunk. Note the erection of the penis (after a photograph)

Sketch 4. Chital stag sniffing the vagina of the oestrus doe. Note the submissive posture of the stag (after a photograph).
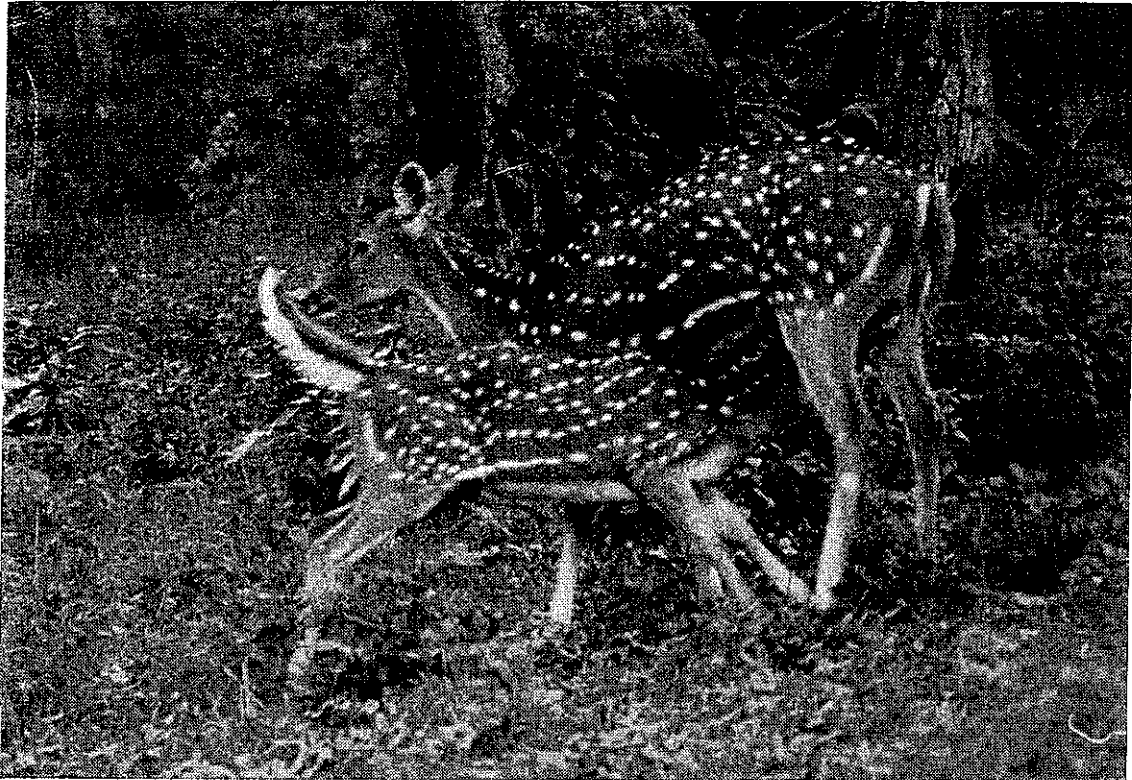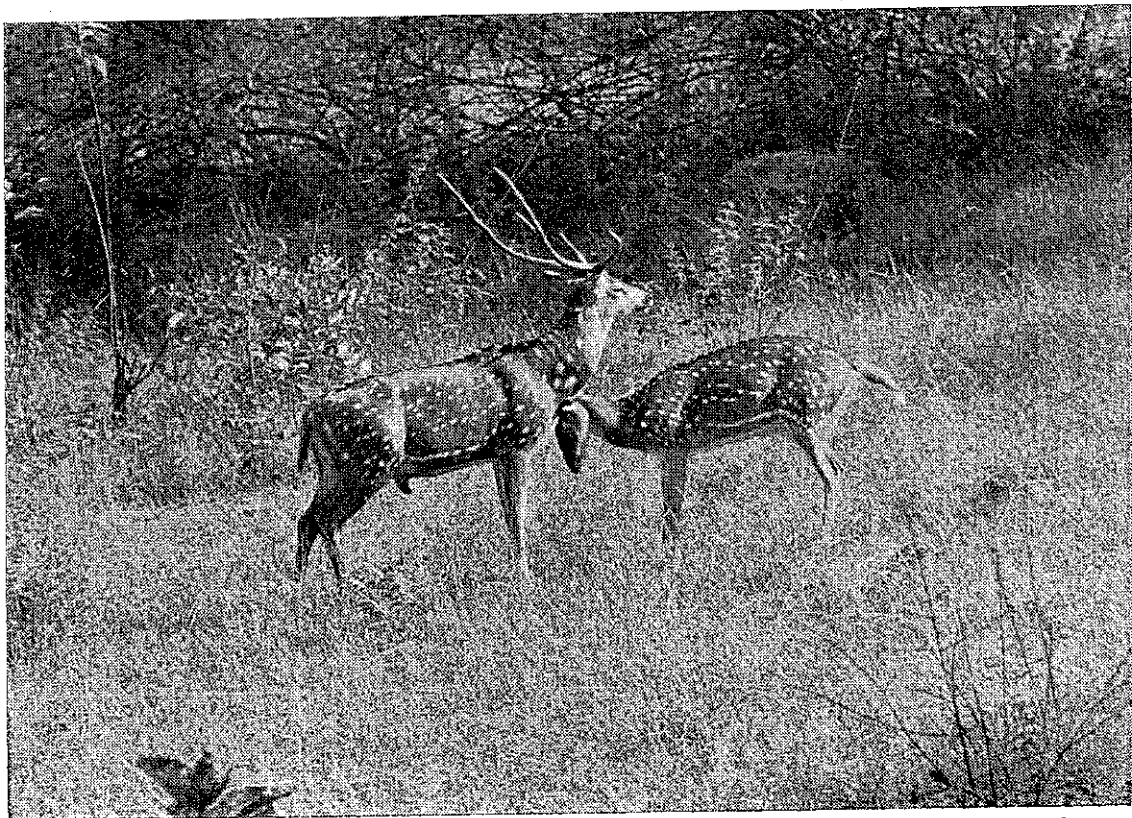
Chital nursing a fawn.

Chital doe pushing another doe.

Sharatchandra and Gadgil: *Axis axis*

Stags challenging each other. Note the position and angle at which the neck is held.

Chital doe courting a stag.

RESULTS

(1) Trophic activities occupy an overwhelmingly large fraction of chital's time followed by anti-predator activities, fighting, displays, locomotion grooming, play and sexual activities (figs. 1 and 2).

(2) Males in hard-antlers devote less time to trophic activities, and much more time to display, fighting and to locomotion than the other life-history stages (figs. 1 and 2).

(3) Females devote a greater fraction of their time to anti-predatory activities (fig. 1).

(4) Play is particularly prevalent amongst juveniles and spike males (figs. 2 and 3).

(5) Sexual activities are restricted to juveniles and hard antlered males. Amongst the latter, they are monopolised by males with antlers over 75 cm in length (figs 2 and 5).

(6) Displays such as preaching, rubbing antlers and hitting antlers are particularly prevalent amongst males with hard antlers between 50 and 75 cm in length (figs. 4 and 5).

(7) Dominance displays are common amongst males with antlers between 25 to 50 cm in length, and over 75 cm in length. Note that the class with intermediate size antlers is notable for lack of dominance displays. At the same time sub-missive displays are almost restricted to males with antlers over 75 cm in length. Fighting is particularly common in males with antlers bet-ween 25 cm and 50 cm and between 50 cm and 75 cm. Pushing is common in males with antlers between 50 to 75 cm in length (figs. 3, 4 and 5).

(8) Sexual activities such as sniffing and mount-ing are quite common amongst the fawns and as mentioned above, to males with hard antlers over 75 cm in length (fig. 5).

DISCUSSION

Two of these results, namely the greater pre-valence of antipredatory behaviour amongst the females, and the distribution of the display, agonis-

tic and sexual behaviour in the various classes of hard-antlered males deserve further discussion.

Antipredatory Behaviour

Chital is a highly social species, and the avoi-dance of predation appears to be the prime moving cause of its sociality (Hamilton 1971). Field observations on the predation on chital by wild dogs indicate that any animal which strays off from the herd is particularly susceptible to predation (A. J. T. Johnsingh, personal communi-cation). When the predators approach a herd of chital, the deer respond by forming a tight bunch. There is no active defence against the predators, and in fact the stronger males force their way into the centre of the herd. This leaves those animals forced to stay on the periphery, mostly females, much more susceptible to predation, and again Mr. Johnsingh's field data seem to indicate that females do suffer heavier mortality through predation. It would therefore appear that females have been selected to be much more alert, since only through an early awareness of the danger could they stand any chance of getting to the safety of the centre of the herd. The stronger males on the other hand can force their way to the centre of the bunch even if they are alerted a little late, and hence do not allocate as much time to antipredatory behaviour as do females. The juveniles are maximally susceptible to predation, but do not exhibit as much antipredatory be-haviour as do the females. Presumably, the juveniles depend on the mothers to be warned of danger, and in fact they always stick to their mothers.

Display, Agonistic and Sexual Behaviour

In chital, as with many other mammalian species, there is evidence that while all females are success-ful in reproduction, only a small fraction of males monopolises all breeding. Sharatchandra and
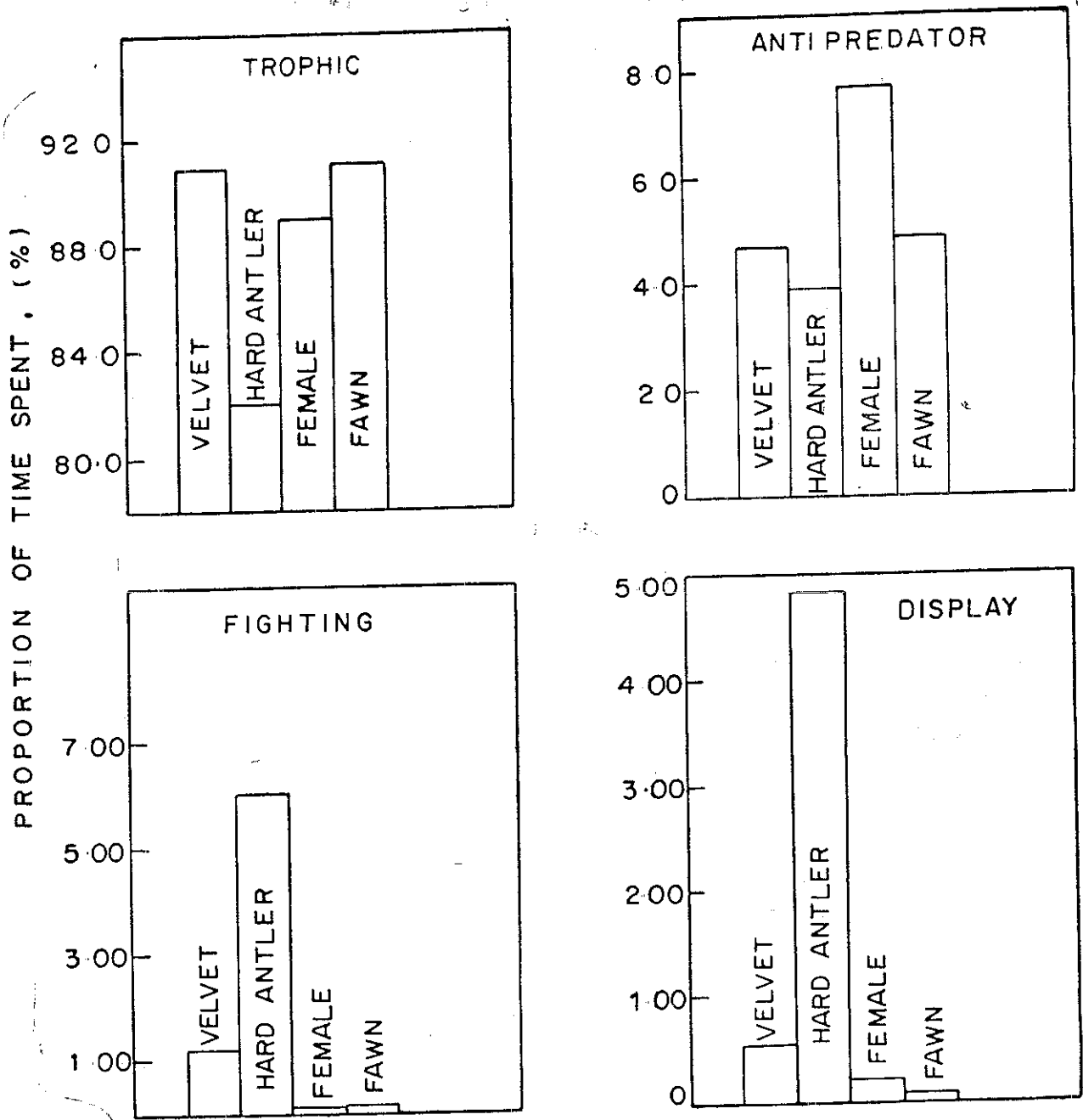
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Fig. 1. Histograms showing the proportion of time spent on trophic, anti-predator, fighting and display activities by different life-history stages of chital
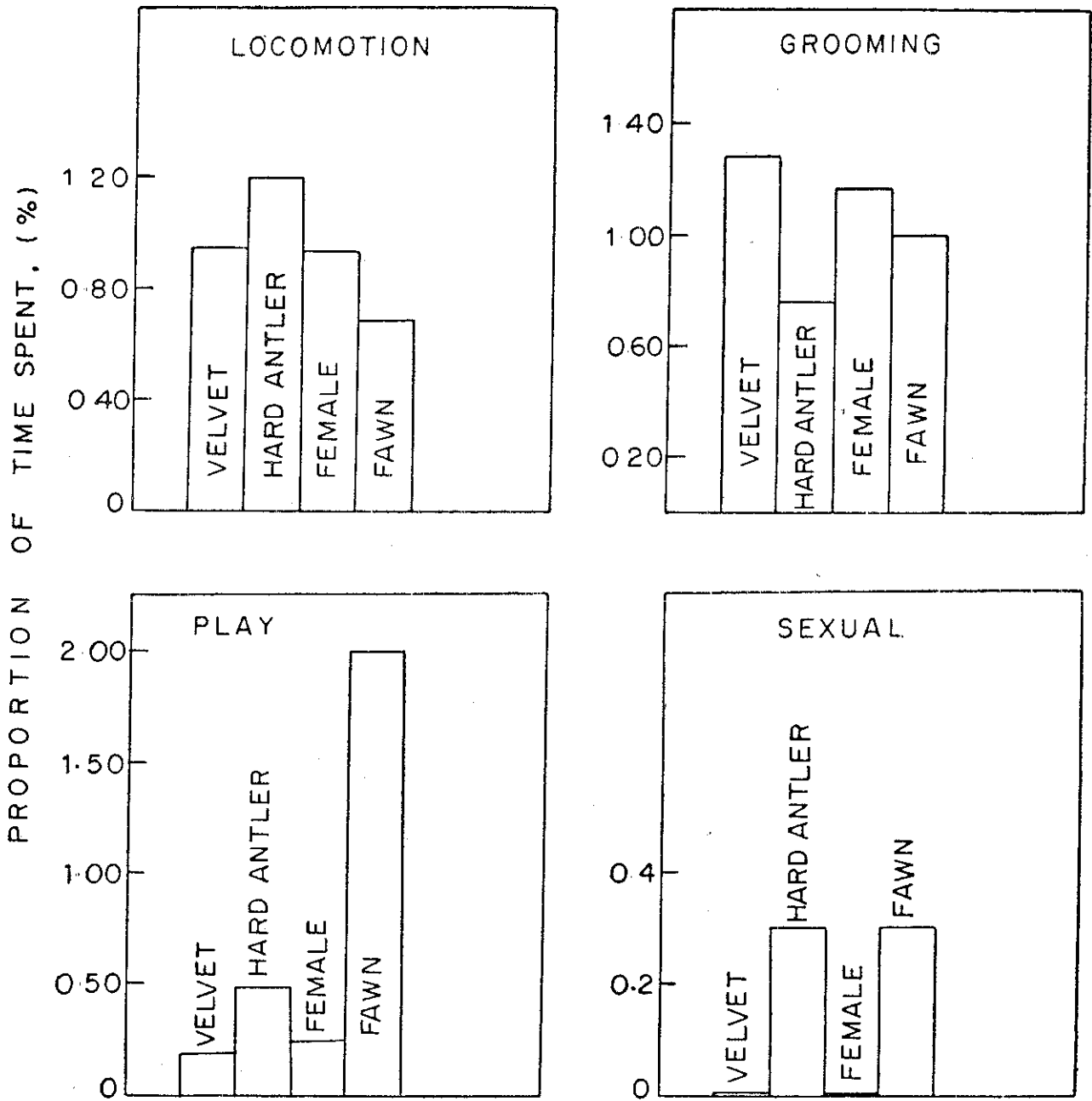
Fig. 2. Histograms showing the proportion of time spent on locomotion, grooming, play and sexual activities by different life-history stages of chital.
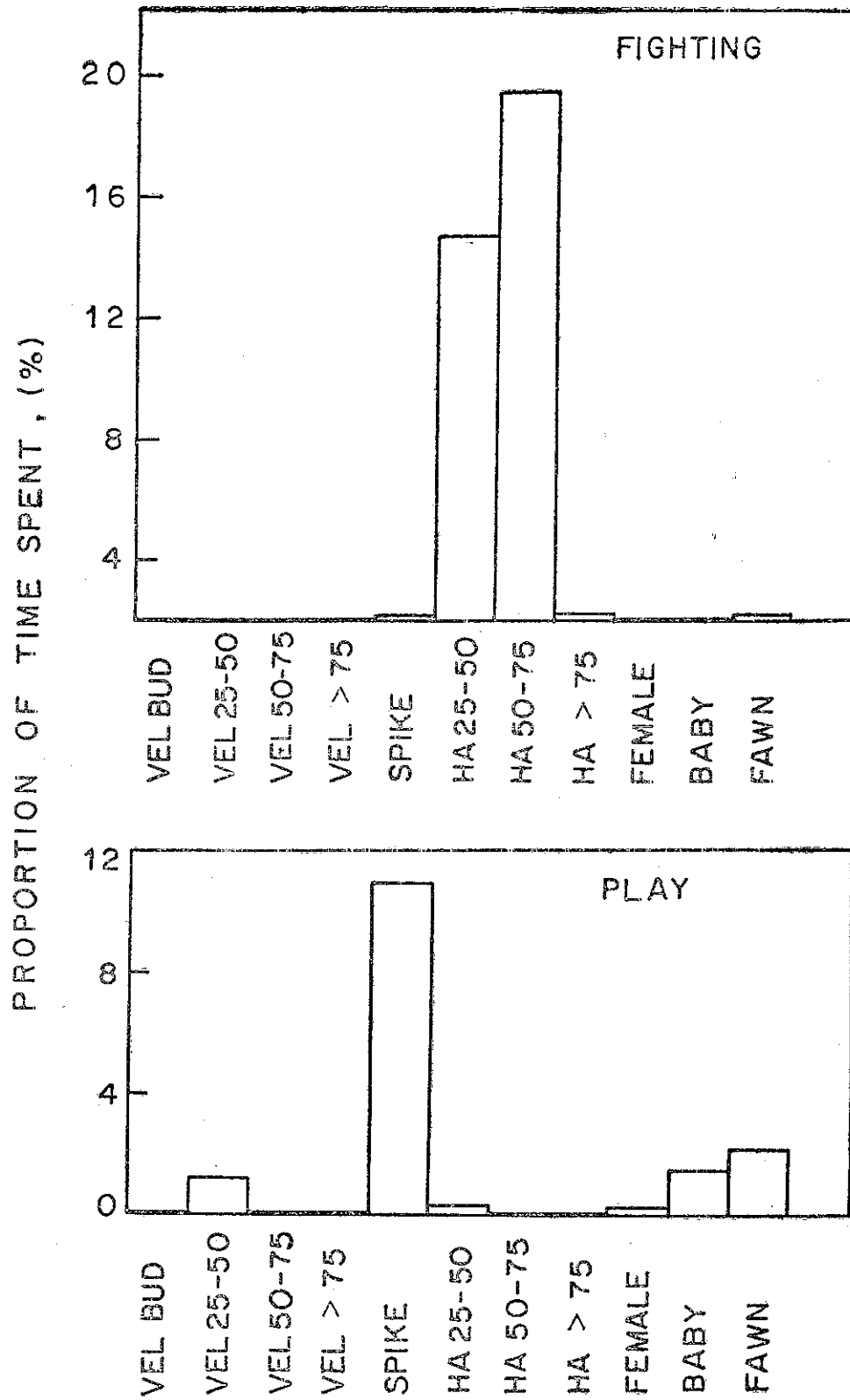
Fig. 3. Histograms showing the proportion of time spent in fighting and play among different life-history stages of males, females, baby and fawn
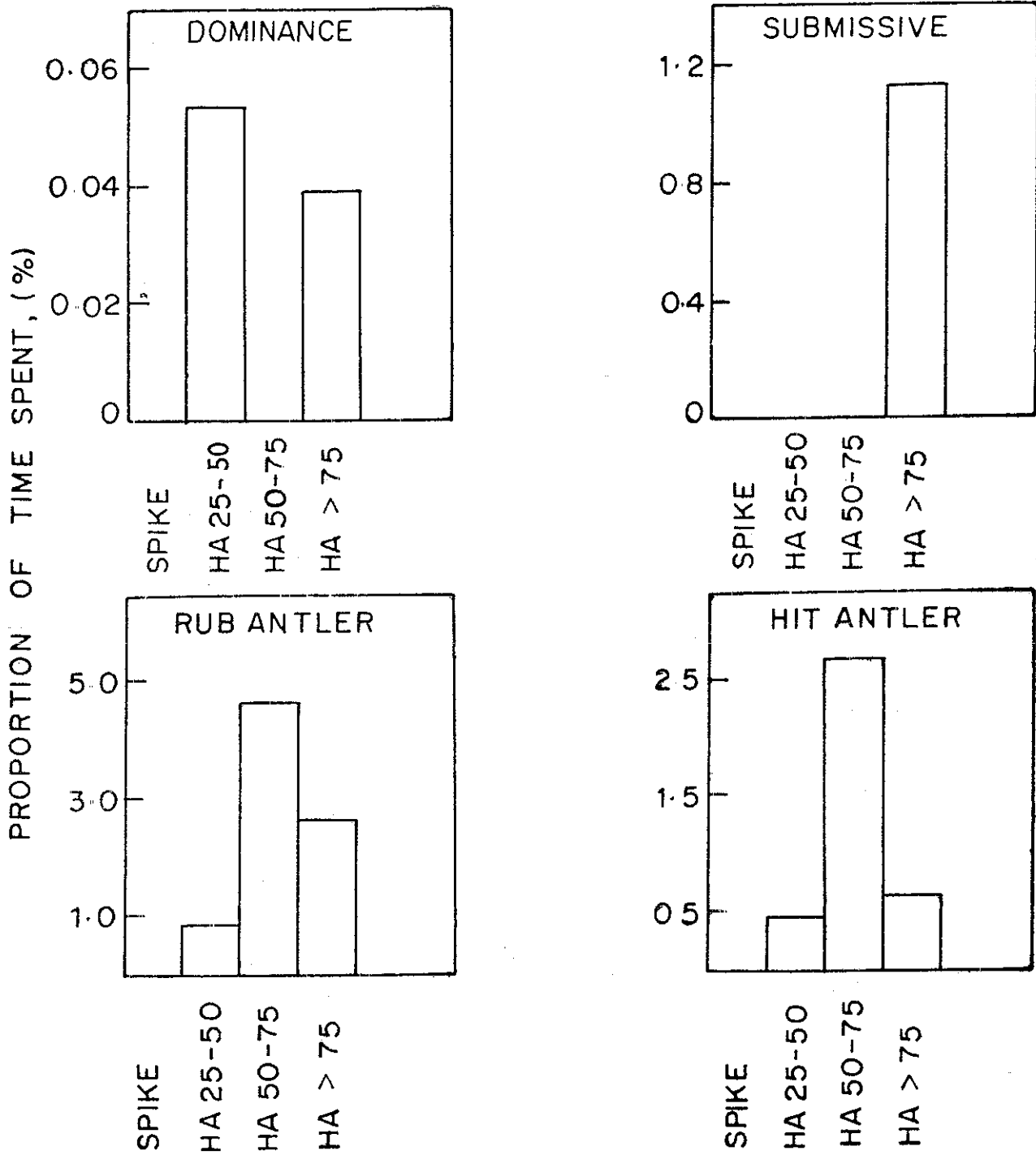
Fig. 4. Histograms showing the proportion of time spent on dominance, submissive, rubbing and hitting antlers among different life-history stages of males in hard antler.
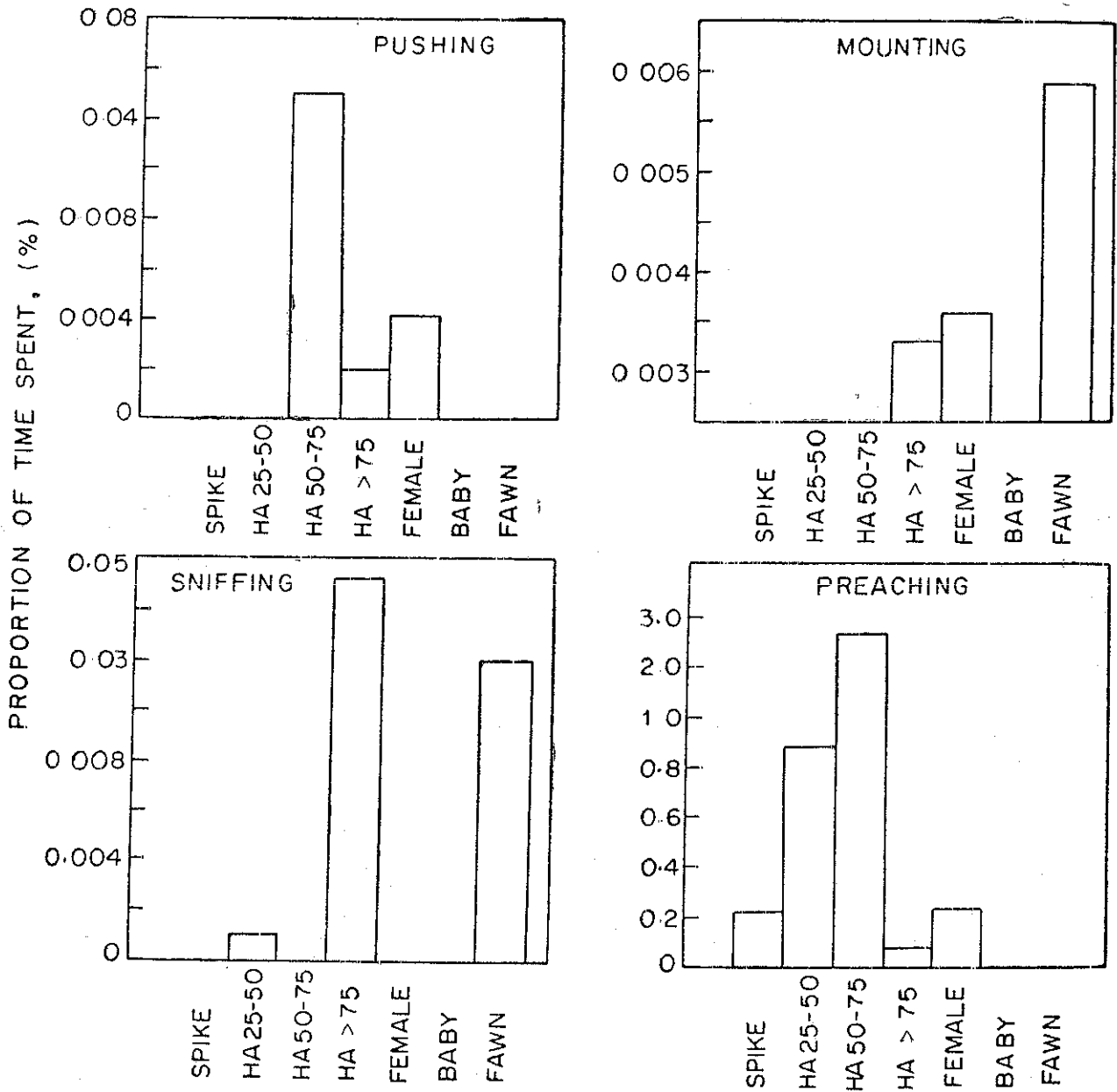
Fig. 5. Histograms showing the proportion of time spent on pushing, mounting, sniffing and preaching activities by different life history stages of males in hard antlers, females, baby and fawn.

Gadgil (1976) from their earlier study of the dynamics of the chital population of Bandipur conclude that the birth rate appears to be such that all adult females fawn once a year. On the other hand, our present study indicates that only males with antlers over 75 cm have sexual access to the females. It is of course possible that even of the males in this class, not all are successful in breeding. In any case, only a small fraction of males can breed successfully, and as Trivers (1972) points out, this would generate intense selection pressures amongst the male sex to be included amongst the males who are successful in breeding. The tremendously higher level of display and agonistic activities amongst the adult males is clearly related to the male-male competition generated by these selection pressures (fig. 1). As this figure shows males indulge in these activities, particularly when they are in the hard-antlered stage, when antlers can be safely employed in sparring.

The male population is composed of several overlapping age and size classes. The males continue to grow in size for several years, and the size of antlers is positively correlated with body size. As the males approach their prime, therefore, they must slowly grow into the size class which includes the males who succeed in breeding. However, if all males automatically grew to the size at which they are successful in breeding, we would not expect the tremendous investment that the males make in display and agonistic activities. It is likely that the growth rate itself depends on success in competition, and also that not all of the bigger males are equally successful in breeding.

It is evident that all adult males are engaged in a continual struggle, particularly during the breeding season, to succeed in reproduction either immediately, or acquire a size and status so as to succeed in reproduction in coming years. The particular combination of display, dominance, submission and agonistic activities employed by a male can then be assumed to have evolved so as to maximise his chances of doing so.

Our results suggest that the strategy adopted by males to accomplish this changes in a most interesting fashion over the four different antler size-classes. The males with spike antlers are first year males. They engage a great deal in what has been classified as play, and involves jumping around vigorously and kicking with hindlegs in the air. They also do some preaching. Apart from this they do not indulge in any display or agonistic activities. Males with antlers between 25 and 50 cm in length engage to a considerable extent in displays like hitting antlers. They also engage quite a bit in fighting and pushing. The fights are initiated generally by a dominance display which may be ignored or responded to with a fight. There is no submissive display. They may sniff female's vagina, but do no mounting. The male-male competition reaches its highest pitch in males with antlers between 50-75 cms in length. This is the size-class, just below the class which breeds successfully. These males give displays such as hitting antlers maximally. The fighting in this group appears compulsive. The fights are initiated not through dominance displays, but by a direct butt with a lowered head. This invariably leads to a fight. These males however do not get a chance at any sexual activity.

The males with antlers over 75 cm in length are the only ones to participate in sexual activities. They indulge very little in other displays such as preaching and hitting antlers. They are the only class of males to give rut calls. They challenge other males with a dominance display. The challenge is generally responded to by a submissive display, and only in a small fraction of cases does it lead to fighting. Overall it appears as if there is a strong selection against actual fighting, perhaps because the energy cost involved or the risk of injuries is very high, or simply because the hierarchy in this group is rather rigidly established, most fights occurring between males of similar sizes. A more detailed explora-

tion of this shift in strategy of male competition with marked individuals, and a theoretical exploration of how changing selection pressures bring about a change in strategy would be most interesting to pursue.

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