Association of seasonal reproductive patterns with changing food availability in an equatorial carnivore, the spotted hyaena (Crocuta crocuta)

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Reproductive seasonality was examined in an equatorial population of free-living spotted hyaenas (Crocuta crocuta) in Kenya. The study population was observed continuously for 10 years, during which time the dates of all births, conceptions, weanings, and cub deaths were recorded. Local prey abundance was estimated two to four times per month, and rainfall was recorded daily throughout the study period. Births occurred during every month of the year, but a distinct trough in births occurred from February to May. This trough occurred approximately one gestation period after the phase of the annual cycle during which prey animals were least abundant in the home range of the hyaenas, and conceptions occurred most frequently when food abundance was greatest. Neither rainfall nor cub mortality were correlated with births or conceptions. Thus, although spotted hyaenas are capable of breeding throughout the year, they exhibit a moderate degree of seasonality that most likely reflects responses to seasonal variation in energy availability.

Introduction

Spotted hyaenas (Crocuta crocuta) are large, gregarious carnivores that occur throughout much of sub-Saharan Africa, from approximately 28° S of the equator to approximately 17° N (Mills, 1990; Estes, 1991). In most populations studied to date, births occur throughout the year, but in many of these populations, patterns of births include distinct seasonal peaks or troughs (Smithers, 1966; Kruuk, 1972; Lindeque and Skinner, 1982; Frank, 1986; Mills, 1990). The environmental factors that account for reproductive seasonality in this species are unknown. In the present study, reproductive data were obtained over 10 years from one large Crocuta clan inhabiting a tropical grassland in eastern Africa. The aims of the study were to determine whether reproduction varies seasonally in this population and, if it does, to identify the environmental factors that might promote such seasonality.

Materials and Methods

Study population

The study site was the Talek area of the Masai Mara National Reserve, in southwest Kenya, situated at 1°40’ S, 35°50’ E, at a mean elevation of 1575 m above sea level. This is an area of open, rolling grasslands year round by large concentrations of several different ungulate species, the most numerous of which are Thomson’s gazelle (Gazella thomsonii), topi (Damiscus korrigum) and impala (Aepyceros melampus). Each year, these resident antelope populations are joined for 3–4 months by large migratory herds of wildebeest (Connochaetes taurinus) and zebra (Equus burchelli). The migratory herds typically arrive in the Talek area in June or July and depart in September. Maximum temperatures in this ecosystem are 27–28°C in every month of the year, and minimum temperatures vary from 13° to 16°C (Sinclair, 1995). In contrast to these constant temperatures, rainfall varies greatly from month to month (Sinclair, 1979).

The subject population was one large Crocuta clan inhabiting a home range of approximately 65 km². The Talek study clan usually contained 20–23 breeding females, 10–12 adult immigrant males, and 30–40 cubs and subadults. Cubs were < 12 months old, and subadults were older individuals that had not yet reached reproductive maturity. All hyaenas in the study clan were known individually by their unique spots, and their sex was determined from the dimorphic glans morphology of the erect phallus (Frank et al., 1990). From June 1988 to April 1998, observers monitored hyaenas in the study area 23–31 days per month, except during April 1991, when Talek hyaenas were observed for only 14 days.

Assignment of dates for births, deaths, conceptions and weanings

In postpubertal male Crocuta, the testes are constantly large and descended, testicular histology does not vary seasonally (Lindeque and Skinner, 1982) and, therefore, fertilizations can occur throughout the year. Female Crocuta
bear their litters in isolated natal dens, and then transfer them to a communal den when cubs are 2–5 weeks old. When cubs were first observed here, at natal or communal dens, their ages were estimated to ± 7 days on the basis of their pelage, size and other aspects of their appearance and behaviour (for example, folded ears, callous pads on carpals, motor coordination). Birth dates were assigned to litters on this basis. Since the duration of gestation is 110 days (Schneider, 1926; Kruuk, 1972), conception dates were calculated by subtracting 110 days from birth dates. Conceptions were inferred exclusively from parturitions, and so conceptions resulting in failed implantation or embryo resorption could not be measured. The date on which any cub was last seen was assigned as its date of death. All hyaenas disappearing before 12 months of age were considered to have died because female Crocuta generally spend their entire lives in their natal groups, and males do not disperse before 2 years of age (Smale et al., 1997). Weaning conflicts and cessation of nursing indicated when cubs were weaned. Weaning conflicts between cubs and their mothers are easily observed in this species because of the characteristic begging behaviour and loud whining exhibited by cubs at this time. All weaning conflicts were recorded in field notes as critical incidents (Altmann, 1974). In determining weaning dates, all field notes were searched for observations of weaning conflicts and nursing behaviour when mother and cubs were found together. If mother and cub were not found together frequently after the last observed nursing bout, the weaning date was identified as being midway between the last nursing bout and the next sighting of mother and cub together without nursing. However, only intervals of ± 20 days were used in this analysis, so all weaning dates used here were accurate to within ± 10 days.

Parity of breeding females

Nulliparous adult females could be distinguished from parous females on the basis of the condition of the pseudopenis. The pseudopenis of a female hyaena is torn when her first litter is born (Frank and Glickman, 1994), leaving a large patch of pink scar tissue on the posterior surface of the phallus. Throughout the current study, the condition of the posterior surface of the phallus in all nulliparous females ≥ 2 years of age was monitored carefully during the phallic erections commonly exhibited when hyaenas greet each other (Kruuk, 1972; East et al., 1993). Thus, even when the first litter of a female was lost before her cubs first appeared above ground, it was possible to determine reliably (± 10 days) when she had delivered her first litter.

Estimation of prey abundance and rainfall

Prey abundance in the Talek area was estimated regularly by counting all antelope and zebra found within 100 m of 4 km transect lines in two different areas of the home range of the study clan. Both transects were run two to four times each month, between 08:00 and 10:00 h. Ungulate census estimates were averaged for each month of the study. Monthly variation in prey counts has been described by Holekamp et al. (1993). The number of prey animals counted per census ranged from 24 to 4306, with a mean of 427 ± 50 (n = 240 censuses). For some analyses, prey abundance each month was divided into five categories on the basis of the mean number of ungulates counted, as follows: ≤ 250, 251–500, 501–1000, 1001–1500, and > 1500. Throughout the study period, rainfall (mm) was recorded at 24 h intervals from a rain gauge situated within the home range boundaries of the study clan, and mean monthly rainfall was calculated from daily records over the 10 year study period.

Data analysis

The number of births, conceptions, weanings and cub deaths were recorded monthly for 113 months. In addition, the percentage of females conceiving litters each month was calculated from the total number of females not currently pregnant ≥ 7 months after parturition with surviving cubs. Seven months after parturition represents the shortest interval at which any Talek female has been known to conceive her next litter (Holekamp et al., 1996), so this percentage represents the proportion of females with potential to conceive that actually did conceive litters that month. Each of these dependent variables was examined in relation to rainfall and prey availability using analysis of variance (ANOVA). In some analyses, the month of the year was included as a covariate with another independent variable of interest, using analysis of covariance (ANCOVA). Mean values were presented ± SEM, and differences between groups were considered statistically significant when P < 0.05.

Results

Seasonal patterns of births and conceptions

During the 10 year study period, 145 litters were born to Talek females, and births occurred during every month of the year. The mean number of births occurring each month was 1.21 ± 0.12 (range, 0–6), but the number of births varied significantly by month (Fig. 1a; ANOVA: F = 2.047, df = 11,102, P = 0.031). There was a distinct annual trough in births from February to May, during which only 16% of all births occurred. The number of adult females known to conceive litters each month ranged from 0 to 6. The number of litters conceived varied significantly by month (Fig. 1b; F = 2.276; df = 11,102, P = 0.016). Females in this population typically conceive 7–15 months after their last parturition. The percentage of females that were ≥ 7 months post partum that actually conceived new litters here varied significantly by month (F = 2.210, df = 11,92, P = 0.020).

Seasonal patterns of cub mortality

The timing of births may be influenced by mortality induced by rains or other sources. Rainfall varied significantly
from month to month (Fig. 2a; $F = 2.482$, df = 11,104, $P = 0.008$). Because some flooding of hyaena dens was observed during heavy rains, the hypothesis that Crocuta time their births to avoid bearing young during the spring rains was considered. However, neither the number of litters born ($F = 0.128$, df = 1,101, $P = 0.721$) nor the number of litters conceived ($F = 0.499$; df = 1,111, $P = 0.481$) in any given month was related to the amount of rain falling during that month, nor was there any significant relationship between the timing of births and early cub mortality. The percentage of all cubs dying during each month of the year varied from 2.2 to 16.1%, but cub mortality did not vary significantly by month ($F = 1.396$, df = 11,91, $P = 0.188$; $n = 93$ cubs dying), and the number of cubs dying each month was unrelated to rainfall ($F = 2.213$, df = 1,100, $P = 0.140$). Furthermore, for all cubs born within a given month, chi-squared comparison of those surviving ≥12 months with those dying before 12 months revealed no significant variation among months of the year (chi-squared = 4.021; df = 10, $P > 0.50$). Thus, seasonal births in this spotted hyaena population did not appear to be influenced by patterns of cub mortality induced by heavy rains or other mortality sources.
Relationships between prey abundance and reproductive parameters

Prey availability was examined as a possible proximal determinant of reproductive seasonality in spotted hyaenas. The mean number of prey animals counted during ungulate censuses varied significantly from month to month (Fig. 2b; \( F = 4.648, \text{df} = 11,105, P < 0.001 \)). The annual influx of several thousand zebra and hundreds of thousands of wildebeest caused a marked increase in food availability for the hyaenas in this study population from June to September. The annual period of lowest prey abundance occurred during the months immediately after the departure of the migratory herds each fall, and prey densities did not then increase to moderate levels until rain stimulated renewed growth of local vegetation. When controlled for month of the year, neither the number of births (ANCOVA: \( F = 1.254, \text{df} = 4,106, P = 0.293 \)) nor the number of weanings (\( F = 0.348, \text{df} = 4,103, P = 0.845 \)) per month was significantly correlated with prey abundance. However, after controlling for month of the year, a strong positive correlation was found between game abundance and the number of litters conceived each month (Fig. 3; \( F = 4.094, \text{df} = 4,109, P = 0.004 \)). There was also a significant relationship between prey abundance and the percentage of females conceiving \( > 7 \) months after parturition (\( F = 7.037; \text{df} = 1,102, P = 0.009 \)). Thus, seasonal changes in prey availability appeared to affect the likelihood of conception. There was no relationship between the number of conceptions and prey abundance during the preceding month (\( F = 0.025, \text{df} = 1,104, P = 0.821 \)). These patterns suggest that female Crocuta are able to adjust rapidly their tendency to conceive new litters in response to changes in the food supply.
Effects of weaning and parity of breeding females

One proximate cause of the seasonal pattern of conceptions in this population could be seasonal changes in the cessation of lactational anoestrus. If this were the case, weaning should vary on a seasonal basis; however, this was not observed in the present study, in that the number of litters weaned did not vary significantly by month (n = 65 litters: F = 1.045, df = 11.96, P = 0.414). The hypothesis proposed by Lindeque and Skinner (1982) that seasonal patterns of conception in spotted hyaenas are facilitated indirectly by seasonal increases in prey abundance that advance the time of weaning of previous litters and, as a consequence, advance the next oestrous period was also tested by comparing conceptions among parous females (n = 94 litters) with those among females bearing young for the first time (n = 33 litters). The seasonal pattern of conceptions among nulliparous females did not differ from that observed among parous females (chi-squared = 2.50, df = 10, P > 0.50), indicating that increased food availability increases directly the probability of conception in both groups of adult females, and that weaning of a previous litter alone is inadequate to explain the reproductive response of female hyaenas to altered prey abundance.

Discussion

Whereas a great deal is known about the social regulation of reproduction in tropical carnivores (for examples, see Malcolm and Marten, 1982; Creel et al., 1992; Holekamp et al., 1996; Creel and Waser, 1997; Moehlman and Hofer, 1997), little is known about the regulation of reproduction in these species by specific environmental factors (Bronson, 1989). The results of the present study, particularly when considered in light of data from other Crocuta populations, permit analysis of both proximal and ultimate explanations for the regulation of reproduction by environmental factors in spotted hyaenas. Although births occurred throughout the year in this equatorial hyaena study population, the annual pattern of births showed a distinct trough from February to May. In attempting to identify the proximal cues by which this seasonal pattern of reproduction is mediated, it was not possible to control any of the relevant environmental variables experimentally, but natural variation in these over time permitted elimination of some causal hypotheses. Because the study area was situated within 2° of the equator, daylength varied by only a few minutes throughout the year. Thus, although it could not be ruled out as a possible cuing mechanism, it appears unlikely that reproductive seasonality in spotted hyaenas is cued by changing daylength as it is in various carnivore species living at higher latitudes (for examples, see Bissonnette, 1932; Dunn and Chapman, 1983; King, 1989). This notion is also supported by the observation of Kruuk (1972) that seasonal patterns of reproduction differ markedly among Crocuta populations inhabiting the Serengeti plains and Ngorongogo Crater, even though these two study areas are separated by <1° of latitude. That photoperiodic cues are unlikely to regulate reproduction even among Crocuta living at relatively high latitudes is suggested by the fact that births occur throughout the year at latitudes 25–28°S, and that the number of births there do not vary significantly with month of the year (Mills, 1990).

Two ecological variables, rainfall and prey abundance, varied seasonally in the current study, although their annual patterns were not isomorphic. That is, the annual influx of migratory antelope occurred each year between June and August, when rainfall was relatively low. Although rainfall is used as a cue to stimulate seasonal reproduction in some tropical mammals, for example rodents (Delaney and Neal, 1969; Taylor and Green, 1976; Walker and Rabinowitz, 1992; ChandrasekarRao and Sunquist, 1996), rainfall could be ruled out as a proximal cue for Crocuta since there was no apparent relationship in the current study between rainfall and either births or conceptions. The hypothesis that Crocuta time their births to minimize cub deaths from flooded dens or other mortality sources could also be ruled out because cub deaths showed no significant seasonal variation.

The annual birth trough observed in the Talek study population occurred approximately one gestation period (3.6 months) after the phase of the annual cycle during which prey animals were least abundant in the home range of the study clan. Litters were least likely to be conceived when game was most scarce, indicating that prey availability has important effects on the timing of reproduction in Talek hyaenas. Furthermore, throughout the range of this species, it appears that reproductive seasonality occurs when prey abundance fluctuates seasonally, and peaks and troughs in the conception rate occur in conjunction with peaks and troughs, respectively, in local food abundance (Kruuk, 1972; Lindeque and Skinner, 1982; Mills, 1990; Cooper, 1993).

Although Crocuta occur from the equator to 28° of latitude, no latitudinal cline in breeding season length is observed in this species as it is in various other mammals ranging from tropical to temperate zones (for example, Peromyscus spp,
Bronson, 1989; Didelphis albiventris, Regidor and Gorostiague, 1996; Akodon azarae, Bilenga et al., 1994). Instead, seasonal patterns of local food availability appear to explain much of the variance observed among spotted hyaena populations with respect to reproductive seasonality. The present study is the first to maintain precise longitudinal demographic and reproductive records for a single population over a period of several years. Nevertheless, shorter term studies have revealed that reproductive seasonality is strongly pronounced in some populations of spotted hyaenas (for example, Cooper, 1993) while it is virtually absent in others (Deane 1962; Pienaar, 1963; Smithers, 1971; Eloff, 1975). Where previous investigators have presented concurrent data documenting both prey availability and female reproductive performance, a strong relationship has appeared between these variables. Lindeque and Skinner (1982) observed a distinct annual peak in the number of conceptions in southern Africa in December and January, which was also the period of peak food abundance. Mills (1990) observed a slight trough in births among Kalahari hyaenas between March and June, approximately one gestation period after the annual period of least game abundance in the area studied. As in the present study, seasonal patterns of prey abundance and rainfall were not isomorphic in the Kalahari. Among hyaenas inhabiting Ngorongoro Crater, Kruuk (1972) observed a peak in numbers of births in April each year, approximately one gestation period after the annual period of peak food abundance, during the wildebeest calving season. In Botswana, Cooper (1993) found that all Crocuta births occurred during the dry season, approximately one gestation period after the annual influx of several thousand migratory zebra.

Interlitter intervals are extremely variable in spotted hyaenas (Holekamp et al., 1996), and females appear to be prepared to breed at any time of year. Throughout the range of this species, it appears that reproductive seasonality is not promoted by a specific predictive cue in the environment, such as daylength or rainfall. Instead, seasonal reproduction in spotted hyaenas appears to be largely a consequence of seasonal changes in immediate availability of food. Crocuta obtain 65–95% of their total food intake from hunting medium and large sized ungulates (Kruuk, 1972; Mills, 1990; Holekamp et al., 1997; Cooper et al., 1999), so they rely heavily on local prey to satisfy their energetic and nutritional needs. Among Talek hyaenas, it appears that some minimum prey abundance may be necessary in the home range of the study clan for conceptions to occur regularly among females. When this minimal prey abundance is not reached, reproduction is inhibited. Thus, for female spotted hyaenas, food availability may function as both a proximal and an ultimate determinant of reproductive seasonality.

In various rodent species with gestation periods lasting only 2–4 weeks, energy shortages at the time of conception often reliably indicate that energy will also be in short supply during the lactation interval (for review, see Bronson, 1989), when energetic costs to breeding females are substantially higher than they are during gestation (for example, see Gittleman and Thompson, 1988; Clutton-Brock et al., 1989). However, because of the long gestation period in Crocuta, energy availability at conception is unlikely to indicate energy availability during lactation. Thus, female spotted hyaenas appear to decide whether to initiate new reproductive effort on the basis of information available to them at the time of conception. Efficient use of this information may reduce the likelihood of implantation failures or early embryo resorptions in spotted hyaenas.

Lindeque and Skinner (1982) suggested that the seasonal peak number they observed in hyaena conceptions in southern Africa was largely the consequence of cubs being weaned when prey were most abundant, and conceptions occurring soon after these weanings. However, this explanation cannot account for the seasonal pattern of hyaena reproduction found in the current study, in which, although conceptions varied significantly among months of the year, weanings did not. Moreover, the finding that primiparous and multiparous females did not differ with respect to their seasonal patterns of conceptions indicated that the timing of weaning is not responsible for reproductive seasonality in spotted hyaenas.

Overall, seasonal reproduction in spotted hyaenas appears to be a direct consequence of seasonal changes in the availability of energy or nutrients. That energy is likely to be a more important determinant of reproductive seasonality than specific nutrients is indicated by data collected from several other mammals examined in both the wild and in captivity (for review, see Bronson, 1989; Wade and Schneider, 1992; Schneider and Wade, in press). A body of research has confirmed that fertility is impaired when food intake is restricted. In all orders of mammals examined to date, ovulatory cycles are lengthened or interrupted by inadequate food intake, or by excessive energy expenditure that is not offset by compensatory increases in food intake (Bronson, 1989; l'Anson et al., 1991; Wade and Schneider, 1992; Foster, 1994; Wade et al., 1996; Schneider and Wade, in press).

In female laboratory rodents and livestock, chronic food restriction suppresses GnRH release and, hence, LH secretion, steroidogenesis and ovulation (for review, see Bronson, 1989; Foster, 1994). Thus, chronic food restriction retards reproductive development and suppresses the oestrous cycle. The mechanisms mediating the interaction between energy balance and endocrine control of reproduction in female mammals has received a great deal of recent attention (for example, see Morin, 1986; Bronson, 1989; Wade and Schneider, 1992). Temporal aspects of reproduction in various species of small mammal have been shown to be correlated with or affected by body mass, body fat stores and the availability of oxidizable metabolic fuels, such as fatty acids and glucose (French, 1982; Barnes, 1984; Bushberg and Holmes, 1985; Wade and Schneider, 1992), all of which are likely to vary with food availability. Similarly, the present data indicate that one of these physiological variables may be associated with seasonal changes in food abundance in Crocuta, and that this may mediate reproductive seasonality in spotted hyaenas.

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