Zoo Biology 2:105–125 (1983)

Behavioral Development in Okapis and Giraffes

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Observations on the behavioral development of two okapi calves and one giraffe calf were made at Brookfield Zoo. The following behaviors were monitored for 4 to 6 mo after birth: nursing duration and nursing attempts, mother-infant distance, bunting the mother's udder, lying, moving, maternal grooming, mother and infant autogrooming, object licking, tail chewing, and contact by others in the herd. Behaviors in both species showed oscillating patterns with high levels of mother-infant contact behaviors at 3–4 wk, 9–11 wk, and 14–15 wk in okapis. Giraffe infants showed similar oscillations with high periods of contact about 2–5 wk later than those in okapis. Other behaviors oscillated in concert with these, with specific correlations occurring between nursing behaviors and grooming behaviors.

A main difference between okapi and giraffe development centered around maternal motivation during the high contact (regressive) periods. In okapis, after 10–12 wk there was a low rate of nursing success, whereas in giraffes the percentage of success in nursing rose with later behavioral oscillations. The regressive periods became conflict periods in okapis, whereas in the giraffe, the mother initiated the periods. This difference was in accordance with the unique strategy of infant rearing in wild giraffes in which there is an extended "hider" period when older calves are left together in shaded areas with an adult sentry. Field studies also indicated probable oscillations of mother-infant contact and a prolonged period of the mother initiating contact with her calf.

Key words: okapi, giraffe, behavioral development, ontogeny

INTRODUCTION

The mammalian mother-infant bond, thought gradually to lessen over time, instead follows a pattern of fluctuations in which the infant grows away from its mother and then regresses in order to grow forward again [Horwich, 1974a]. This growth pattern is better likened to a spiraling of development [Gesell, 1939; Ames and Ilg, 1964]. The function of this fluctuating growth varies; in social mammals such as the Siberian ibex, it may function to maintain the matrifocal herd structure

Received for publication January 4, 1983; accepted February 11, 1983.

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during rut and calving periods [Horwich et al, 1977, 1982], whereas in *Colobus* monkeys it seems to function in general troop cohesiveness [Horwich and Wurman, 1978]. However, the fluctuating nature of development seems to be a genetically basic phenomenon which occurs in less social species as well.

Regressive periods are periods of mother-infant conflicts of interests. Trivers [1974] noted that during such conflict one tactic an infant can employ to extend contact is the use of regressive behaviors which may cause the mother to respond to the infant with additional parental care. Okapi and giraffe development exhibit a contrast in "conflict" during regressive periods which is related to the species' general social structure. Since okapis are thought to be less social than giraffes we hypothesized a difference in 1) whether or not regressive periods occur in both species and 2) whether they would be periods of equal mother-infant conflict.

METHODS

Observations were made on mother-infant interactions between an adult okapi, Fredericka, and her two successively born infants. The first female infant observed, Mufuh, was born July 14, 1973. Observations were made on her from July 14 to November 2, 1973, for two 1.5-h periods per week for a total of 50 h. The second infant, Doko, a male, was born on March 14, 1976, and was observed between March 25 to July 3, 1976, for 1-h periods between 7–8 AM and 5-6 PM for a total of 102 h. The okapis were contained in an indoor cage about 20 ft square which was connected to an outdoor yard 40 by 100 ft. Both indoor and outdoor enclosures were ordinarily on display to the public. Mother and male infant were housed apart from the other okapis until April 3, 1976, when a pregnant female, Osceena, was introduced to them.

A third calf, a female giraffe, Ann, was observed in order to compare her development with the development of the okapis. This infant, born to Joy on November 22, 1974, was observed from the time of birth until May 17, 1975, initially during morning hours (9–11 AM) and later from 1–3 PM for 1.5–2-h periods. Initially the mother and infant were caged alone indoors in two cages with an open door between them (total dimension 40 by 50 ft). During week 10 a second male calf was born to the herd, and all giraffes except the new mother and calf were squeezed into one small cage, making observations difficult. Observations were resumed the following week when the cage doors were reopened. In mid-April all giraffes were let outdoors when weather permitted into an enclosure 40 by 100 ft. Additional data on a male calf born to the giraffe herd on July 3, 1975, were taken by Stokes [1975], initially under the guidance of one of the authors (R.H.H.) and will be discussed with the other data.

Behaviors observed in one or more of the calves included the following weekly data averaged per hour of observation: duration of nursing, mother-infant distance noted at 1 min intervals, frequency and success of nursing attempts, frequency of bunts directed at the mother's udder, minutes during which the infant was lying and moving, number of minutes during which maternal grooming and mother and infant autogrooming occurred, number of minutes during which licking of objects occurred, the frequency of tail chewing on others, the frequency of contact (touching or licking) by other herd members. Observation periods were chosen for convenience of the researcher and to work around existing zoo schedules and regulations.

RESULTS

Okapis

Both Okapi calves showed similar fluctuations in nursing time (Fig.1) which initially peaked at weeks 3 and 4, then decreased considerably during weeks 5-8, and increased in the first regressive period during weeks 9–11. Nursing decreased again only to show a third peak during weeks 14–15, Mufuh showing a more marked peak, during this time. In concert with nursing duration, Figure 2 shows the percentage of time spent by Mufuh within 4 and 16 ft of her mother. After 6 wk, she was almost always within 16 ft of Fredericka. The greater time spent away from the mother during the early weeks was due to the "hider" tendency of this species in which the calf is usually left alone lying in the forest or in the outdoor yard in this case, and the calf does not follow its mother around much during this period [Rabb, 1978; Lent, 1974]. However, after 6 wk, two peaks in mother-infant distance association were apparent at 8 wk and at 12–14 wk, just preceding and merging with the high nursing times.

Figure 3 considers the frequency of nursing attempts by the two calves. Both clearly show a later increased number of unsuccessful attempts (after 11 wk in Doko and 14 wk in Mufuh). The percentage of successful nursing attempts in both calves (Fig. 4) is very high until 10 wk, after which a radical change occurs. In Doko at week 16 nursing again becomes successful, even though by this time the nursing level is quite low. The two calves deviate in bunting the mother's udder with their nose (Fig. 5). Mufuh shows high peaks of bunting during nursing regressive periods and periods of high levels of unsuccessful nursing. With Doko the higher bunting levels increase after 9 wk (except week 14) with a major rise in week 16. This matches the low percentage of successful nursing except during week 16, which had a high success rate for nursing.

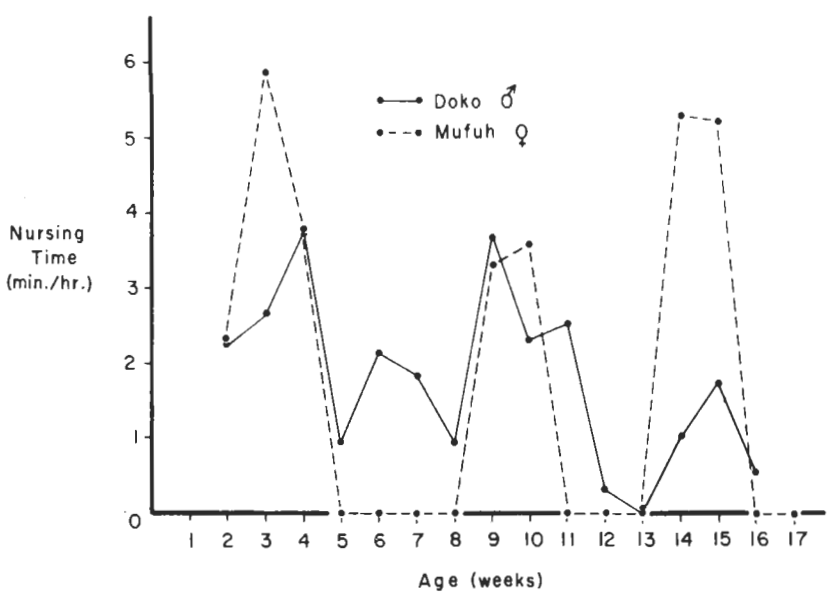

Fig. 1. Nursing time in minutes per hour as a function of age in weeks for two okapi calves.

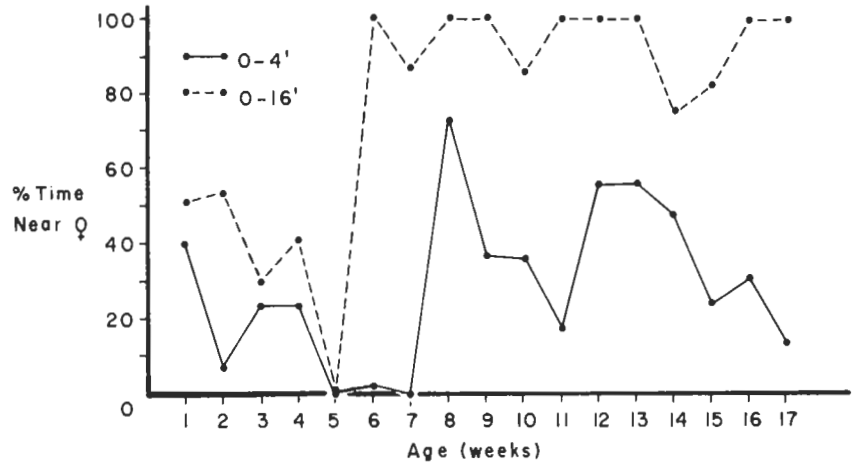

Fig. 2. The percentage of time (1-min interval samples) in which Mufuh was within 4 and 16 ft of her mother as a function of age in weeks.

Figure 6 shows the inverse relationship between lying and moving. Basically, after 13 wk the amount of lying decreases and the moving around the cage increases.

Licking behavior or grooming takes a number of forms in okapis which all seem interrelated and connected with nursing as well. Figure 7 shows maternal licking of her two calves. Comparison of nursing (Fig. 1) with the time during which Fredericka licked them (Fig. 7), shows how clearly she responded to the infant's nursing periods. Similarly Osceena, the pregnant female who was caged with Fredericka and Mufuh, showed a tendency to groom Mufuh at these same times. Autogrooming also seems correlated with nursing (Fig. 8). Both calves show an initial grooming of themselves between 2–6 wk, a second peak between 8–12 wk, and a smaller rise at 15 wk. Figure 9 exhibits Fredericka's autogrooming. She showed high autogrooming and licking of Mufuh during the first two of Mufuh's autogrooming peaks. With Doko a similar but weaker trend occurred. Doko's grooming of Fredericka was never high during the study, but two rises at 9 and 14 wk were in accordance with the other grooming and nursing periods. Mufuh's grooming of Fredericka occurred mostly after 9 wk and was not so distinctly periodic but seemed to be interspersed between Fredericka's grooming her. It seemed to somewhat overlap and conform to the nursing cycling with high periods occurring at 10 wk, 12–14 wk, and at 16 wk. Two other instances of licking behaviors were recorded. One was the infant's licking of inanimate things, which included food, water, salt, hay, and the bars. Figure 10 shows that this behavior fluctuates inversely with nursing periods. The other behavior is anal licking by the infant of itself or by the mother of the infant. The infant's self licking is at a low level that fluctuates with the regressive periods, except for a peak at 7 wk. Maternal anal licking (Fig. 11) is very high during the first week, then resumes a low level until weeks 8–9 and 12–14, when it was high. This is interesting in that it precedes the general maternal grooming (Fig. 7). Anal licking is important to okapis because of a specific rectal anatomy which makes it necessary for

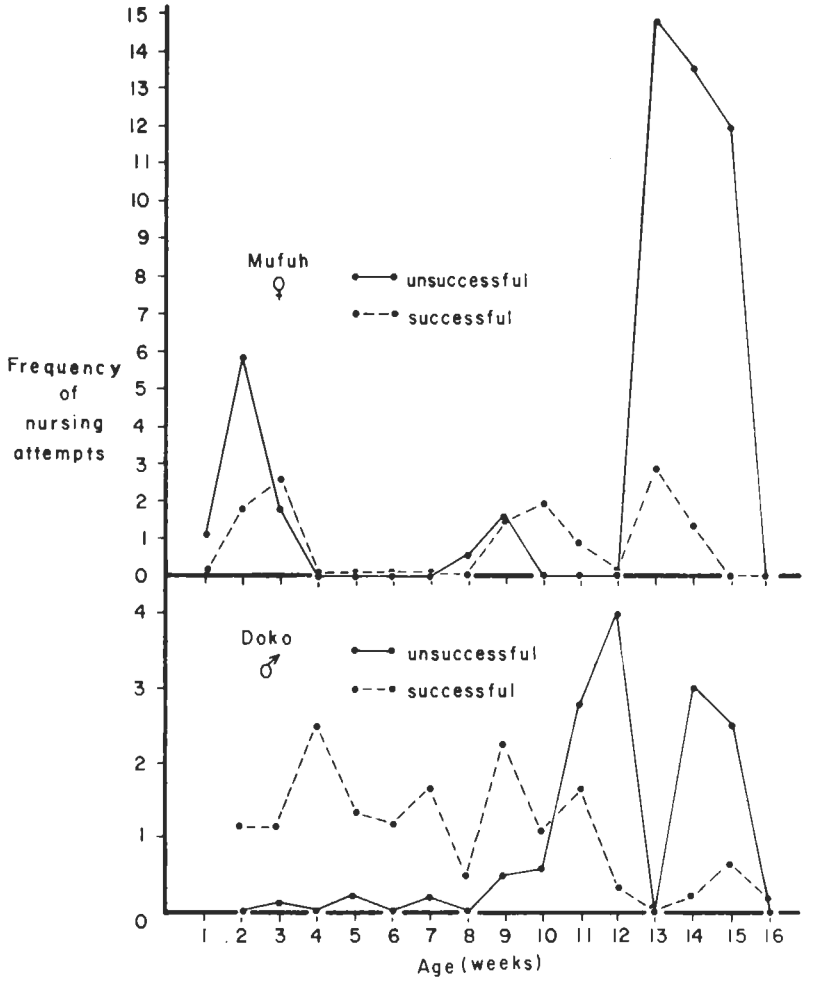

Fig. 3. The frequency of successful and unsuccessful nursing attempts by okapi calves, Mufuh (top) and Doko (bottom), as a function of age in weeks.

the mother to lick out feces for the first two months and to have the rectum cleaned out in hand-reared infants [Rabb, 1978].

Giraffe

Although it was thought that okapis and giraffes differed in development, okapis initially being hiders and giraffes followers [Kitchen, 1977], it has been found that giraffes are hiders as well [Langman, 1977]. Thus in making observations on a giraffe calf, we were seeking to find what developmental differences occurred between the two species.

Figure 12 shows that in duration of nursing two regressive periods occur at 11 wk and 20–22 wk. Both peaks are 2–5 wk later than those in okapis. Data on a male

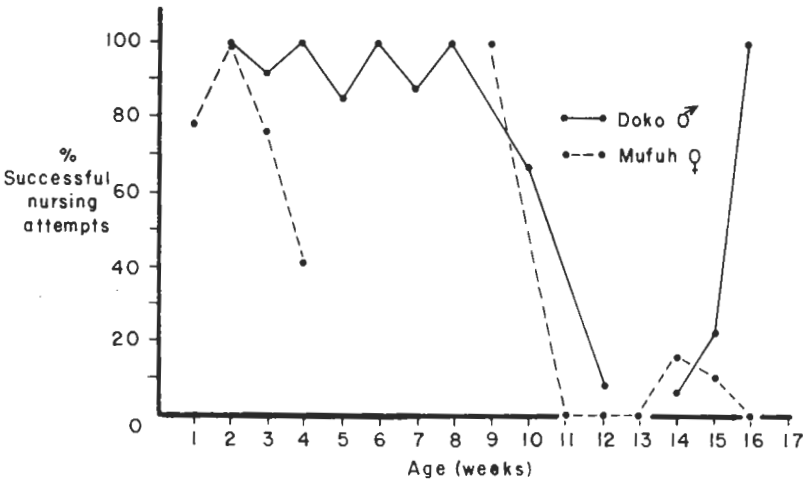

Fig. 4. The percentage of successful nursing attempts by the two okapi calves as a function of age in weeks.

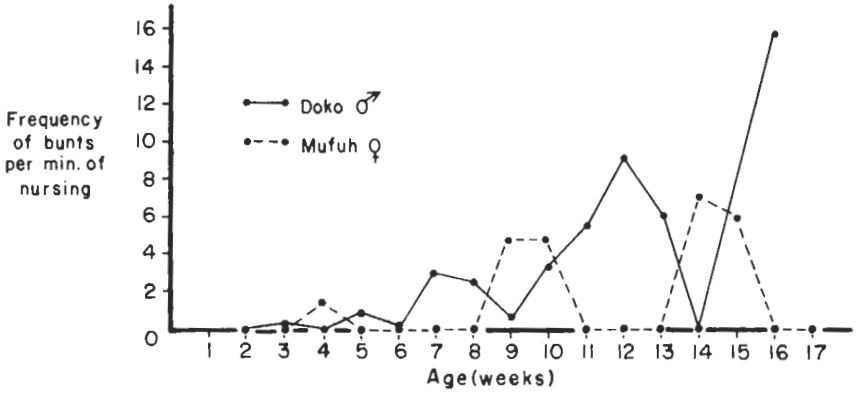

Fig. 5. The frequency of bunting per minute of nursing in the two okapi calves as a function of age in weeks.

giraffe calf born in July 1975 [Stokes, 1977] confirms this data indicating a slight increase in nursing at 10–12 wk and a much greater peak at 18 wk, slightly later than in okapis. Data on a calf observed for three months showed only rare nursing after 25 days [Kristal and Noonan, 1979]. These authors note that this is consistent with other weaning ages. Figure 13 shows nursing attempts. In all cases except during the first week, unsuccessful attempts are higher. Data from Stokes [1977] agree with this. However, Figure 14 shows that the percentage of success closely follows the nursing fluctuations with greater success at 1, 10–13, and 19–22 wk. This contrasts with

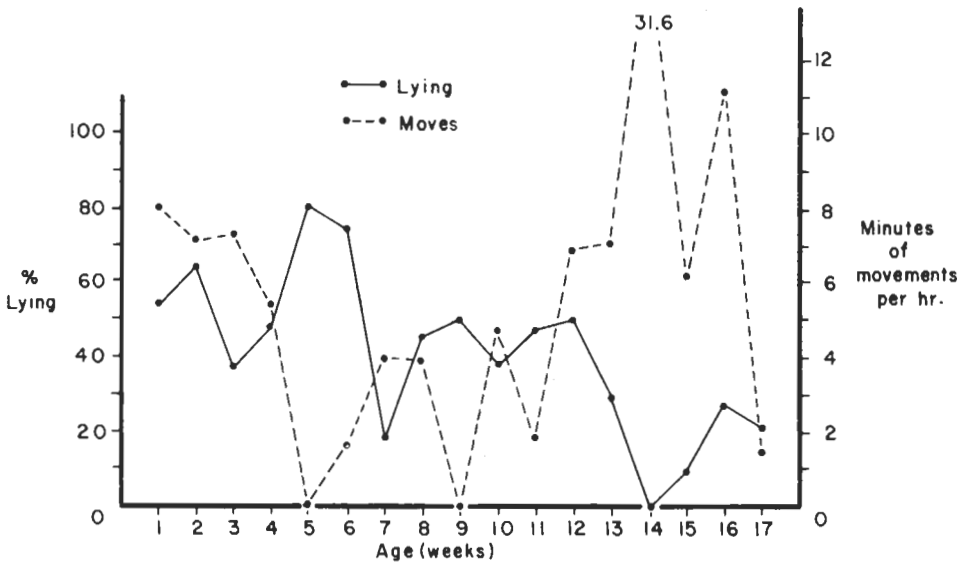

Fig. 6. The percentage of time lying or minutes in which moving occurred in Mufuh as a function of age in weeks.

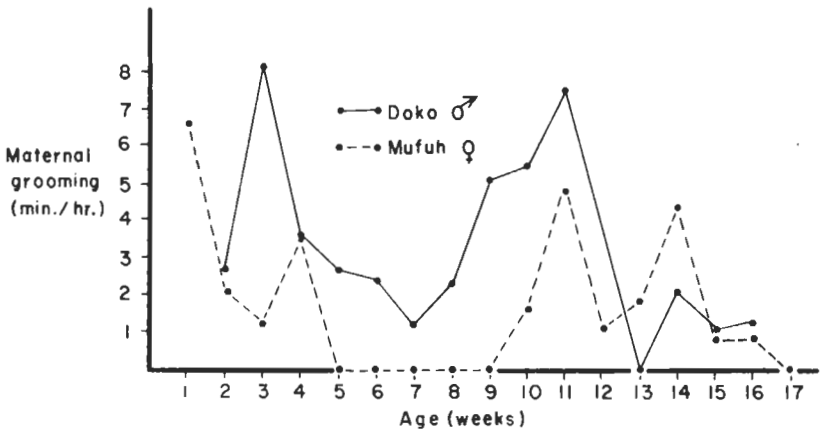

Fig. 7. The minutes per hour in which Fredericka groomed her two calves as a function of age in weeks.

okapis, which show an early success and a later lack of sucesss, except for Doko's last regressive period. Stokes's calf [1977] shows a high rate of success during the first 4 wk and from 15–18 wk, but intermediate data are sketchy. The giraffes rarely show bunting during nursing. We never observed bunting, while Stokes [1977] noted it only once during week 23, when it was done hard enough to induce the mother to move.

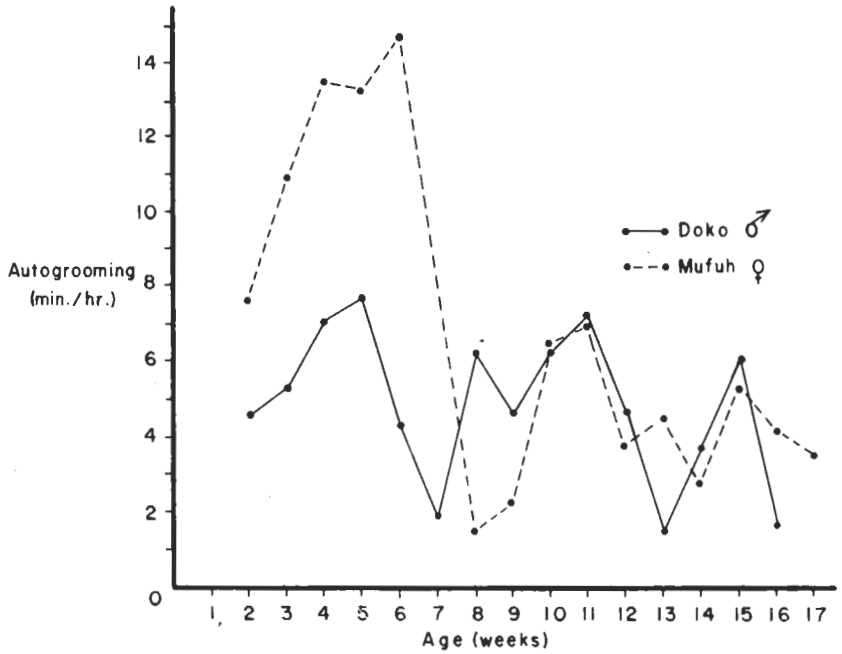

Fig. 8. The minutes per hour during which autogrooming occurred by the two okapi calves as a function of age in weeks.

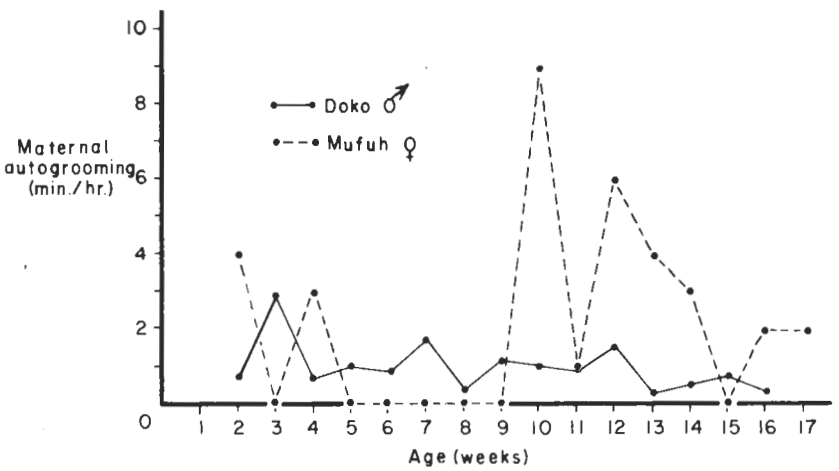

Fig. 9. The minutes per hour during which the mother groomed herself as a function of the age in weeks of her two calves.

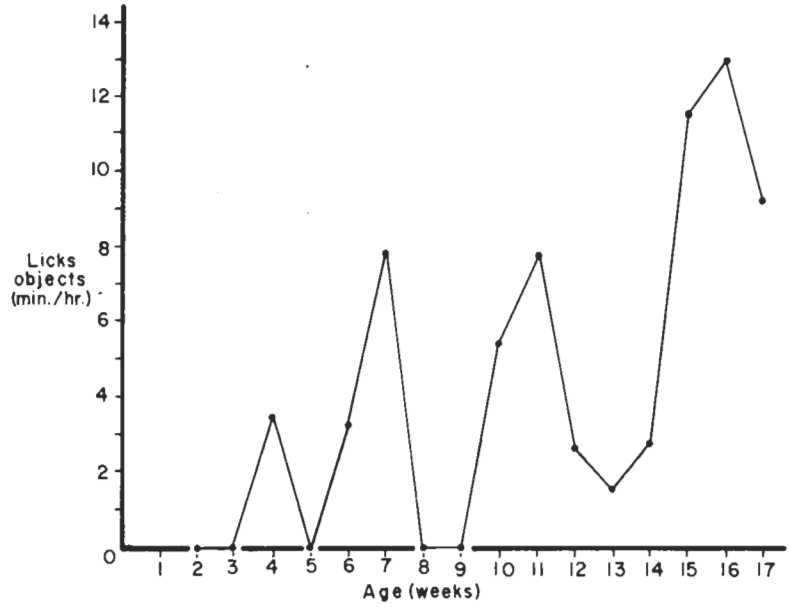

Fig. 10. The minutes per hour during which Mufuh licked inanimate objects as a function of age in weeks.

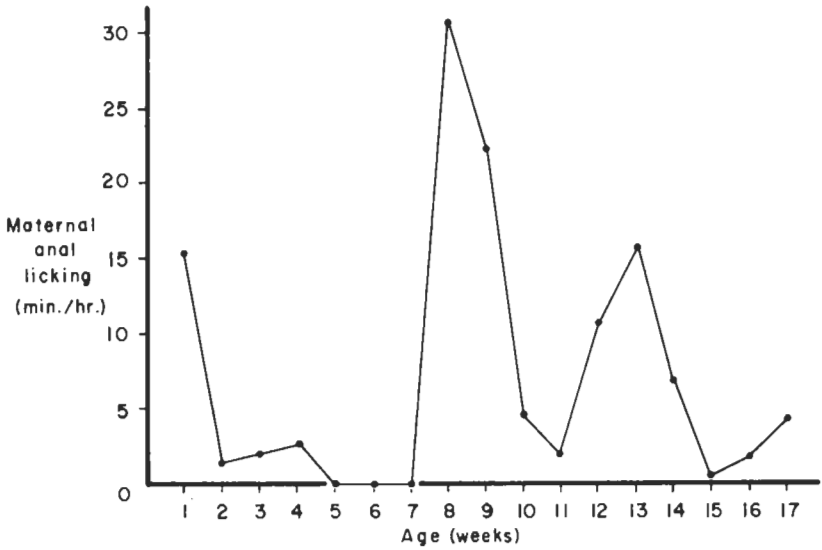

Fig. 11. The minutes per hour during which Fredericka licked Mufuh's anus as a function of age in weeks.

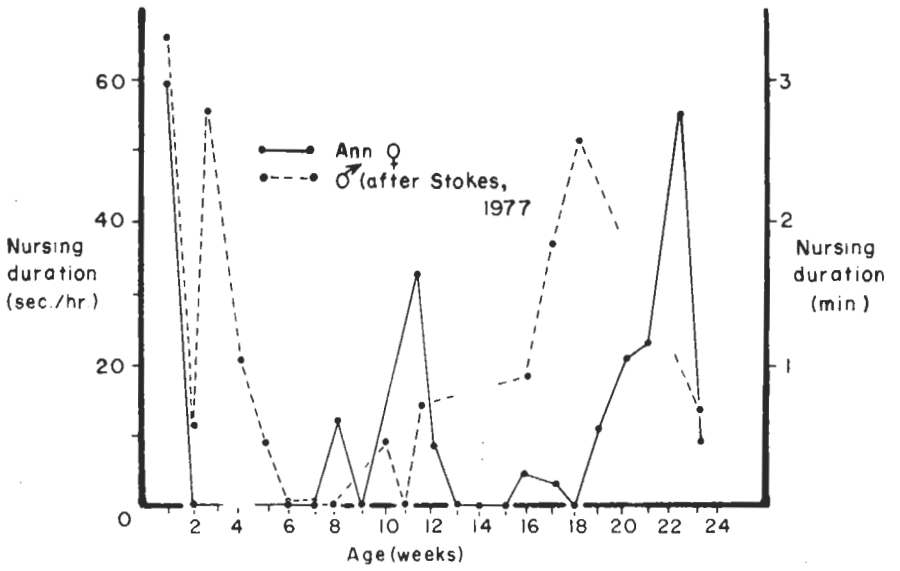

Fig. 12. Nursing time in minutes per hour as a function of age in weeks for the giraffe calf, Ann, and the calf studied by Stokes [1977].

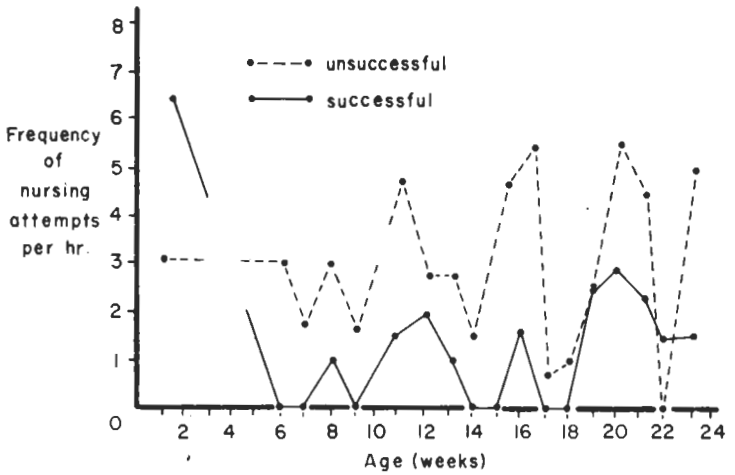

Fig. 13. The frequency of successful and unsuccessful nursing attempts by the infant giraffe as a function of age in weeks.

Tail chewing on the mother or other giraffes, which is not seen in okapis, shows an inverse relationship to nursing with high rates at 7–11 wk, and again at 14–18 wk (Fig. 15). This is a similar relationship to that of a langur's thumb-sucking to nursing [Horwich, 1974b].

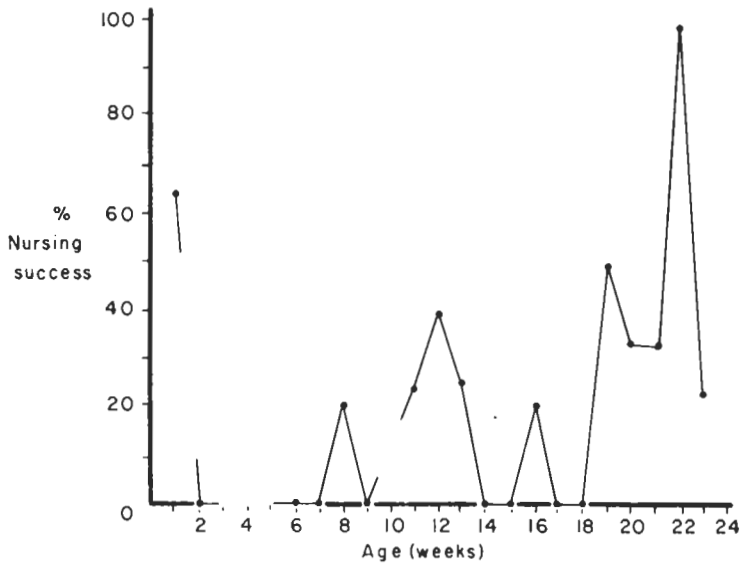

Fig. 14. The percentage of successful nursing attempts by the giraffe calf as a function of age in weeks.

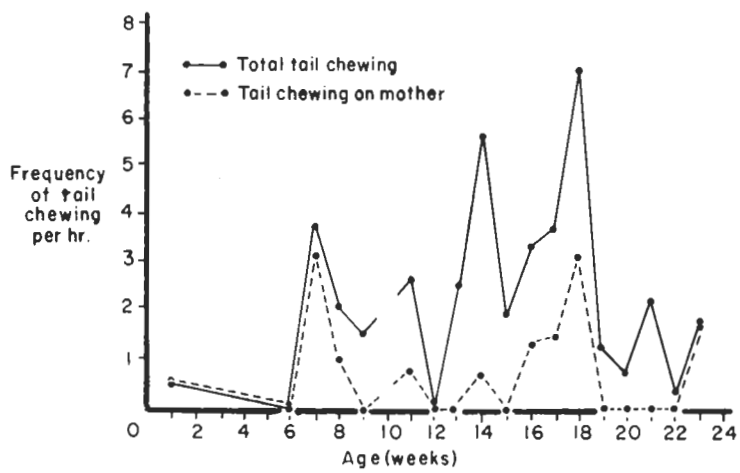

Fig. 15. The frequency per hour of tail chewing by the giraffe calf on her mother and other herd members as a function of age in weeks.

The frequency of mother-calf contact, which includes naso-nasal contacts as well as licking bouts (Fig. 16), shows high maternal attention during the first 7 wk and again at 12 wk. Stokes's [1977] mother shows a high rate of contacting her calf in the first 3 wk and again at 15–18 wk. Our calf, Anne, contacts her mother at a high

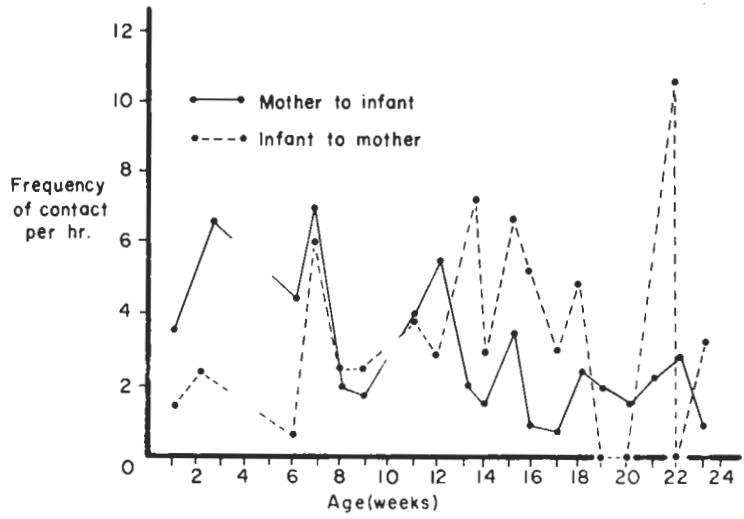

Fig. 16. The frequency of contact behaviors initiated by the giraffe mother and calf as a function of age of the calf in weeks.

rate at 7 wk, 13–16 wk, and again at 21 wk. The Stokes calf shows high rates during weeks 1 and 3, and again at 17-18 wk. The ratio of mother/infant contact (Fig. 17) exhibits a clear picture with a high ratio at weeks 1-6, 12, and 19-22, all in syncrony with nursing and regressive peaks. This later maternal interest in her calf contrasts with okapi maternal care.

Other animals in the group also show an interest in our infant, particularly during the first regressive peak (Fig. 18). Their interest is most pronounced from 7–15 wk with other high points at 19 and 22 wk. Stokes also noted interest in her calf by other herd members at 7–10 wk. Our infant, in contrast, is most interested in contacting others from 13–18 wk and again at 21–22 wk.

Behavioral Correlations

Using the Spearman rank correlation tests it can be seen that each calf showed somewhat different correlations while certain patterns emerged (Figs 19–21). The main point is that behavioral oscillations occur and that some behaviors follow similar oscillations.

In all three calves there was an interrelation of nursing-closeness parameters. The giraffe showed positive associations of nursing duration with successful nursing attempts and with mother-infant distance, as well as successful nursing attempts with distance. Both okapi calves showed positive associations of nursing duration with successful nursing attempts.

In regard to nursing behaviors and those which might be thought to be antithetical, such as unsuccessful attempts and bunting, there is little agreement. The giraffe and Mufuh show positive correlations, whereas Doko shows a negative correlation of nursing duration and bunting.

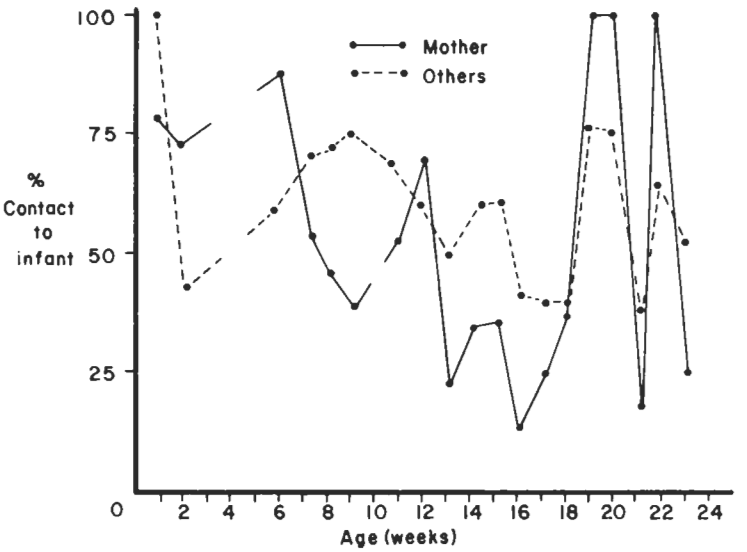

Fig. 17. The percentage of contacts initiated by the mother or other herd members of the total contact between them and the giraffe infant as a function of the infant's age in weeks.

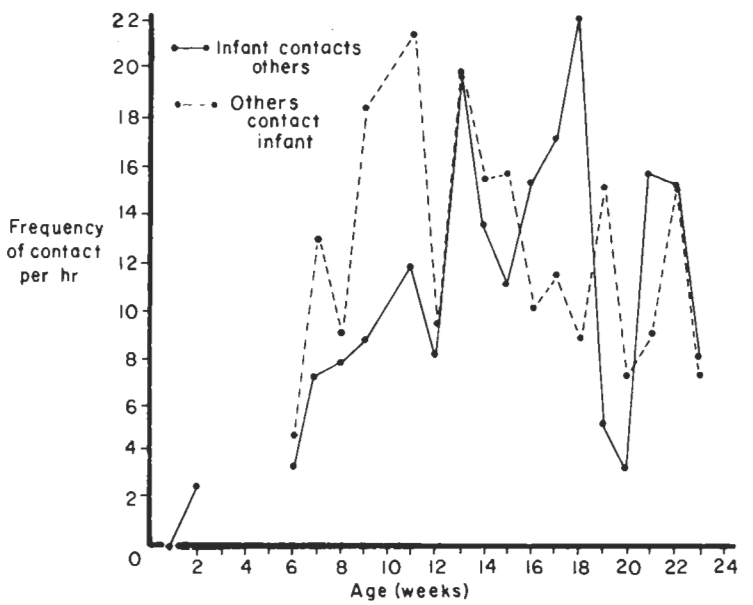

Fig. 18. The frequency of contacts per hour between the giraffe calf and other herd members as a function of its age in weeks.

	Nursing duration	Mother-infant distance	Successful nursing attempts	Unsuccessful nursing attempts	Bunting	Maternal grooming	Maternal anal licking	Maternal autogrooming	Infant autogrooming	Infant anal licking	Infant licking objects	Infant grooming mother	Lying	Moving
Nursing duration	—	NS +.14	** +.66	** +.83	** +.74	* +.44	NS +.10	NS +.07	NS +.06	* +.45	NS +.13	NS +.04	NS −.27	NS +.42
Mother-infant distance		—	NS +.23	NS +.19	NS +.34	NS +.28	** +.88	NS +.37	** −.75	NS −.19	NS −.16	* +.60	NS −.18	NS +.40
Successful nursing attempts			—	* +.53	* +.48	** +.82	NS +.15	* +.46	NS +.13	* +.45	NS +.07	NS +.34	NS +.24	** +.48
Unsuccessful nursing attempts				—	** +.68	* +.42	NS +.01	NS +.16	NS +.05	NS +.34	NS +.19	NS +.41	NS +.39	** +.65
Bunting					—	NS +.28	NS +.23	NS +.10	NS +.23	NS +.20	NS +.16	NS +.30	NS +.31	NS +.13
Maternal grooming						—	NS +.22	** +.62	NS +.11	NS +.33	NS +.06	NS +.38	NS −.02	** +.63
Maternal anal licking							—	NS +.36	** −.76	NS +.17	NS +.33	NS +.29	NS −.11	NS +.15
Maternal autogrooming								—	NS +.14	NS +.06	NS +.10	** +.62	NS −.03	* +.46
Infant autogrooming									—	NS +.24	NS +.02	NS +.28	NS +.38	NS −.08
Infant anal licking										—	* +.46	NS −.07	NS +.38	NS +.30
Infant licking objects											—	NS +.34	* −.56	NS +.07
Infant grooming mother												—	NS +.38	** +.64
Lying													—	NS −.34
Moving														—

The okapis show similar trends between nursing behaviors and autogrooming. Both calves show positive correlations of nursing duration with autogrooming behaviors. Both also show positive correlations of maternal grooming with maternal autogrooming.

The giraffe calf seemed to treat other herd members as mother substitutes, which is exemplified by the positive correlation of infant to mother contacts with infant to others contacts. However, behaviors involving other herd members contacting the calf were negatively correlated with the infant contacting its mother or others, and with its own autogrooming. This seems to indicate a lack of attractiveness on the part of the infant when it was seeking contact.

Figure 19 presents Mufuh's developmental trends. She shows correlations of nursing duration with maternal grooming and her own anal licking. This may indicate that maternal grooming stimulates the calf's autogrooming. In contrast, maternal anal licking is negatively correlated with Mufuh's own autogrooming, indicating the complimentary roles of the two. Mufuh also licks objects in correlation with licking

	Nursing duration	Successful nursing attempts	Unsuccessful nursing attempts	Bunting	Maternal grooming	Maternal autogrooming	Infant autogrooming
Nursing duration	—	** +.81	NS −.02	* −.60	** +.66	NS +.40	* +.44
Successful nursing attempts		—	NS −.02	* −.44	* +.54	* +.49	* +.54
Unsuccessful nursing attempts			—	NS +.27	NS +.31	* +.47	NS +.26
Bunting				—	NS −.24	NS −.04	NS −.11
Maternal grooming					—	* +.64	* +.52
Maternal autogrooming						—	NS +.27
Infant autogrooming							—

Fig. 20. Correlations within Doko's behaviors using the Spearman rank correlation test: *, .05 level; **, .01 level; +, positive value; −, negative value; NS, not significant.

Fig. 19. Correlations within Mufuh's behaviors using the Spearman rank correlation test: *, .05 level; **, .01 level; +, positive value; −, negative value; NS, not significant.

	Nursing duration	Mother-infant distance	Successful nursing attempts	Unsuccessful nursing attempts	Mother contacts infant	Others contact infant	Infant autogrooming	Infant chewing mother's tail	Infant chewing other's tail	Infant contacting mother	Infant contacting others
Nursing duration	—	** +.66	** +.81	NS +.36	NS −.07	NS +.34	NS −.06	NS +.24	NS +.36	NS +.32	NS +.16
Mother-infant distance		—	** +.62	NS +.20	NS −.30	NS .00	NS +.10	NS +.16	NS −.05	NS +.10	NS −.08
Successful nursing attempts			—	** +.55	NS −.09	NS +.33	NS +.20	NS −.38	* +.43	NS −.24	NS −.14
Unsuccessful nursing attempts				—	NS −.17	NS +.15	NS −.21	NS −.13	NS −.12	NS +.21	NS −.17
Mother contacts infant					—	NS +.14	NS +.18	NS −.13	NS −.32	NS +.03	NS −.37
Others contact infant						—	* −.41	NS −.35	* −.42	* −.56	** −.64
Infant autogrooming							—	NS +.20	NS +.24	NS +.20	* +.44
Infant chewing mother's tail								—	** +.67	NS +.34	NS +.19
Infant chewing other's tail									—	** +.69	** +.67
Infant contacting mother										—	** +.63
Infant contacting others											—

Fig. 21. Correlations within giraffe calf's behaviors using the Spearman rank correlation test: *, .05 level; **, .01 level: +, positive value; −, negative value; NS, not significant.

her own anal area. Close mother-infant distance is slightly out of phase with nursing duration, and thus the two do not correlate. However, it does correlate with maternal anal licking and correlates negatively with Mufuh's autogrooming. Mufuh's autogrooming does not occur while near her mother.

There is also an interrelation of mother and calf grooming. Fredericka's autogrooming correlates with her grooming of Mufuh and with Mufuh's grooming of her.

Other correlations include a negative correlation between lying and object licking, and moving with maternal grooming, maternal autogrooming, and the infant grooming her mother. Very little can be said of nursing attempts because successful and unsuccessful attempts fluctuated in syncrony, both correlating with nursing duration, moving, maternal grooming, or anal licking and bunting. Only successful attempts, however, correlate with Fredericka's autogrooming and Mufuh's self anal licking.

Doko's behaviors (Fig. 20) show correlations of nursing duration with successful nursing attempts, Doko'a autogrooming, maternal grooming, and a negative

correlation with bunting. Doko's very aggressive bunting shows a negative correlation with successful nursing attempts as well. Successful attempts positively correlate with Doko's autogrooming and autogrooming of his mother as well as Fredericka's grooming of him. Maternal grooming and Doko's autogrooming correlate as well as maternal grooming with maternal autogrooming.

Nursing duration in the giraffe calf (Fig. 2l) correlates with close mother-infant distance and with succcessful nursing attempts. Close distance also correlates with successful nursing attempts. The infant's self-touching correlates with the infant's contacting others. Tail chewing of others correlates with chewing the mother's tail and with the infant's contacting both her mother and other giraffes as might be expected. It also correlates with successful nursing attempts. The frequency of the infant's contacting others correlates with the infant's contacting her mother. Finally, successful and unsuccessful nursing attempts correlate positively.

DISCUSSION

Developmental Differences Between Okapis and Giraffes

It was thought that major differences would emerge in fluctuations of the mother-infant bond in okapis and giraffes because of species differences in sociality despite the close evolutionary relationship. Earlier investigations of Siberian ibex [Horwich et al, 1977], a very social species, show a clear indication of regressive periods which extend until reproductive maturity and seem to play a role in maintaining social bonds beyond the physical need of the young ibex [Horwich et al, 1982]. Thus it was expected that such an asocial* species as the okapi would not show regressive periods in development but would rather show a quicker and more radical break between mother and infant while the giraffes would instead follow the ibex pattern. Instead, both species show similar regressive nursing patterns, with the more solitary okapi showing a stronger tendency to nurse. The giraffe periods occur 2–5 wk later than those of the okapi. However, *the most significant difference noted was that during the regressive periods, the okapi infants were very aggressive in seeking maternal attention and nursing, which led to a real conflict between the mother and calf.* The calves bunted the mother's udder, and she would either walk away or actively reject the calf by kicking it. However, the okapi infants' persistence paid off as it did generally increase their success in nursing from the mother during regressive periods.

The giraffes had a very different approach. *The giraffe mother in this study was very attentive, and the increased nursing periods seemed due to the mother rather than the infant, who would approach and induce nursing during the regressive periods.* Figure 17 shows how the ratio of mother-to-infant contact increases dramatically during weeks 11–12 and weeks 19–22. Data on the male infant [Stokes, 1977] also show high levels of maternal initiated tactile encounters during the early weeks and again at weeks 17–18. Similarly, a high percentage of success in nursing occurs during the first 4 wk and again during weeks 16–18. Ruthe, who observed our infant, specifically noted that it was the mother who brought on this regression. However, the evidence that other animals in the group were also interested in grooming the infant during these times lends us to suspect that some change in the infant or action

*A recent study of wild okapi (Bodmer, R.E. and K.R. Gubista, Some Aspects of the Behavior and Ecology of Wild Okapi, ms.) has shown by indirect methods of observation that okapis may be more social than had been previously thought.

on its part, not perceived by Ruthe, made the infant more attractive to the mother at this time who thus allowed it to nurse more during these periods.

Trivers [1974] has constructed a hypothetical model which deals with mother-infant conflict and the amount of parental investment toward the offspring. He discusses a benefit/cost ratio (relating to reproductive success) which may take a certain graphic trend for any species over time. At a specific time in development, a conflict will arise as to whether parental care should continue or not. Weaning in mammals is an example of this conflict [Trivers, 1974] and Trivers also mentions that the infant can competitively deal with this conflict by employing regressive behaviors it had used at an earlier stage to get care it needed then. During regressive periods [Horwich, 1974a,b; Horwich and Manski, 1975; Horwich and Wurman, 1978; Horwich et al, 1977] infants revert to behaviors of an earlier age, staying closer to the mother, nursing or remaining on the tit more, crying more, etc. These regressive periods may coincide with Triver's periods of parental-infant conflict. In the okapi, maternal care in the form of grooming is high for the first four weeks while the infant nurses a great deal. Then care reduces presumably in relation to the infant's demonstration of its needing less. The infant lies less, nurses less, shows more movement and more independence. The mother monitors this and eases her care-giving. She then is not prepared for the infant's radical desire for more care again, and a conflict develops, probably the beginning of the weaning process. This was also noted in a spectacled langur [Horwich, 1974b]. As he began to regress, the mother showed a greater rejection of his nursing attempts, and as he persisted, she allowed him to proceed into the first regressive period at about 3 mo. Regressive periods may become peak times for the weaning process or other conflicts to occur. In Siberian ibex, regressive peaks in yearling primiparous females lead to direct reproductive conflict with the mother who is having her new calf and does not want the siblings around to interfere with it. The older siblings develop regressive tendencies at this time to maintain their herd bonds when they are most likely to be stressed [Horwich et al, 1977; Horwich et al, 1982].

In the giraffe infant, during at least the first and second regressive peaks, the mother, in contrast, took an active role in maintaining contact with her calf and no real conflict was noted at these times. During week 22 the mother actually approached the infant and would proceed to lick or touch it after which the calf would nurse. Indeed, nursing success during the regressive periods slowly increased, in contrast to the okapis, which showed a decrease. In the okapis, during the first period the female no longer approached the calf, and by the second regressive period she no longer groomed it and actively rejected it. The intensities of conflict increased radically in the form of calf bunting and kicking by the mother. This suggests that the parental-investment curve as suggested by Trivers [1974] may be more gradual in giraffes than okapis and that the real giraffe conflict period has not yet occurred by 22 wk.

Giraffe Mother-Infant Stategy: Supportive Field Data

Early studies of giraffes indicated they were poor mothers with weak mother-young bonds [Innis, 1958; Foster, 1966; Dagg, 1971; Foster and Dagg, 1972], mothers weaning and abandoning the calves as early as 1 mo of age [Foster and Dagg, 1972]. More recent studies have shown the mother-calf relationship lasts until 14–16 mo [Langman, 1977] or even 22 mo [Pratt and Anderson, 1979]. In addition, Langman [1977, 1982] has indicated that giraffes have a very specific and unique

mother-infant relationship based on the giraffe's unusual physiology. Of the two main early ungulate mother-infant contact systems, some calves are "followers" of their mothers immediately after birth while others are "hiders," ie, the newborn calves remain hidden most of the time during the first weeks while the mothers feed and return at intervals to nurse them [Lent, 1974; Langman, 1977; see Walther in Langman, 1977]. Both the giraffe and okapi are of the hider type. However, the giraffe seems to have extended this hiding period [Langman, 1982]. The initial period of hiding, which may last as long as a month, is similar to that of other "hiders" in which the calf remains hidden but isolated from other giraffes. After this time, giraffe mothers deposit their calves during the day in a shaded area with other calves, and usually one mother remains behind. This mother acts as a sentry who, when danger approaches, alerts and flees with her own calf. The other calves then follow her away from the danger as well [Langman, 1982]. Langman [1982] has found that this extended hiding period serves to protect the young giraffes from the heat and water loss since they have the same physiology as adults but do not actively drink water in the wild.

The mothers do not abandon the young but rather have evolved a system for extending the hiding and protection of the calf. In agreement with this extended mothering, this study indicates that mother giraffes show more interest in their calves at later stages than other mammalian mothers which we have studied thus far. Kristal and Noonan [1979] also noted an indication of this bond when a mother was separated from her 90-day-old calf. The mother bucked and kicked at the cage door in response to the calf's bleating. During early regressive periods we found that it was the giraffe mother who took the initiative in contact rather than the calf as in okapis. In the field as well when the mother giraffe returns to a calving pool, the young one, rather than approaching, stands and watches its mother's approach. After the mother contacts (nudging and licking) the calf, it then nurses [Langman, 1977]. We would hypothesize that at some later stage after this extended hiding period, a reversal would occur in which the mother would show less interest and the calf would have to be more persistent in its contact.

Indeed, field data indicate that there are later mother-calf reattachment periods. Mother-calf distances observed but lumped at irregular intervals [Pratt and Anderson, 1979] indicate trends similar to the zoo situation. The percent of 5-min intervals when mother-calf distance was under 6 m was high until 2 mo, radically dropping at 3–4 mo and increasing again at 5–7 mo. Since the data of older calves was increasingly lumped into larger time blocks as the calves aged, oscillations are not evident. However, the data clearly show an increase after 5 mo, continuing to a substantial increase in older calves (13–22 mo), indicating probable regressive periods during the yearling age [Pratt and Anderson, 1979]. Data on the life history of a young male in the wild [Dagg and Foster, 1976] support the above evidence as well. Observations on when the mother was present or absent indicate her presence during the first 3 mo with her absence during months 4 and 6 and her presence in month 5, which corresponds to the captive data of 18–22 wk (Fig. 12). Thereafter, from 7 until 22 mo the mother was present. Although the data is sketchy, it indicates a lull in contact with a reattachment period from 7 to 22 mo, as does the data of Pratt and Anderson [1979]. Closer observation of individuals would probably indicate oscillations between those months. Data on suckling also indicate a longer bond, with calves observed continuing to suckle until 9–10 mo (one captive male suckled until 13 mo) [Guggisberg, 1969],

and even captive adults may attempt to suckle [see Dagg, 1970 in Dagg, 1971; Innis, 1958].

CONCLUSIONS

1. Okapi and giraffe calves both show developmental behavioral oscillations.
2. The calves of both species show early regressive or maternal reattachment periods, with those of the giraffes being 2–5 weeks later.
3. During these early regressive periods the okapi calves were more aggressive in maintaining contact, while the giraffes were more passive.
4. The giraffe mothers were more attentive in maintaining contact during these early regressive periods, which seems related to the giraffe survival strategy in the wild.
5. General mother-infant contact in giraffes appears more passive in nature. There is not a relationship of maternal grooming with nursing in the giraffes as there is in okapis. This may be related to giraffe mother-infant contact prior to nursing as noted in the wild.

ACKNOWLEDGMENTS

We would like to thank keepers Merle Nelson, Ann Norkey, Tony Blueman, and Ann Owens for help and information on the animals. Thanks also go to Dr. Marie Tucker for encouraging and commenting on the work. This study was done with the help and consent of the Chicago Zoological Park and its director, Dr. George Rabb.

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