

Mother-Young Relationships in Captive Ungulates: Spatial and Temporal Patterns

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Ungulates are often divided into two groups—the followers and the hiders—characterized by differing spatial and temporal patterns of mother-young behavior. We assessed the relative roles of mother and young in maintaining these patterns by recording standardized quantitative measures on 37 mother-young pairs representing eight species. We found no differences between followers and hiders on any of our measures. The mother was largely responsible for maintaining the species characteristic spacing distances between mother and young, although young sometimes contributed. The mother usually initiated activity bouts of the young. Activity bouts of young were longer and more frequent when the mother was active than when she was lying down. Young often stood when their mother was lying, but these activity bouts were brief. Young usually terminated their own activity bouts. Hinde's measure, a measure designed to quantify the relative roles of primate mother and young in maintaining proximity, proved less satisfactory for ungulates, due to the multiple interpretations possible for low values of the measure and the difficulty of adequately defining approaches and departures.

Key words: follower, hider, ungulate, mother-young

INTRODUCTION

Most ungulate species can be placed into one of two groups, the "followers," in which young are in close proximity to their mother from birth, or the "hidiers," in which young spend most of the first days or weeks of life at some distance from their mother, often concealed in vegetation [Walther, 1961, 1964, 1965, 1966; Talbot et al, 1965; Fraser, 1968]. Mother and young of follower species interact frequently, but contact between hider mother and young is restricted to as few as two to three times per day during the hiding period [Lent, 1974].

What are the relative roles of mother and young in producing these characteristic spatial and temporal patterns? In hider species, young appear to select their own hiding places [Bubenik, 1965; McCullough, 1969; Jungius, 1970; Gosling, 1969; Schaller, 1967; Walther, 1979], which prompted Lent [1974] to suggest that young

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hidiers make their own spatial decisions. Temporal patterns are usually defined in terms of the initiation and termination of activity periods. Hider mothers often approach their lying young to initiate nursing and are therefore thought to be largely responsible for initiating activity periods [Lent, 1974; Leuthold, 1977; Walther, 1979]. After nursing, the young actively move away from the mother [Walther, 1979], thus terminating activity periods.

The roles of follower mother and young in determining spatial and temporal patterns are less clear. Lent [1974] views follower mother and young as continuously responding to each other's spatial position and suggests that follower young are more likely than hider young to initiate activities such as nursing and play on their own. Walther [1979] discusses following largely in terms of the behavior of the young; movements and vocalizations of the mother are thought to elicit the following response.

The collections of the National Zoological Park (NZIP), Washington, D.C. and the Metropolitan Toronto Zoo (MTZ), Toronto, Ontario, provided us with the opportunity to compare several species using standardized quantitative measures. Previously, we reported on similarities and differences between followers and hidiers on several measures of mother-young association and the percentage of time the young spent lying [Ralls et al, 1986] and changes in these measures as the young matured; [Ralls et al, 1987]. Here, we assess the relative roles of mother and young in maintaining spatial and temporal patterns.

METHODS

Thirty-seven mother-young pairs representing eight species and two families (Table 1) were observed for a total of over 600 hours between 1977 and 1982. Common names of these species are used in the text and tables; scientific names are given in Table 1.

Pairs were observed at NZIP; NZIPs Conservation and Research Center (CRC), Front Royal, Virginia; and MTZ. Enclosures were large (ranging from 0.11 ha to 12.14 ha) and contained ample hiding places (eg, tall grass, fallen logs, and rocky outcrops). Social groupings in captivity resembled those in the wild.

An attempt was made to observe each mother-young pair for 1 continuous hour per day, at least 3 days per week, for the first 7 weeks after birth of the young, but scheduled observations were occasionally missed, and individual animals were not always visible for the entire observation period. The total number of hours during which both mother and young were visible for each species is shown in Table 1. Observations were made in the morning (0800-1000) or in late afternoon (1600-1800), when the animals tended to be most active.

Thirty-two trained volunteers collected the data; each observed one or more mother-young pairs from the birth of the young until the end of the seven-week observation period. Data were recorded on a simple checksheet. Because the species observed were relatively large and slow moving and the behaviors scored were familiar and easily recognized, we achieved better than 92% agreement between observers. An analysis of the mean weekly coefficients of variation for several measures of mother-young association showed that these were not consistently related to the number of observers contributing data for a particular species, the number of pairs of each species observed, or the time of day at which observations were made [Ralls et al, 1983].

TABLE 1. Scientific names of species, number of mother-young pairs of each species observed, total number of hours both mother and young were visible, and type of mother-young relationship*

Taxon	No. of pairs	Hours visible	Type of mother-young relationship		References
			Ralls et al	Lit.	
Cervidae					
<i>Rangifer tarandus</i> (reindeer)	5	64	F	F	Espmark, 1971
Bovidae					
<i>Bison bison</i> (bison)	3	58	F	F	McHugh, 1958
<i>Hippotragus niger</i> (sable)	4	97	H	H	Grobler, 1974
<i>Oryx dammah</i> (oryx)	9	117	H	H	Walther, 1979
<i>Connochaetes taurinus</i> (wildebeest)	3	90	F	F	Estes and Estes, 1979
<i>Gazella dorcas</i> (Dorcas gazelle)	7	147	H	H	Walther, 1966, 1979
<i>Hemitragus jemlahicus</i> (Himalayan tahr)	3	41	F	I	Schaller, 1977
<i>Capra ibex</i> (Ibex)	3	50	F	I F	Schaller, 1977 Walther, 1979

*Based on Ralls et al [1986] and according to the literature. Species listed in taxonomic order. F, follower; H, hider; I, intermediate.

At the end of each minute, observers recorded whether mother and young were lying or standing (which included moving) and the distance between them in terms of mother-lengths. Changes in activity state (as from lying to standing) and approaches and departures of one pair member to or from the other were recorded whenever they occurred.

An approach was scored if an animal moved to within one mother-length of the other, a departure if it moved beyond this distance. A measure developed for primates by Hinde [1974], "the percentage of approaches by the young minus the percentage of departures by the young" (Hinde's measure) was calculated as an indicator of the relative roles of mother and young in maintaining proximity. Positive values of Hinde's measure are thought to indicate that the young plays a greater role in maintaining proximity between mother and young; negative values that the mother plays a greater role [Hinde, 1974].

The Mann-Whitney U-test was used to examine differences between followers and hidiers [Siegel, 1956]. The sign test [Siegel, 1956] and test of proportions [Neter et al, 1978] were used for differences between mothers and young.

RESULTS

Species listed in Tables 2-7 are classified as "followers" or "hidiers" according to a cluster analysis based on three measures of mother-young association recorded during the first week after birth [Ralls et al, 1986]. In six of the eight species, our

TABLE 2. Total number of approaches and departures by mother and young, percentage made by the young, and value of Hinde's measure during week 1 and weeks 2-7 after birth*

	Type of mother-young relationship ^a	Approaches		Departures		Hinde's measure
		Total	% By young	Total	% By young	
Week 1						
Ibex	F	53	58	56	71	-13
Oryx	H	72	21	67	23	-2
Wildebeest	F	23	39	22	41	-2
Reindeer	F	107	19	104	20	-1
Sable	H	3	0	3	0	0
Gazelle	H	68	41	74	31	10
Tahr	F	50	36	55	25	11
Bison	F	36	44	42	29	15
Weeks 2-7						
Oryx	H	545	51	533	48	3
Tahr	F	106	51	111	43	8
Sable	H	138	70	137	59	11
Reindeer	F	424	62	410	46	16
Bison	F	91	64	80	45	19
Gazelle	H	586	70	584	47	23
Wildebeest	F	275	70	275	40	30
Ibex	F	285	74	271	39	35

*Ranked on Hinde's measure.

^aF, follower; H, hider.

assignments agree with those in the literature (Table 1). There is no consensus in the literature regarding the placement of species in the tribe Caprini (goats and sheep). We classified the ibex as a follower; others have considered it either a follower [Walther, 1979] or an intermediate between followers and hidiers [Schaller, 1977]. We also classified the tahr as a follower although Schaller [1977] considers it intermediate.

There were no significant differences between followers and hidiers on any of the measures reported here (Tables 2-7, Mann-Whitney U-test); thus we combined the two groups when examining behavioral differences between mothers and young.

Spatial Patterns

Hinde's measure. In week 1, values of Hinde's measure fell within a relatively narrow range (-13 to +15, Table 2) despite considerable variation across species in the percentage of approaches and departures made by the young. In subsequent weeks, young made a greater percentage of approaches (Table 2), resulting in higher values of Hinde's measure for all species but the tahr.

Distance between mother and young when both were lying. The tendency for mother and young of follower species to lie much closer together than those of hider species was apparent throughout the 7-week study period, although spacing between mother and young changed over time [Ralls et al, 1987]. A detailed week-by-week tabulation of the data for each species indicated that these characteristic spacing patterns were maintained regardless of whether mother or young was the second to lie (data summarized in Table 3).

TABLE 3. Percentage of times mother or young was second to lie at various distances from the other

	Distance (ML) ^a		
	< 1	1-2	> 2
Followers			
Mother	54	15	31
Young	73	12	15
Hiders			
Mother	11	13	76
Young	14	24	62

^aML, mother-lengths.

TABLE 4. Percentage of times mother or young was the first of the pair to stand*

Species	Type of mother-young relationship ^a	First to stand (%)		Sign test ^b
		Mother	Young	
Oryx	H	96	4	+
Wildebeest	F	95	5	+
Reindeer	F	81	19	+
Bison	F	79	21	+
Sable	H	72	28	+
Gazelle	H	71	29	+
Tahr	F	69	31	+
Ibex	F	66	34	+

*Ranked on "mother first to stand."

^aH, hider; F, follower.

^bFor the sign test, +, mother was first to stand more often than young ($P = .008$, two-tailed).

Temporal Patterns

Initiation of activity periods. The mother was usually the first of the pair to stand after a period when both animals had been lying (Table 4). We calculated the proportion of time the young "followed" its mother, ie, stood within five minutes of the mother standing; the mean across-species was 47% (range 33-74%, data not shown).

With the exception of the ibex, young were more likely to stand if their mother was standing than if she was lying (Table 5). Furthermore, young of all species tended to stand for longer periods when the mother was standing than when she was lying (Table 6). We examined the possibility that this was due to mothers standing for longer periods than they lay; there was no significant difference in the average duration of mothers' standing and lying bouts ($P = .29$, data not shown).

Termination of activity periods. The young was usually the first of the pair to lie down after a period when both mother and young had been standing (Table 7). In reindeer, oryx, bison, sable, and wildebeest, the young was first to lie more than 90% of the time. Mothers "followed" their young, ie, lay within 5 minutes after their young, an average of only 19% of the time (range 10-30%, data not shown).

TABLE 5. Percentage of standing bouts of young when mother was standing and when mother was lying*

Species	Mother-young relationship ^a	Mother (%)		Sign test ^b
		Standing	Lying	
Reindeer	F	94	6	+
Wildebeest	F	90	10	+
Oryx	H	87	13	+
Gazelle	H	70	30	+
Tahr	F	65	35	+
Bison	F	58	42	+
Sable	H	53	47	+
Ibex	F	45	55	-

*Ranked on "young stand while mother standing."

^aF, follower; H, lider.

^bFor the sign test, +, young standing bouts were more frequent when mother was standing than when mother was lying; the sign, -, indicates that young standing bouts were less frequent when mother was standing than when she was lying in this species ($P = .07$, two-tailed).

TABLE 6. Mean duration (in minutes) of standing bouts of young when mother was standing and when mother was lying down*

Species	Type of mother-young relationship ^a	Mother		Sign test ^b
		Standing	Lying	
Wildebeest	F	6.8	2.0	+
Gazelle	H	6.3	3.0	+
Sable	H	5.8	3.0	+
Oryx	H	5.8	2.3	+
Reindeer	F	4.8	2.4	+
Bison	F	4.4	2.6	+
Tahr	F	2.9	1.4	+
Ibex	F	2.8	2.0	+

*Ranked on "young stand while mother standing."

^aF, follower; H, lider.

^bFor the sign test, +, young standing bouts were of greater duration when mother standing than when mother lying ($P = .008$, two-tailed).

TABLE 7. Percentage of time mother or young was the first of the pair to lie*

Species	Type of mother-young relationship ^a	First to lie (%)		Sign test ^b
		Mother	Young	
Reindeer	F	2	98	+
Oryx	H	5	95	+
Bison	F	6	94	+
Sable	H	6	94	+
Wildebeest	F	9	91	+
Tahr	F	13	87	+
Gazelle	H	24	76	+
Ibex	F	25	75	+

*Ranked on "young first to lie."

^aF, follower; H, lider.

^bFor the sign test, +, young was the first to lie more often than mother ($P = .008$, two-tailed).

DISCUSSION

Spatial Patterns

Hinde's measure. Hinde's measure was designed to quantify the relative roles of primate mother and young in maintaining proximity. In the rhesus monkey, it changes from negative to positive as an infant matures, indicating that maintenance of proximity is due mostly to the mother in the early weeks and to the infant in later weeks [Hinde and Atkinson, 1970].

Our values for Hinde's measure and the percentages of approaches and departures made by the young (Table 2) suggest that the young played a greater role in maintaining proximity after week 1. Although this result seems intuitively reasonable, we believe that it should not be accepted without further research as we encountered serious methodological problems with these measures. Hinde's measure proved less satisfactory for ungulates than for primates for two reasons: 1) There are three possible interpretations of small values, and 2) it is difficult to adequately define approaches and departures.

Our values for Hinde's measure during the first week were relatively small. The three sets of circumstances that can lead to small values are 1) The mother makes the majority of both approaches and departures, 2) the young makes the majority of both approaches and departures, and 3) each of the pair makes about the same number approaches and departures. Our week 1 data contained examples of all three. The mother made the majority of both approaches and departures in oryx, reindeer, and sable, the young made the majority of both in ibex, and mother and young contributed about equally in the wildebeest.

In Hinde's rhesus study, an approach was scored when the distance between mother and young changed from more than 60 cm to less than 60 cm and a departure when the distance between them changed from less than 60 cm to more than 60 cm. We modified these definitions for ungulates by scoring an approach when the distance between mother and young decreased to less than 1 mother-length and a departure when this distance increased to more than 1 mother-length. Lickliter [1984] independently adopted these definitions in his study of the domestic goat, and apparently encountered no problems with them.

However, we found both definitions inadequate. Mothers of many hider species do not approach to within one mother-length before making contact with their young. Rather, they pause several meters away [Walther, 1979; Murdock et al, 1983] and make soft vocalizations, apparently calling the young out of hiding [Lent, 1974; Leuthold, 1977; Walther, 1979; Murdock et al, 1983]. In followers also, maternal cues such as tail-wagging or head-bobbing may induce the young to approach [Lent, 1974; Walther, 1979]. In both cases, we would credit the young with an approach, although the mother initiated the interaction. Thus, we strongly suspect that the use of this definition underestimates the role of the mother. The definition of a departure proved unsatisfactory because a distance of one mother-length is too small to distinguish movements of the young during activity periods from departures that terminate these periods.

Hinde recognized a similar problem in primates. As the young mature, "the mere crossing of an arbitrary boundary could become potentially misleading as a guide to who was responsible for the change in the proximity" [Hinde, 1974]. This problem may be more severe in young ungulates as they are born at a more advanced

stage of development than young primates, and long distance communication between mother and young begins early in life.

Distance between mother and young when both were lying. As suggested by Walther [1979], the distance between mother and young when both were lying proved more useful in separating followers from hiders than the distance between them, irrespective of activity state [Ralls et al, 1986, 1987]. During the first week after birth, follower mother and young lie close together, and hider mother and young lie far apart. In both followers and hiders, mothers were more often the second of the pair to lie and thus appeared to be largely responsible for these characteristic spacing patterns.

Temporal Patterns

Our data on changes in activity state suggest that the mother plays the major role in initiating activity periods in both followers and hiders. Mothers were usually the first to stand after both animals had been lying and young often stood within the next 5 minutes. It is likely that young respond to their mother's stand in part because it represents a potential suckling opportunity.

The activity state of the mother influenced the duration of the young's activity bouts. Most bouts were very short (less than 3 minutes), although some were considerably longer (5 to 15 minutes). Short bouts occurred regardless of the mothers activity state, but longer bouts usually occurred when the mother was standing. During activity bouts, young are particularly vulnerable to detection by predators. By restricting activity to times when the mother is active (thus relative vigilant), young may reduce their risk of predation.

Walther [1979] states that young hiders normally do not stand until the mother approaches the hiding place to initiate an activity period. However, many of the short bouts (≤ 3 min) we observed in hider young (37% in the gazelle and 56% in the sable) occurred while the mother was lying. During such bouts, the young stood, stretched, and repositioned itself before lying down again. During longer bouts it suckled, played, and interacted with its mother.

Young were usually the first to lie down after both mother and young had been standing, suggesting that they terminate their own activity periods when they tire. Mothers rarely followed suit by lying within 5 minutes (in contrast to the high frequency with which young stood within 5 minutes of their mother).

CONCLUSIONS

1) Despite striking differences between followers and hiders in spacing between mother and young and the frequency of mother-young interactions, we find no differences between the two groups in the way spatial and temporal patterns are maintained.

2) Follower mother and young lie close together and hiders far apart. The mother is largely responsible for maintaining these characteristic spacing patterns, although appropriate distances are maintained when the young is the second to lie.

3) The mother usually initiates activity bouts of the young.

4) Activity bouts of the young are longer and more frequent when the mother is standing than when she is lying.

5) Young often stand when their mother is lying, but these activity bouts tend to be relatively short (≤ 3 min).

6) Young usually terminate their own activity bouts.

7) Hinde's measure proves less satisfactory for ungulates than for primates due to the multiple interpretations possible for low values of the measure and difficulty in adequately defining approaches and departures.

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