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Seasonal Variation in Mother-Daughter Groupings in Siberian Ibex *(Capra ibex siberica)*

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The association of three pairs of mother-yearling Siberian ibex was recorded by noting the distance between the mothers and daughters at 5-min intervals for 1–2-h observation periods for 1 yr at the Brookfield Zoo. Monthly averages of climatological data were obtained. All three pairs showed a seasonal fluctuation of association, with a higher level during spring and fall-winter and a low degree of sociality in midsummer and late winter. Within the high social periods, short 1–3-wk periods of low association occurred, which were correlated to actual rut and calving times in individual females. The mother-daughter associations were most highly correlated to day length and sunrise of the climatological measures. These data seem to support the original hypothesis that these social periods, which began as developmental associations in the infant, aid in keeping the matrifocal herd structure together despite aggression at the times of rut and calving. It seems also that the social cycling, although linked to reproductive cycling, has its own physiological mechanism.

Key words: breeding, grouping, ibex, seasonality, sociality, ungulates

INTRODUCTION

As in many species of mammals [Horwich, 1974a], behavioral ontogeny in young Siberian ibex follows developmental oscillations in which the calves spend periods close to their mother followed by periods when they are not as close to her [Horwich et al, 1977]. We hypothesized that these periods of close contact, which have been termed *regressive periods,* are at the roots of mammalian sociality. Such periods have their origins in infantile nursing and are periods of reattachment to the mother. The weakening of the mother-infant bond is gradual and there is evidence

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that suckling occurs well beyond the age when it is needed for physical nourishment, occurring in many yearling ungulates [Lent, 1974, Horwich et al, 1977] and even in animals over 2 yr of age [Schloeth, 1966]. The social relationships, especially in females, extend beyond weaning and are sometimes prolonged for generations, as in red deer [Darling, 1937]. Eisenberg [1966] notes that the mother-infant grouping is one of the origins for sociality in mammals. Further, the normal oscillations of infant regressive periods are a mechanism which allows for close group contact, particularly at times when the social bonds may be stressed by crisis periods such as rut and calving. We wished to know if these oscillations continued into adulthood and what happened when the yearling bred and had her own calves. Second, we were interested in how the developmental oscillations related to seasonal cycles.

METHODS

Since earlier behavioral studies of ibex had shown mother-calf distance to be a good indication of social attachment [Horwich et al, 1977] we used it to look at maternal attachment in older ibex. As infants age, many mother-infant contact behaviors drop out. Consequently, in older animals distance is one of the few consistently reliable measures of attachment. Using an approximation of ibex body length, we recorded distances in four foot lengths (1.22 m) for three mother-yearling pairs at 5-min intervals for 1–2-h periods on a naturalistic oval (65 m × 40 m) gunite island at Brookfield Zoo for a total of 260 h from April 1975 to May 1976. Since earlier work had shown that 16 ft was the most meaningful for yearlings, we lumped all interval distances into less or greater than 16 ft (four body lengths = 4.88 m) between mother and yearling. Additional data from a preliminary study of matrilineal affiliations during September to December 1975 showed a clear difference between mother-daughter pairs and nonrelated females. From 16 h of 5-min interval samples on the three mothers in this study, the mother-daughter pairs averaged 74% of the time within 16 ft (4.88 m) of each other, while nonrelated females averaged only 4% of the time within 16 ft (4.88 m) of the same females. Despite this low association, there was an indication of an increase of contact between nonrelated females, following the same seasonal pattern as observed in the following results.

Additional data on courtship and other behaviors were noted during the rut season and the dates of calving were recorded. An estimation of the individual estrus periods was calculated from the times of calving, using a gestation period for ibex of 150–180 d [Asdell, 1964]. Monthly climatological data for Midway Airport, collected by the National Climatic Center, for the observation periods were used to test for correlations between weather factors and the mother-daughter distances using the Spearman Rank Correlation test.

RESULTS

Figure 1 shows the individual developmental record of the three yearlings starting at 46 wk of age. Jenifer (top) showed a period of frequent contact with her mother, Gazelle, until a sudden drop in contact at wk 53 due to the birth of a new infant to Gazelle. This was followed by several short returns to a high level of contact and then a low level of contact at 63 wk. There was an increase of contact after wk 65 which gradually increased to a very high level after wk 78. Close contact was

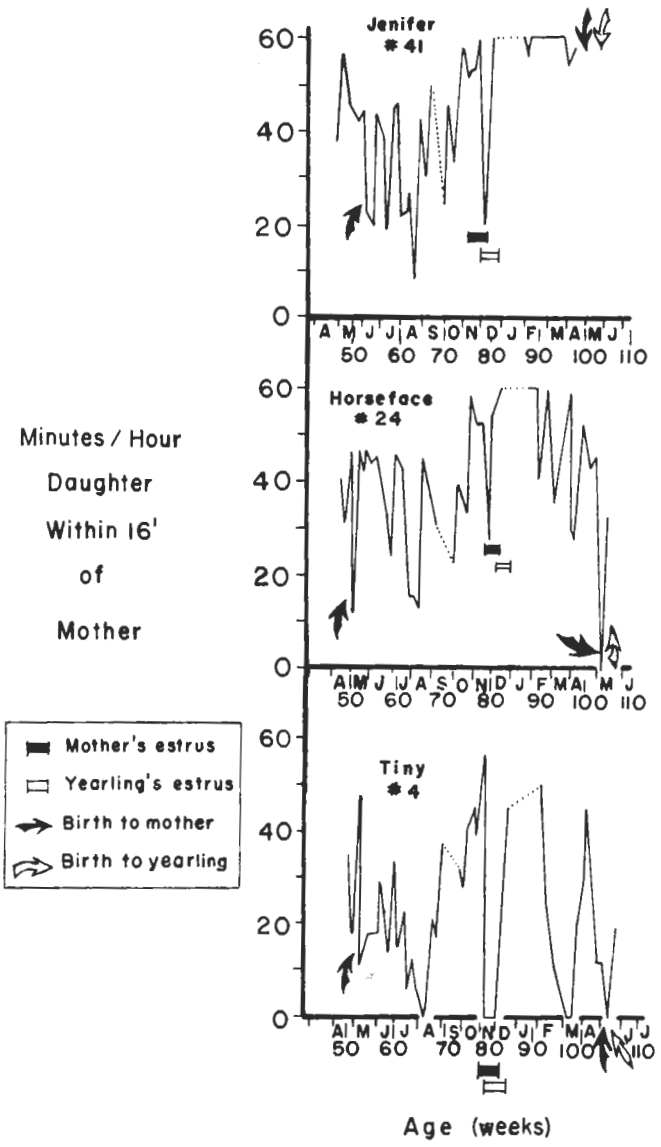

Fig. 1. Minutes per hour of observation when mother and daughter ibex were within 16 ft of each other, as a function of age of the daughter (weeks) and of the season (based on 5-min interval samples).

maintained with her mother for the rest of the observations, which terminated with the death of her mother during a stillbirth in April. There was a 1-wk exception during wk 79 which was probably related to Gazelle's estrus.

Horseface (Fig. 1, middle) showed a similar pattern of contact with her mother, Lucy. There was a relatively high rate of contact for wk 50–57 except for the week following the sibling birth. Then a fluctuating, decreased contact during wk 58–75 was followed by an increase to a high level of proximity in wk 76–90. Week 80 showed a marked decrease, again related to estrus. During that week, Lucy was

consistently courted by the dominant adult male. After wk 90 there was a fluctuating decrease and then an increase again between wk 97–103. At wk 104 Lucy had a calf and her contact with Horseface was reduced to no time spent within 16 ft (4.88 m) of her. Closeness increased the following week and no data were taken after that. Horseface had her own calf 2 wk later.

Tiny's mother, Mama, was a very aggressive female who did not allow Tiny as much contact with her when compared to the other mother-yearling pairs. Consequently, the fluctuations in the time spent between mother and daughter (Fig. 1, bottom), were much more clear-cut and perhaps more indicative of the changes which occurred. As with the other young, a high level of contact occurred to wk 52. After the birth of Tiny's sibling, during wk 52, a marked drop in contact occurred. Although Tiny often attempted to be near Mama, she was consistently threatened. Her response was to remain in visual contact, watching her mother from a considerably greater distance. This continued until Tiny was able to regain close contact 3 wk after the birth. Then, as with the other yearlings, she showed a decrease in contact through wk 66. A marked increase in contact was reached by wk 70 and it remained high until wk 97 except for a 3-wk period during wk 79–81. During this period Tiny was actively courted by the other large adult male. Judging from the birth of Mama's infant the following spring, Mama was also in estrus within a week or two of Tiny. This may have accounted for the 3-wk drop instead of 1 wk as in the other yearlings. After wk 91 there was a drop in contact between the two females and an increase after wk 99. Both Tiny and Mama had their infants within a week of each other on wk 106 and 105, respectively. Tiny's baby was born dead, after which she increased contact with her mother. Observations were terminated after that.

Figure 2 shows the mother-daughter contact lumped for all three pairs. There was a comparatively high rate of contact (regressive period) during the calving season (wk 46–61). Fluctuations (wk 51–54) were based on the birth of siblings. A low period of progressive growth (wk 62–70) followed and another regressive period occurred from wk 70 through 90. A dip at wk 80–85 showed response to estrus periods. High contact was maintained to 100 wk, after which a drop-off occurred, related to the new sibling births.

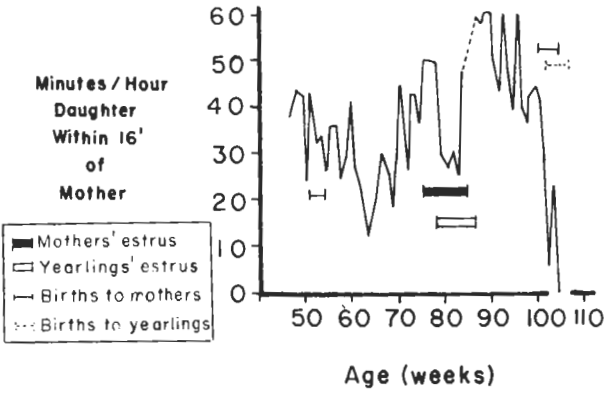

Fig. 2. Averaged data of three mother-daughter pairs indicating minutes per hour of observation when pair members were within 16 ft of each other, as a function of age of the daughters (weeks; based on 5-min interval samples).

Figure 3 makes the picture clearer, showing the data lumped on a seasonal basis, the three yearlings having all been born within a month of each other. There was a clear pattern indicating a high level of contact during April-May, the calving season. Major fluctuations were seen in April due to the three sibling births (Fig. 3, bottom). This was followed by a seasonal reduction in mother-daughter contact until the lowest level was reached in July-August. Then in November, prior to rut, there was a rapid increase in contact which remained high through early February. A major dip was seen in November which coincided with the collective mother and daughter estrus periods; but mother-daughter proximity was quickly resumed in December at a very high level. In February-March a decrease in contact again occurred. Again in March-April, prior to calving, an increase in contact occurred but it rapidly dropped in April-May with the sibling births. The last observation week in May showed a probable increase after that.

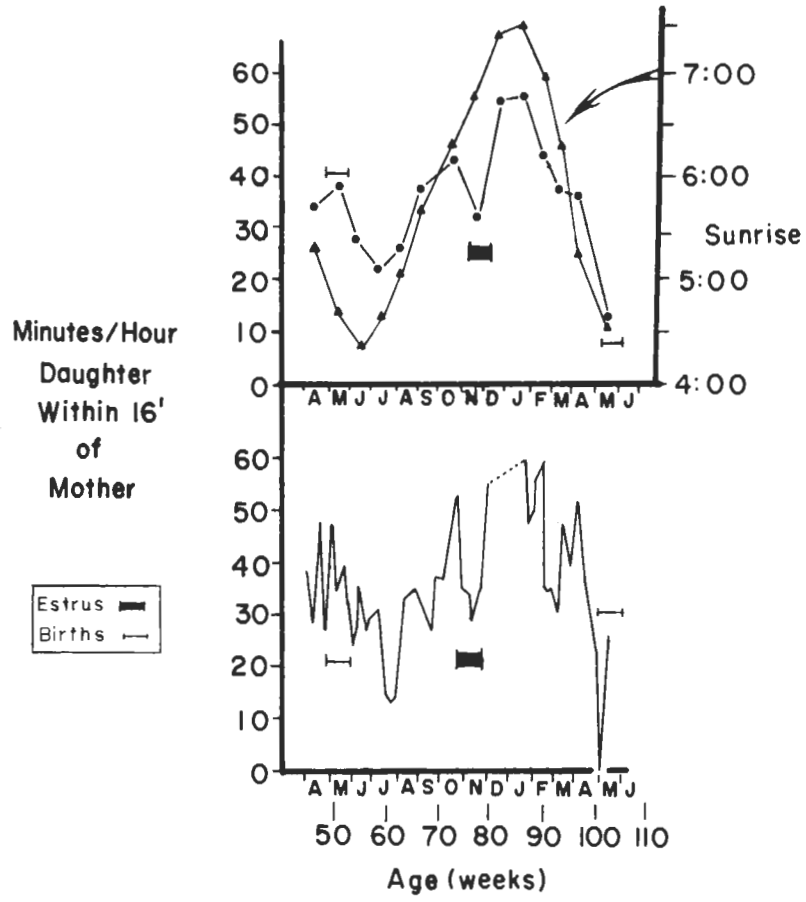

Fig. 3. Averaged data of three mother-daughter pairs indicating minutes per hour of observation when pair members were within 16 ft of each other, as a function of age of the daughters (weeks) and of the season (based on 5-min interval samples). Top: data plotted monthly along with monthly averages of time of sunrise. Bottom: data plotted weekly.

In order to understand how weather affected social actions of the ibex, monthly averages were compared to each other and to the seasonal changes in mother-yearling distance using the Spearman Rank correlation test. Table 1 shows the correlation values, which are arranged in descending order of values indicating probable behaviorally important factors.

As can be seen from the correlation of ibex distances with weather factors, correlations existed with measures of sunshine, temperature, and wind in that order, with no correlations shown to barometric pressure, precipitation, or 24-h sky cover. This seems to indicate that day length and/or time of sunrise are the most important factors and the correlations between weather factors indicate their dependence on the light-seasonal changes. Figure 3 (top) shows the correlation graphically.

DISCUSSION

Oscillating Growth and Mother-Infant Bonds

For a great number of mammalian species, the development of behaviors proceeds in a spiral/cyclic fashion of regressive-progressive periods [Horwich, 1974a,b]. The regressive periods which are essentially maternal reattachment periods are characterized by the infant's successful attempts to maintain contact with its mother at a level higher than the preceding period and are thus reminiscent of its early infancy. This occurs despite actual weaning. These oscillations are the raw material which can be modified for varied social purposes, such as to synchronize troop sociality, as in *Colobus* monkeys [Horwich and Wurman, 1978], or as noted in ibex, to maintain the herd structure despite other social stresses to it. Indications of oscillations are also noted in suckling success in some populations of bighorn sheep at approximately 8 wk [Berger, 1979], in suckling in okapis and giraffes [Kitchen, 1977; Horwich et al, unpublished data], and in play in domestic sheep [Sachs and Harris, 1978].

There is relatively little information on the weakening of the mother-infant bond [Lent, 1974]. Literature shows conflicting times of weaning for many species of ungulates. For example, in 1962 Courturier [Lent, 1974] notes that ibex are frequently weaned by 3 months yet he also notes that they are suckled through winters with better than average grazing conditions. In a wide variety of ungulates, suckling in yearlings has been observed [Lent, 1974; Horwich et al, 1977] and Lent further notes that weaning and bond breakdown are not synonymous, close mother-daughter relationships occurring much beyond weaning. Darling [1937] indicated matriarchal groups of four generations of female red deer and Lent [1974] notes that these bonds may be disrupted at parturition only to be renewed later. This study shows that mother-daughter associations may break down gradually, never actually dissolving but continuing to cycle year after year. What may begin as a developmental oscillation showing a species-specific developmental time scale, in ibex, then grades into a seasonal cycle of sociality which extends into breeding adulthood.

Developmental Oscillations and Seasonality

The function of such regressive actions on the part of both mother and infant was hypothesized to aid in keeping the matrifocal herd structure together despite the crisis periods of calving and rut when the herd structure has other social forces pushing it apart [Horwich et al, 1977]. We feel that the data for one complete season supports this original hypothesis. The regressive periods start prior to both the calving

TABLE 1. Correlation values of mother-daughter distance with environmental factors and between environmental factors from the Spearman Rank Correlation test

	Sun measures					Temperature				
	Sun-rise	Day length	Total hours sun	% sun	24-h sky cover	Dew point	Avg temp	Avg wind speed	Avg barom press	Avg pptn
Mother-daughter distance	+.78 **	−.78 **	−.58 *	−.49 *	+.25 NS	−.73 **	−.67 **	+.53 *	+.34 NS	−.33 NS
Sunrise		−.98 **	−.88 **	−.73 **	−.61 *	−.82 **	−.82 **	+.66 **	+.50 *	+.39 NS
Day length			+.95 **	+.75 **	−.65 **	+.80 **	+.83 **	−.61 *	−.52 *	+.36 NS
Total hours of sunshine				+.75 **	−.44 NS	+.68 **	+.71 **	−.54 *	−.45 NS	+.39 NS
% of possible sunshine					−.77 **	+.69 **	+.73 **	−.53 *	−.23 NS	+.06 NS
24-hr sky cover						−.40 NS	−.19 NS	+.40 NS	−.02 NS	+.42 NS
Dew point							+.99 **	−.89 **	−.22 NS	+.13 NS
Average temperature								−.88 **	−.24 NS	+.17 NS
Average wind speed									−.07 NS	+.08 NS
Average barometric pressure										−.41 NS
Average precipitation										

*Indicates significance at .05 level.
**Indicates significance at .01 level.

and estrus periods and a high level of contact is attained before either of these periods emerge, thus establishing the regressive periods as entities in themselves which may be linked with the physiological changes of estrus and birth but are not direct responses to either of the reproductive events. Data on female-female grouping in walia ibex, which are less social and show a somewhat reverse rut-calving season, showed a higher sociality during June-November, which encompasses the birth season, and a slight peak during the breeding season [Nievergelt, 1974].

Immediate responses to new infants and to the estrus periods were obvious from the data and those changes lasted less than 3 wk and usually only 1 wk, after which the higher mother-daughter contact was reestablished.

Studies linking hormonal events with mother-infant contact are difficult to find because hormones are mainly thought to act at the adult level. However, in a preliminary search we have noted one study in prepubertal ponies which indicates a bimodal peak in plasma follicle stimulating hormone (FSH) at about 10 wk and 34 wk in normal spring-born colts [Wesson and Ginther, 1979]. This resulted in higher levels in late June-July and again in late December-January. Later-born fillies showed an unclear pattern probably exhibiting the conflict of developmental and seasonal oscillations. Data on LH and testosterone in young rams also indicate a bimodal peaking at about 4 and 20 wk [Ducharme et al, 1979], thus showing an inverse relationship with the play oscillations [Sachs and Harris, 1978].

A hypothetical figure (Fig. 4) based on this study and that of Horwich et al [1977] shows what we think is the pattern over 2 yr in the development of a young female ibex in reference to maternal contact from birth through reproductive maturity to the birth of her first calf. Data from an excellent field study on yearling red deer [Guiness et al, 1979] show seasonal mother-yearling associations comparable to those shown by this study. However, due to the difference in data collection methods it is difficult to coordinate the results of the two studies. In the red deer study, sampling involved only one mother-young count per day when mothers were within 50 m of their young (ie, within the same group). Our study involved discrete recordings over

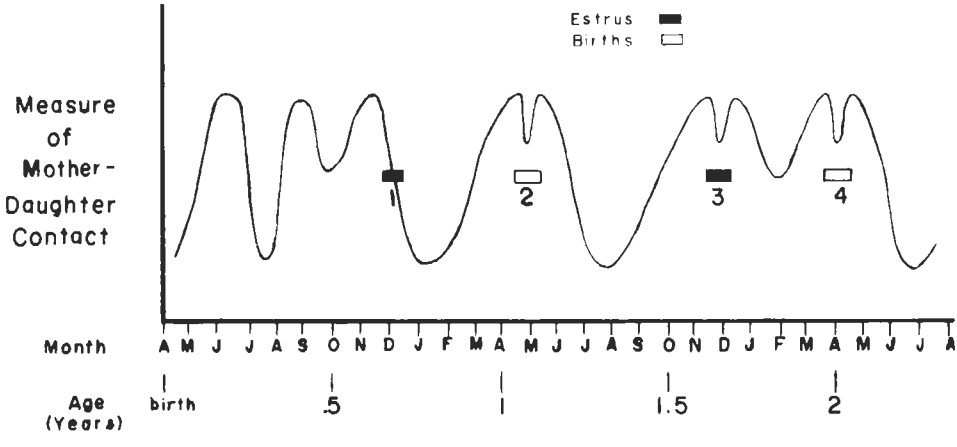

Fig. 4. A hypothetical measure of mother-infant contact as a function of developmental age and the seasons (in months).

a continuous observation period of mother-daughter associations (within 16 ft or 4.88 m of each other). Thus, the red deer study shows trends which are similar to the ibex trends but the ibex data additionally includes a rhythm of sociality that seems to be present over and above the reproductive cycling.

Guiness et al [1979] found that although red deer form a matriarchal herd, the mother-yearling associations decrease at times of the year which are particularly dependent on the rut and calving periods, and specifically dependent upon whether or not a mother is pregnant and nursing a calf. They found that female offspring associate with the mother more than males do. Additionally, yearlings associate with nonbreeding mothers more often than those which have had a new sibling and specifically, at the time of calving, there is a decrease in association. This was true for the ibex, the period of decrease lasting from 1 to 3 wk. At birth the female red deer show increased aggression and do not tolerate the yearling being nearby. They also noted that all hinds associate less with male yearlings during the rutting month. This seems due to aggression of stags toward the younger males who have already developed breeding capability. The main difference between the deer and ibex studies was that Guiness et al [1979] found that females showed little change in association with mothers throughout the year as yearlings. This difference could be related to the difference in sensitivity between the two methods of measuring mother-daughter associations.

In summary, ontogenetic oscillations of mother-infant contact eventually grade into and synchronize with seasonal cycling. The high rate of sociality during winter and spring seasons coincide and are superimposed on the rut and calving periods and thus function to maintain the matrifocal bonds despite the stress to these bonds due to the males' interference during rut and the mothers' aggression during calving [Horwich et al, 1977]. There are longer, less social periods—one of long duration during summer and a shorter dip between the rut and birth periods. Although linked behaviorally to the reproductive cycling this tendency toward sociality seems to have its own schedule and may be regulated by a separate hormonal mechanism, perhaps related to FSH or estradiol.

Growth Oscillations and Herd Management

Ibex developmental and seasonal oscillations suggest that young animals are more secure during certain periods than others. For herd management, when separation of individuals is required, these data indicate that separation might be less traumatic if done in concert with observations on what period the animal is in. In the ibex, 10–15 wk and 29–30 wk of age, and during the summer months seems the least social time and thus the least traumatic times for separation. Additionally, since ibex form close mother-daughter bonds, it may be better to thin groups along matrilineal lines with mothers and daughters separated and sold together as units.

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