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Diurnal Births and Perinatal Behavior Among Wild Patas Monkeys: Evidence of an Adaptive Pattern

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Data from a 2-year field study of patas monkeys (Erythrocebus patas) *in Kenya support our earlier suggestion that diurnal births are a species-typical pattern of patas. In this respect patas are very unusual, as all existing information shows that nocturnal births are typical of both captive and free-ranging monkeys. Patas do not give birth at night because to do so would render ineffective their night-resting strategy which reduces vulnerability to predation at night. Giving birth during the day, however, does not eliminate the risk of being preyed on; nor are all times of day equally favorable for giving birth. Our field data suggest that a patas female gives birth at those times of day when she is least likely to lose contact with her group or to encounter predators.*

KEY WORDS: patas monkeys; field study; diurnal births; perinatal behavior; predation; adaptive behavior.

INTRODUCTION

Reviews written in the early 1970s, primarily on the basis of captive studies, indicated that nocturnal births are normal for Old World monkey species (Brandt and Mitchell, 1971; Jolly, 1972). Since the publication of these reviews, a few additional reports of diurnal births in the field have appeared (e.g., Dunbar and Dunbar, 1974; Nash, 1974; Abegglen and Abegglen, 1976; Oppenheimer, 1976; Altmann, 1980; Teas *et al.*, 1981). When the number of these reports is compared to the number of hours spent watch-

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ing Old World monkeys in the field, however, it is clear that diurnal births are rare events.

Jolly (1972) and Altmann (1980) have suggested why nocturnal births might be advantageous: the birth process is potentially exhausting to a female and it is likely that the mother and her infant are at considerable risk if birth does not occur when the group is stationary for a substantial period as at night, so that mothers may rest after birth without risking separation from the group. Infant survival may be improved if mothers, released from the energetic demands of moving with the group, are able to clean, support, and nurse their newborns for several hours without interruption.

Given the foregoing, our previous finding (Chism *et al.,* 1978) that captive patas monkeys *(Erythrocebus patas)* frequently give birth during the day was unexpected. From our observations of captive patas, we advanced the hypothesis that diurnal births are characteristic of patas monkeys. This hypothesis is now supported by a 2-year field study of patas in Kenya which indicates that patas group composition and habitat combine to make this species particularly vulnerable to predation at night. In response, patas have evolved a night-resting strategy which uses unpredictability, dispersal, and concealment to lessen vulnerability to nocturnal predation. Nocturnal births, because of the cues they provide to predators, are clearly incompatible with this strategy.

Giving birth during the day does not eliminate the risk of predation. Females which give birth during the day risk separation from their group when it moves rapidly over long distances to avoid certain predators or even during normal, rapid group progression. Females can reduce this risk by giving birth at times of day when the group is likely to be moving shorter distances and when predators are least likely to be encountered.

We present evidence for the adaptiveness of diurnal births for patas based on the frequency of their occurrence and timing during the day and observations of the perinatal behavior of females. These data are evaluated in relation to the timing of predator occurrences and patterns of day ranging at the study site.

STUDY SITE, SUBJECTS, AND METHODS

The study site was in the Laikipia District of Kenya (0°5′N, 36°42′E) at an altitude of 1900 m. Vegetation within the 75-km^2 study area was predominately *Acacia–Themeda* wooded grassland [*sensu* Lind and Morrison, 1974] in which the whistling-thorn acacia, *Acacia drepanolobium,* was the dominant woodland species.

Observations carried out by Chism and Olson from June 1979 through July 1981 focused on two groups of patas and comprised approximately 3500 contact hr. During the course of the study, one group ranged in size from 15 to 25 individuals (Mutara 1), and the other ranged from 42 to 54 individuals (Mutara 2). Both groups were well habituated, and animals in both groups were individually recognizable.

Data collection methods included *ad libitum* recording, scan sampling, focal animal sampling, and the compilation at half-hourly intervals of a day-range map and record of habitat use patterns. *Ad libitum* records provided the data on timing of births as well as the data on predator occurrence reported in this paper. Detailed descriptive data on parturition and perinatal behavior were extracted from focal animal samples. *Ad libitum* records and focal animal samples also provided data on sleeping site choice and night-resting behavior. Ranging data for this paper were derived from day-range maps compiled for each study group during the 1980–1981 birth season and from a matched sample of day ranges outside the birth season.

Further detailed descriptions of the study site, subjects, and methods will appear elsewhere (Olson and Chism, in preparation).

RESULTS

Timing of Births

Free-ranging patas monkeys are highly seasonal breeders (Hall, 1965b; Struhsaker and Gartlan, 1970). In the Laikipia District, mating occurs from June through August, and births are concentrated between mid-December and mid-February.

Twenty-five births occurred in the two study groups in the 1980–1981 birth season. Two births were witnessed in their entirety, and an additional five births occurred while the groups were under observation. All seven of these births were diurnal, occurring between 0800 and 1800 hr (Table I). Five of these seven diurnal births occurred during the first half of the day (between 0700 and 1300 hr), one took place between 1200 and 1430 hr, and one occurred during the last half of the day, between 1400 and 1800 hr. In an eighth case, a newborn was spotted before noon, but a predawn birth could not be ruled out, because the mother had not been seen early in the morning. In no other case did we join the study groups early in the morning and find infants which had been born during the previous night. Thus, 87.5% of the infants (7 of 8) observed on their first day of life were known

Table I. Timing of Births in Two Study Groups

Study group	Female	Date of birth	Time of birth[a] (hr)	Additional observations
Mutara 2	AG, multiparous	14 Dec. 1980	1015–1145 (estimated)	Probable stillbirth; fetus not found. AG seen at 1145 being approached, sniffed, and visually inspected by adult females. AG has blood on perineum, sides, and hands. Birth estimated to have occurred not more than 90 min prior to 1145.
Mutara 2	BE, multiparous	19 Dec. 1980	1102	Birth observed.
Mutara 1	BG, nulliparous	21 Dec. 1980	1144	Birth observed.
Mutara 1	CL, multiparous	15 Jan. 1981	0800–1000 (estimated)	Initial sighting at 1000. Based on appearance of mother and infant, birth estimated to have occurred not more than 120 min earlier.
Mutara 1	RU, multiparous	26 Jan. 1981	1200–1430 (estimated)	Female seen repeatedly between 0900 and 1200 without an infant. Female seen with new infant at 1530. Based on appearance of mother and infant, birth estimated to have occurred not less than 60 min prior to 1530.

to have been born diurnally, and at least 28% of all births (7 of 25) which occurred during the birth season were diurnal.

Parturition and Perinatal Behavior

Behavior immediately prior to, during, and following the two observed births closely resembled the behavior of patas giving birth in captivity (cf. Chism *et al.,* 1978). One of these births was to a multipara and the other to a 3-year-old nullipara. The following descriptions of perinatal behavior and parturition are abstracted from focal animal samples taken during the course of the birth process.

Both observed births took place on the ground. The multipara was recognized to be in second-stage labor (for terminology see Atwood, 1976)

Table I. continued

Study group	Female	Date of birth	Time of birth[a] (hr)	Additional observations
Mutara 1	MA, multiparous	31 Jan. 1981	Possibly predawn; probably 0830–1030	MA first seen with new infant at 1030; she was not observed prior to 1030. Mother and infant both clean when first observed.
Mutara 2	FL, multiparous	31 Jan. 1981	1400–1800 (estimated)	FL first observed at 1840, under poor observation conditions, to have a very bloody perineum and a new infant.
Mutara 2	WI, multiparous	14 Feb. 1981	0800–1000 (estimated)	WI observed with new infant at 1010. Infant has piece of umbilical cord attached; mother cleaned self and infant. Birth estimated to have occurred not more than 120 min earlier.

[a] Each estimate of the time of birth was based on the appearance of mother and neonate when first seen. Criteria resulted from our observations of births in wild and captive patas groups: birth was judged to have occurred within the preceding 2 hr of first sighting if a female's hands, legs, and perineum were covered with fresh blood; birth was judged to have occurred at least 1 hr but not more than 2 hr prior to first sighting if the mother was clean but her infant was still wet or bloody. Behavior of mothers and infants (e.g., mother moving slowly or at rear of group, infant clinging high on ventrum in tightly curled position, mother continuously supporting infant with one hand while moving) was not used in these evaluations because the relationship of behavior to time of birth varies with factors such as maternal parity, degree of difficulty of birth, and infant health.

by her repeated quadrupedal crouching/lordosis postures associated with obvious contractions and straining and by her repeated touching of the perineal area and vulva followed by sniffing and licking of the fingers. In the 10 min prior to parturition the female's group was moving, and she moved and stayed with the group, near the rear, for approximately 150 m while actually in second-stage labor. Labor was observed for 7 min prior to delivery, although it may have been considerably longer in duration since the observer did not necessarily see its onset.

Immediately after the female had pulled the infant free of the birth canal, neither she nor the infant could be seen for 2 min. When she was next visible, the female was consuming the placenta, and her newborn was lying beside her in the grass. The mother fed on the placenta for about 8 min before she picked up the neonate and licked it for 5 sec, after which she placed it in the grass beside her and resumed eating the placenta. The mother repeated this sequence of behavior a minute later, and in neither in-

Fig. 1. Multiparous female eating the placenta while newborn clings to her ventrum 13 min postpartum.

stance did the infant cling, although it squealed loudly the second time it was picked up. Thirteen minutes after birth, the female picked up her infant and it clung to her ventrum while she alternately fed on the placenta and cleaned herself (Fig. 1).

The mother remained in the place where the birth had occurred for 18 min after birth. As soon as she had completely eaten the placenta she moved to rejoin the group, which was dispersed over more than 300 m and whose rearmost members were not more than 50 m from her.

After the female had gone, the place where the birth occurred was recognizable by a matted, bloodied area of grass about 30 cm in diameter.

Behavioral indicators of labor shown by the nullipara were identical to those of the multipara. On the day she gave birth, the nullipara had been observed intermittently for more than 1 hr before labor was apparent. Once second-stage labor began, she was observed continuously through delivery and for 75 min after birth. The duration of second-stage labor in this instance is thus known to have been 36 min.

The nullipara's group was moving while she was in labor, and she moved with the group for approximately 150 m while engaged almost exclusively in labor-associated behavior. During this period she climbed 5 m up into the crown of an acacia and remained there crouching, straining, and touching her perineum and vulva for 11 min. Three minutes before delivery, the crown of the infant's head appeared briefly in the birth canal during one set of contractions while the nullipara was still in the tree.

Two minutes before birth, the nullipara climbed down out of the tree and moved a short distance on the ground before giving birth. The observer's view of mother and infant was obstructed for 12 min following the birth, although intermittently the mother could be seen trying to bite through the placenta's attachment to the umbilical cord and cleaning herself. Each time the mother could be briefly but clearly seen, her infant was lying beside her in the grass.

After 12 min, the mother picked up the newborn and it clung to her ventrum as she moved toward other group members which were 50 m ahead of her. The mother sat down after moving 25 m and cleaned herself and the infant.

Twenty minutes postpartum, it was clear that most of the placenta was still attached to the newborn's umbilical cord. When the mother moved short distances carrying her infant, the placenta dragged on the ground. The mother stopped more than once to look down at the placenta before moving farther. It was not until 25 min postpartum that the mother began to consume the placenta, by which time she had moved less than 50 m from the site where the birth had occurred. The placenta was completely consumed within 12 min. After eating the placenta, the mother resumed cleaning herself and the infant.

The mother had rejoined the rest of her group by 45 min after birth; she had never been separated by more than 50 m from the nearest group member, and the group's pre- and postpartum dispersal had been approximately 150 m.

Neither female attempted to isolate herself from other group members prior to or during birth. In fact, each female was approached and briefly watched from within 3 m by one or more adult females and immatures before and during the birth process. The females giving birth completely ignored the other group members. The adult male in each group showed no interest whatsoever in the births. In both instances, mothers became separated from their respective groups by 50 m while they were engaged in cleaning themselves and their newborns and while eating the placenta in the postpartum period. The distance of separation in both of these cases was insignificant considering the overall dispersal of each group at the time.

The entire birth process from the time when each female was first continuously engaged in second-stage labor until the time when she resumed moving with her group after birth took 20 min for the multipara and 68 min for the nullipara.

Relationship Between Timing of Births and Risk of Predation

Predators

There were 12 species of mammals in the study area which were potential predators: 5 felids (lion, *Felis leo;* leopard, *Panthera pardus;* cheetah, *Acynonyx jubatus;* caracal, *Felis caracal;* and serval, *Felis serval*); 5 canids (black-backed, common, and side-striped jackal, *Canis mesomelas, C. aureus,* and *C. adustus;* wild dog, *Lycaon pictus;* and domestic dog, *C. familiaris*); and 2 hyaenids (spotted hyena, *Crocuta crocuta;* and striped hyena, *Hyaena hyaena*). There were also at least four species of large raptorial birds (eagles and owls) present which could potentially prey on patas, although none was ever observed to attempt to do so. Interactions between patas and raptors have been described elsewhere (Olson and Chism, 1981).

Patas responded to wild and domestic dogs by rapid, long-distance flight. While fleeing from dogs it was not unusual for the patas to move more than a kilometer in less than 30 min. Their response to other predators was much more variable: patas were seen to respond to some felids by vocalizing and moving toward them, thus advertising the predator's position and keeping it in sight.

In the following two sections we provide data on the risk of predation and characteristic patas responses to this risk. Both risk and response are presented as factors which may influence the timing of patas births in the wild.

Nocturnal Predation: Sleeping Site Choice and Night-Resting Behavior

Our data on patas sleeping site choice and night-resting behavior confirm and amplify those of Hall (1965b). In both studies, a consistent pattern of behavior was observed at sleeping sites.

In our study, each patas group had a relatively large number of sleeping sites ($N > 100$ for each group during a 1-year period). Furthermore, patas in neither group ever slept in the same sleeping site on two consecutive nights even though their day ranges occasionally brought them at dusk to within a few hundred meters of their sleeping site of the previous night. Thus, although patas might sleep in the same area more than once during a year, they did so infrequently and unpredictably.

Once a sleeping site had been chosen, patas dispersed widely in their sleeping trees over an area of several hundred square meters. Each patas (with the exception of adult females with dependent infants) remained alone throughout the night in the crown of its sleeping tree. At the study site, patas slept in the crowns of whistling-thorn acacias (*Acacia drepanolobium*), generally favoring trees with small, straight boles having no large branches less than 1.5-2 m above the ground. Heights of sleeping trees fell within the range of 4-8 m with very few exceptions. Within the tree crown, individuals slept either on the smallest possible branches or amid dense growths of crown parasitic plants which made patas virtually invisible either from a distance or from directly below the tree.

One in their sleeping trees, patas remained silent and immobile even in the presence of potential predators: when a wild dog (*Lycaon pictus*) hunted at dusk in the patas' sleeping area, directly below trees in which the patas had settled moments before, the entire group remained silent while the dog was present and none shifted its position within the sleeping trees.

The importance of nighttime dispersal and concealment to patas is underscored by the fact that on the rare occasions when a group member tried to enter a tree that was already occupied, the first animal in the tree, whether adult or juvenile, threatened or attacked the other until it left. Even after they had settled for the night, individual patas would sometimes threaten a patas in an adjacent tree, apparently in an attempt to force the animal to move farther away.

At Hall's Uganda study sites and at our site in Kenya, the most likely predator of patas at night is the leopard. All age-sex classes of patas are vulnerable to leopards. During the present study, on two occasions within a period of 2 weeks an adult female patas disappeared between dusk and early the following morning. Both of these females had infants less than 1 month old, and both were in good health immediately prior to their disappearance.

In neither case did careful searching within the sleeping site and adjacent areas, through which the group had moved in the early morning, reveal any clues to the fate of these individuals. We conclude that in these two cases predation was likely, probably by leopards.

Diurnal Predation: Temporal Patterns of Predation Occurrence and Day Ranging

Females make themselves vulnerable to predators while giving birth during the day in two ways: by giving birth on the ground and by becoming separated from the group during delivery or in the postpartum period. We considered both encountering potential predators and becoming separated from the group as risks, and we examined temporal patterns of predator occurrence and day ranging to see whether some times of day are less risk-prone than others. If there are periods which are distinctly less risk-prone, births ought to be clustered at those times.

To determine the temporal distribution of predator occurrence, the day was divided into six consecutive 2-hr blocks beginning at 0700 and ending at 1900 hr. (Patas rarely began to move, feed, or forage before 0700–0730 hr and were almost never moving after 1900 hr.) Predator occurrences include predator encounters and predator sightings. A "predator encounter" was recorded whenever either patas group was in the presence of a potential predator. A "predator sighting" was recorded whenever either observer saw a potential predator within the patas' home ranges but at a time when neither study group was present. Sightings comprise 11.5% of the predator occurrences (12 of 104) and are included in the analysis because they reflect times of day when predators were active and likely to be encountered. All instances in which patas responded as though a predator were present but without the observer(s) being able definitely to confirm its presence have been omitted from the analysis.

The frequency at which predators were encountered or sighted was not randomly distributed among the six 2-hr blocks spanning 0700–1900 hr (Kolmogorov–Smirnov one-sample test $D = 0.179$, $N = 104$, $P < 0.01$). Rather, predator occurrence exhibited distinct temporal patterning as shown in Fig. 2, which represents the predator occurrence calculated for each 2-hr block as the rate of occurrence/100 hr of observation. Temporal patterning of predator occurrence is further illustrated in Fig. 3: hyaenids were observed early in the morning or late in the day; felids were never observed between 1100 and 1300 hr. Jackals, which accounted for 85% of the canid occurrences (78 of 92), were most frequently seen before 0900 or after 1500 hr (70% of the jackal occurrences; 55 of 78).

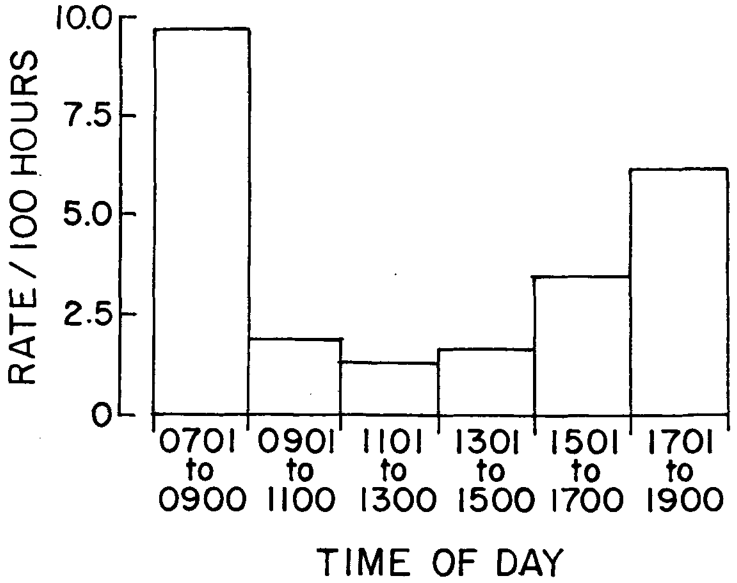

Fig. 2. Temporal distribution of rate of predator occurrence (*N* = 104 occurrences during 3500 observation hr).

All age-sex classes of patas are not equally vulnerable to each predator species. Adult females at all times are vulnerable to the large felids (leopard, lion, cheetah), wild and domestic dogs, and hyenas. Jackals, caracals, and servals are probably not potential predators of adult patas except in unusual circumstances (i.e., only when an adult is ill, injured, or otherwise incapacitated). A parturient female giving birth on the ground could be such an instance of adult vulnerability. Vulnerability of the parturient female would be greater if more than one predator were present (e.g., a pair of jackals), if the female were experiencing a difficult delivery, or if the female were not close to a suitable tree into which she might quickly retreat.

Day-Ranging Patterns

A patas group is not likely to stop moving while a female is giving birth or in the period immediately postpartum. Consequently, a female about to give birth must keep moving in order to stay with her group: both of the females observed giving birth moved 150 m while engaged almost exclusively in second-stage labor, and neither permitted herself to become separated from her group by more than 50 m during the birth process.

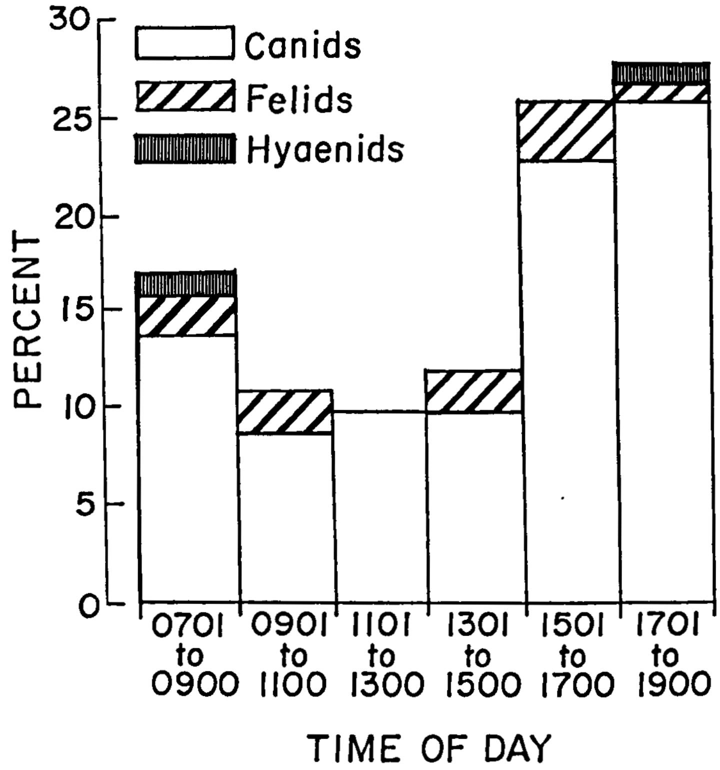

Fig. 3. Temporal distribution of predator occurrences by percentage of predators which were canids, felids, or hyaenids ($N = 104$ occurrences).

Given these observations, we reasoned that it would be most adaptive if a female gave birth at those times of day when the rate of group movement is likely to be lowest and the effort of keeping up least. Such behavior on the parturient female's part would lessen the likelihood of her becoming separated from the group and thus more vulnerable to predation. It would also facilitate her postpartum recovery and her ability to attend to her newborn. As a result, the probability of the neonate's survival might be increased.

To determine whether timing of births within the day was related to rate of group travel, 20 complete day ranges (10 for each group) collected during the 1980–1981 birth season were analyzed. All of the days included in the analysis were days on which there was at least one infant less than 2 weeks old in the group. Births actually occurred on 5 of the days included.

Days were divided into six consecutive 2-hr blocks between 0700 and 1900 hr in the same way data were analyzed with respect to predator occur-

Table II. Temporal Patterns of Day Ranging

Time block (hr)	Birth season		Non-birth season	
	Rank[a]	Mean distance traveled[b]	Rank	Mean distance traveled
		Mutara 1		
0700–0900	2	460*	2	703
0900–1100	1	390*	1	678
1100–1300	3	544	4	715
1300–1500	4	596	3	709
1500–1700	5	769	6	869
1700–1900	6	1132**	5	749
		Mutara 2		
0700–0900	2	657	1	692
0900–1000	3	685	4	882
1100–1300	1	515*	5	913
1300–1500	5	728	2	732
1500–1700	6	913**	6	1025
1700–1900	4	726	3	839

[a] Time blocks ranked from lowest (value of 1) to highest (value of 6).

[b] Means are based on complete day ranges: $N = 10$ for each group during the birth season, and $N = 10$ for Mutara 1 and $N = 9$ for Mutara 2 during the non-birth season. All distances given as meters.

*Significantly less than expected, $P < 0.001$ (χ^2).

**Significantly greater than expected, $P < 0.001$ (χ^2).

rence. Distance traveled during each 2-hr block was measured directly from day-range maps which had been compiled at half-hourly intervals at a scale of 1:12,500.

Data for both groups (Table II) show that patas moved farther in the last half of the day (1300–1900 hr) than they did in the first half (0700–1300 hr). Furthermore, rank ordering of time blocks on the basis of mean distance traveled reveals that patas in both groups were likely not to travel as far during any given morning block as they did during any given afternoon block.

Data on distance traveled during each 2-hr block were further analyzed with a χ^2 test. For each study group, the mean for observed distance traveled in each 2-hr block was compared to an expected value under H_0 of equal distance traveled in each. As shown in Table II, distance traveled in each block was significantly less than expected in either group only among blocks in the first half of the day (0700–0900 and 0900–1100 hr for Mutara 1; 1100–1300 hr for Mutara 2). Distance traveled was significantly greater than expected only among time blocks in the last half of the day (1700–1900 hr for Mutara 1; 1500–1700 hr for Mutara 2).

We also compared the sample of birth-season day ranges for each group with a sample of each outside the birth season. (The non-birth-season sample was drawn from an equivalent time interval and was closely matched with the birth-season sample for climatic variables of rainfall and mean minimum and maximum temperatures.) The comparison showed that whereas day ranges for both groups were shorter on average during the birth season, there was no significant difference in day-range length for either group (Mutara 1—Mann-Whitney $U = 36$, $N_1 = 10$, $N_2 = 10$, $P > 0.05$; Mutara 2—Mann-Whitney $U = 32$, $N_1 = 9$, $N_2 = 10$, $P > 0.05$). In fact, one of the two longest day ranges recorded during the entire study for either of the patas groups (9.275 km) occurred on a day when a female in the group had given birth.

The birth-season pattern of moving less in the hours 0700–1300 than during the hours 1300–1900 did not appear, however, in the non-birth-season data for either group (Table II). This difference may arise from the effect that pregnant and newly parturient females have on group activity patterns during the birth season. Pregnant females, especially those near term, are very often torpid particularly in the morning. New mothers were relatively inactive during the first 2–3 days after giving birth and often lagged at the rear of the group. The magnitude of the effect of pregnant females and new mothers on group ranging patterns may depend on the proportion of such females in the group at the time. In the study groups, for example, pregnant females accounted for 42% (8 of 19) of Mutara 1 group members and 33% (15 of 46) of Mutara 2 group members at the outset of the 1980–1981 birth season.

DISCUSSION

The Problem of Giving Birth at Night

Observations of wild patas in Kenya, as well as of captive patas, suggest that patas typically give birth during the day. Such a pattern of diurnal rather than nocturnal births is very unusual among Old World monkeys. In one birth season in Kenya we recorded nearly half as many diurnal births as have been reported in the past decade for all monkey species observed outside captivity. Why, then, are patas so unusual? Why are diurnal births also not typical of other monkeys, especially of baboons, which often live in very similar habitats? Part of the answer lies in asking the question a different way: Given the potential advantages of nocturnal births, why do patas not give birth at night? We believe the answer lies in the vulnerability of patas to nocturnal predators, particularly leopards (Hall, 1965a), and in the evolution among patas of a unique behavioral complex serving to reduce this vulnerability.

Patas adaptations reducing nocturnal predation risk become apparent when their behavior at sleeping sites is compared with that of baboons. Altmann and Altmann (1970), whose discussion of baboon behavior at sleeping sites remains the most detailed, report that baboons repeatedly use a small number of sleeping sites and frequently use the same sleeping site on consecutive nights. At the chosen sleeping site, preferably cliffs or trees which are large or difficult of access, members of the group stay close together; when they sleep in trees, several animals rest in the same tree. Their position in the tree is based on the animal weight and branch size, and Altmann and Altmann suggest that such nonrandom positioning results in the likelihood that an adult male will be between smaller animals and a predator's route of access into the tree crown. Baboons at the Altmanns' Amboseli study site usually fell silent when they were completely settled for the night and could be quite inconspicuous when resting in well-foliated trees. Our own experience with baboons in Uganda (Rowell, 1966) and at several places in Kenya has been that baboons react noisily when disturbed during the night, with barking by males and screeching and squealing by others. Intense bouts of vocalization by male baboons during the night have been reported by Stoltz and Saayman (1970) as a probable response to nocturnal predators. It is possible that concerted barking, combined with branch shaking and other displays, may successfully disrupt the activity of predators at night in the same way that this behavior has been observed to do during the day (see Saayman, 1971).

Patas' choice of sleeping sites and night-resting behavior differ from those of baboons in ways which demonstrate the importance to patas of avoiding detection by nocturnal predators. Baboons depend less on avoiding detection than they do on mounting a successful defense once a predator has found them. The difference between the two species is probably due primarily to the fact that baboons nearly always have more than one adult male present at sleeping sites, whereas patas groups nearly always have only a single male (Hall, 1965a; Struhsaker and Gartlan, 1970; this study). Adult male baboons acting together can successfully defend their group against predators (DeVore and Washburn, 1963; Stoltz and Saayman, 1970), whereas successful defense by a single adult male patas against a nocturnal predator such as a leopard is, we believe, unlikely (see also Hall, 1964). Thus, the best night-resting strategy for patas is one which relies on unpredictability, dispersal, and concealment rather than on defense. By having a large number of sleeping sites and never using the same site on consecutive nights, patas make it difficult for predators to predict where the group might be found. By dispersing widely within the sleeping area, sleeping singly, and remaining still and silent once in the sleeping trees, patas make it difficult for a predator to find individuals should it move through the sleeping area. We suggest that these behaviors have been selected for because they reduce the risk of predation at night: cues to nocturnal predators about either the group's location or that of individuals are minimized.

Clearly, a patas female could increase the risk of predation to herself and others nearby by giving birth at night since parturition is not a cryptic process. It is, in fact, an activity which provides abundant cues to predators because of movements, sounds, and odors: the movements of the female in the crown of the tree or climbing to the ground during labor, the sounds associated with such movements or the squeals of a neonate, and the odors of blood, amniotic fluid, placenta, and neonate would all combine to advertise the presence of a parturient female. Indeed, we suggest there has been strong selection against patas' giving birth at night. The fact that patas births continue to occur in daylight even in captivity in North America (Chism *et al.*, 1978) reinforces this conclusion.

The Problem of Timing of Births During the Day

Even in daylight, birth is a process which may draw the attention of predators. The thoroughness with which females cleaned themselves and consumed the placenta after birth suggests that it is important to avoid leaving cues for predators hunting by scent. In the wild and in captivity this cleaning of the mother and eating of the placenta take priority over cleaning and holding the infant, which is often left lying on the ground until the process is nearly complete.

A female giving birth during the day risks separation from her group if she is unable to keep up. Her inability to keep up will be greatest when the group is progressing rapidly under normal conditions or when the group flees over long distances to avoid predators such as dogs. The patas pattern of habitat use including large home ranges, long day ranges, and unpredictable sleeping site use would make it particularly difficult for a female to relocate her group once separated from it. During the day, the combined vigilance of group members is an important aspect of predator avoidance. If a female becomes separated from her group, she increases the risk to herself of being preyed on because she can no longer benefit from the vigilance of others.

Both females we observed during parturition continued to move with their respective groups even during second-stage labor; both closely monitored the movement of the group while giving birth and immediately postpartum; and both moved to rejoin the group as soon as they were able to do so. Neither female became separated from her group by more than 50 m, a distance which was one-third or less of the overall dispersal of each group at the time. In both cases, females were able to stay near their groups due to the relatively slow rate of group progression at the time when the births occurred.

In general, the effectiveness of a parturient female's behavior in maintaining contact with her group and so reducing the risk of predation will be greatest when the group is moving most slowly. We found that during the birth season patas groups moved slowly before 1300 hr. After 1300 hr they began to increase their rate of travel and often covered much of their day range in the last 2-3 hr of the day. As Table II shows, in the time taken to give birth the groups were likely to travel no more than 200-325 m during the morning, a distance over which a patas, in most circumstances, could easily remain in sight and catch up. In the afternoon, a female could fall behind her group by 500 m or more during a 60-min birth. Thus, a female which gives birth as early as possible in the day runs the smallest risk of being left behind during normal group progression. In addition, she has more time to recover from the birth before rapid afternoon travel begins.

The disadvantages of a late-afternoon birth due to fast normal progression rates are reinforced by the greater likelihood of encountering predators after 1500 hr, while the frequency at which predators are likely to be encountered before 0900 hr tends to cancel the advantages of giving birth in the early morning. Consideration of both predator occurrence and day-ranging patterns together suggests that the best time to give birth is during the period between 0900 and 1300 hr. All but one of the births for which times were known took place within or close to this period. These observations suggest that there is a mechanism for effective selection of birth timing such that births will occur during an optimum period of the day.

Outside the birth season, patas groups did not consistently move more slowly in the morning than during the rest of the day; that pattern of movement seemed to be an effect of the presence of numerous heavily pregnant females and mothers with young infants. The possibility of taking advantage of a lengthy period of slow group movement for giving birth is, therefore, available only to females whose births are synchronized closely with those of other members of the group. This may provide one of the selection pressures which has led to the unusually short birth season of the patas monkey.

Birth synchrony among females and nonrandom timing of births during the day also have been reported for wildebeest: Sinclair (1977) shows not only that wildebeest in the Serengeti have a very short, highly synchronized birth season, but also that they concentrate nearly all births between 0800 and 1100 hr, thus avoiding their main predator, the hyena. In this instance, it seems that the behavior of both ungulate and primate has converged: both patas and wildebeest reduce the risk of predation by selectively giving birth at those times of day when the likelihood of encountering predators is relatively small.

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