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# Intraspecific Variation in the Behavioral Ecology of a Tropical Carnivore, the Spotted Hyena

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KAY E. HOLEKAMP and STEPHANIE M. DLONIAK

DEPARTMENT OF ZOOLOGY, MICHIGAN STATE UNIVERSITY,  
EAST LANSING, MICHIGAN, USA

## I. INTRODUCTION

Spotted hyenas (*Crocuta crocuta*) are large terrestrial predators found throughout much of sub-Saharan Africa. They are far more abundant than any other large carnivore on the African continent (Estes, 1991), and they are second only to lions (*Panthera leo*) with respect to body size. Spotted hyenas occur from approximately 17° N of the equator to 28° S. Thus, although they are not found exclusively between the Tropic of Cancer and the Tropic of Capricorn, the vast majority of the range of this species lies in the tropics. Spotted hyenas occupy an extraordinarily diverse array of habitats, including savanna, deserts, swamps, woodland, and montane forest up to 4000 m of elevation. They do not thrive in uninterrupted low-elevation rain forest habitats, but they appear to do well in montane forests, forest-savanna mosaics, and tropical forests containing open clearings or “*bais*,” as occur in certain parts of the Congo basin. Spotted hyenas occur at low densities in many arid and semiarid habitats. Hyenas occupying such areas do not derive any significant fraction of their water intake from drinking; instead, these hyenas apparently obtain most of their water from the bodies of their prey (Green et al., 1984). Even lactating females can survive without water for over one week. The highest population densities reported for this species occur on the prey-rich savannah plains of Kenya and Tanzania, and surprisingly, in the montane forest of Aberdare National Park in Kenya. In these areas, densities of spotted hyenas often exceed one animal per square kilometer.

Since the late 1960s, the spotted hyena has been the subject of a surprisingly large number of scientific studies, and these have provided us with data from many of the different habitat types occupied by this species (Table I). We currently know a great deal about the behavioral ecology of spotted hyenas in certain habitats, and in fact, because these animals are relatively easy to study, we know more about spotted hyenas than we do about most other large carnivores. These myriad studies have revealed that spotted hyenas exhibit remarkable behavioral plasticity: they can reproduce at any time of year, be active during day or night, survive on foods ranging from termites to elephants, and even coexist with humans in some urban areas, as in Harar, Ethiopia (M. Baynes-Rock, personal communication). The behavioral plasticity documented in the spotted hyena is far greater than that evident in any other large carnivore on the African continent. On the other hand, the studies listed in Table I have also shown that certain aspects of the hyena's behavioral biology appear to be constant among diverse habitats, such that they seem highly inflexible or fixed. Determining which aspects of the hyena's biology fail to vary significantly across a wide range of environmental conditions can shed light on the limits to their behavioral plasticity and yield information useful in the long-term conservation and management of spotted hyenas and other large African carnivores.

Here we first review the aspects of the behavioral ecology of spotted hyenas that appear invariant across study areas, and then those that vary markedly among populations, and inquire why certain behaviors fall into each category. We then make a detailed comparison of the hyena's behavioral ecology as it has been documented in the two longest-running studies of wild spotted hyenas. Finally, we conclude by evaluating the current and potential effects of human disturbance on the behavioral ecology and ultimate persistence of this species. As human population density in Africa continues to increase, and habitats continue to be modified by human activity, this analysis should suggest viable strategies for conserving these fascinating and ecologically important animals.

## II. INVARIANT ASPECTS OF THE SPOTTED HYENA'S BEHAVIORAL ECOLOGY

Certain aspects of the behavioral ecology of the spotted hyena appear to be remarkably constant among populations, and it is these "invariant" traits on which we focus in this section. These traits can be grouped into categories associated with clan structure, male-biased dispersal behavior, certain aspects of the hyena's reproductive biology, social dominance of females over males, and rank-related maternal effects.

TABLE I  
SIGNIFICANT STUDIES OF THE BEHAVIORAL ECOLOGY OF *Crocuta crocuta*

Location <sup>a</sup>	Latitude, longitude (degrees)	Habitat	Elevation (m)	Temperature (°C)	Precipitation (mm)	Prey base <sup>b</sup>	Years	Topic	Number of clans studied	Hyena density <sup>c</sup>	Sources
Niokolo Koba NP, Senegal	12°45' N, 10°00' W	Savanna to dense woodland	< 150	18–33	900–1000	R	1995–1996	Diet	– <sup>d</sup>	–	Di Silvestre et al. (2000) <sup>g</sup>
Comoe NP, Cote d'Ivoire	8°45' N, 3°49' W	Gallery forest	250	26	700–1170	R	1992–1998	Census, habits	–	–	Korb (2000) <sup>h</sup>
Faro NP, Cameroon	8°54' N, 12°63' E	Wooded savanna	250–500	21–34	1300	R	2000–2001	Diet	–	–	Breuer (2005)
Aberdares NP, Kenya	00°08' S, 36°32' E	Montane forest	1920–2500	14–27	1090	R	1986–1987	Population ecology	2	1.34	Sillero-Zubiri and Gottelli (1992)
Masai Mara NR, Kenya	1°40' S, 35°50' E	Savanna	1575	12–32	1305	R, M	1979–1987	Socioecology	1	0.86	Frank (1986a,b)
Masai Mara NR, Kenya	1°40' S, 35°50' E	Savanna	1575	12–32	1305	R, M	1988–present	Behavior	6	0.94	Holekamp and colleagues
Serengeti NP, Tanzania	2°25' S, 24°50' E	Savanna	1200–1800	11–32	500–1000	R, M	1965–1967	Behavior, hunting	> 1	0.17	Kruuk (1972)
Serengeti NP, Tanzania	2°25' S, 24°50' E	Savanna	1200–1800	11–32	500–1000	R, M	1987–present	Socioecology	7	0.82–1.1	Hofer and East (1993a)
Amboseli NP, Kenya	2°40' S, 37°15' E	Dry savanna	1250	11–33	347	R	2002–2005	Population ecology, interspecific interactions	2	1.65	Watts and Holekamp (2008, 2009), Altmann et al. (2002)
Ngorongoro CA, Tanzania	3° S, 35° E	Savanna	1800	5–30	750	R	1965–1967	Behavior, hunting	7	1.7	Kruuk (1972)
Ngorongoro CA, Tanzania	3° S, 35° E	Savanna	1800	5–30	750	R	1996–present	Population dynamics, behavior	8	0.59–0.89	Höner et al. (2007, 2002, 2005), Wachter et al. (2002)
Selous GR, Tanzania	9° S, 38°1' E	Miombo woodland	350	19–37	1406	R	1991–1996	Density, interspecific interactions	–	0.31	Creel and Creel (2002) <sup>i</sup>
Hwange NP, Zimbabwe	18°30' S, 25°45' E	Woodlands	1000	–9–40	714	R	1999–2003	Space-use	4	0.07	Salnicki (2004)
Etosha NP, Namibia	19°0' S, 16°30' E	Arid savanna	1000	10–44	351	R, M	1982–1986	Demography, feeding	3	0.05	Gasaway et al. (1989, 1991)

(Continued)

TABLE I (Continued)

Location <sup>a</sup>	Latitude, longitude (degrees)	Habitat	Elevation (m)	Temperature (°C)	Precipitation (mm)	Prey base <sup>b</sup>	Years	Topic	Number of clans studied	Hyena density <sup>c</sup>	Sources
Etosha NP, Namibia	19°0' S, 16°30' E	Arid savanna	1000	10–44	351	M	2000–2001	Spatial organization interspecific competition	3	0.02	Trinkel and Kastberger (2005), Trinkel et al. (2004)
Moremi GR, Botswana	19°10' S, 23°45' E	Seasonal floodplains and swamp	960	14–24	525	R	Early 1970s	Hunting	–	–	Child and Robbel (1975)
Kruger NP, South Africa	23°30' S, 31°30' E	Open woodlands and plains	300	4–40	300–700	R	Early 1970s	General ecology	–	0.21	Smuts (1978), Reason et al. (2005)
Kruger NP, South Africa	23°30' S, 31°30' E	Open woodlands and plains	300	4–40	300–700	R	1974–1980	Reproductive physiology	0 <sup>e</sup>	–	Lindeque (1981) <sup>f</sup> , Lindeque and Skinner (1982)
Kruger NP, South Africa	23°30' S, 31°30' E	Open woodlands and plains	300	4–40	300–700	R	1982–1984	Diet, sociality, dispersal	1	0.13	Henschel and Skinner (1987, 1990a,b)
Kruger NP, South Africa	23°30' S, 31°30' E	Open woodlands and plains	300	4–40	300–700	R	1982–1984	Socioecology	1	0.09	Henschel (1986)
Kruger NP, South Africa	23°30' S, 31°30' E	Open woodlands and plains	300	4–40	300–700	R	1984	Census	–	0.09	Mills (1985b) <sup>g</sup>
Kruger NP, South Africa	23°30' S, 31°30' E	Open woodlands and plains	300	4–40	300–700	R	1985	Foraging, breeding	—	0.07–0.2	Mills (1985a)
Namib Desert, Namibia	23°34' S, 15°03' E	Desert	0–2000	6–35	15–18	R	1976–1979	Socioecology, feeding	1–3	0.004–0.0085	Tilson et al. (1980), Skinner and van Aarde (1991) <sup>f</sup> , Tilson and Hamilton (1984), Tilson and Henschel (1986), Henschel and Tilson (1988) <sup>m</sup> , Skinner et al. (1992)
Chobe NP, Botswana	23°50' S, 25°10' E	Savanna	960	5–38	400–550	R, M	1986–1988	Socioecology	5	0.44	Cooper (1989), Cooper (1990)
Timbavati, South Africa	24°35' S, 31°14' E	Dry woodland	350	0–43	483–532	R, M	1973–1975	Feeding ecology, interspecific interactions, fecal marking	1	0.48	Bearder (1975) <sup>n</sup> , (1977), Bearder and Randall (1978) <sup>o</sup>

Southern Kalahari, South Africa and Botswana	26° S, 20°30' E	Semidesert	950	-10–40	200–300	R, M	1979–1984	Socioecology	6	0.009	<a href="#">Mills (1990)</a>
Mkuze, GR, South Africa	27°36' S, 32°12' E	Bushveld and pans	100	5–35	406–866	R	1989	Diet	1	0.13	<a href="#">Skinner et al. (1992)</a>
Hluhluwe-iMfolozi NP, South Africa	28°13' S, 32°00' E	Thornveld <sup>f</sup>	40–590	0–34	750–1000	R	2003–2004	Density	–	0–1.25	<a href="#">Graf et al. (2009)<sup>g</sup></a>
Umfolozi NP, South Africa	28°25' S, 31°50' E	Thicket and woodland	91–579	0–34	703–900	R	1973–1981	Density, body measures, food intake	1–3	0.36–0.46	<a href="#">Whateley (1980<sup>h</sup>, 1981), Whateley and Brooks (1978), Green et al. (1984)</a>

<sup>a</sup>NP, National Park; NR, National Reserve; CA, Conservation Area; GR, Game Reserve.

<sup>b</sup>R, resident; M, migratory.

<sup>c</sup>Hyena densities are reported as number of hyenas per square kilometer.

<sup>d</sup>Data not available or not applicable.

<sup>e</sup>Hyenas under study were culled.

<sup>f</sup>Fenced area.

<sup>g</sup>Di Silvestre, I., Novelli, O., Bogliani G., 2000. Feeding habits of the spotted hyaena in the Niokolo Koba National Park, Senegal. *African J. Ecol.* 38, 102–107.

<sup>h</sup>Korb, J., 2000. Methods to study elusive spotted hyenas in the Comoe National Park. *IUCN/SSC Hyaena Specialist Group Newsletter*. 7, 3–11.

<sup>i</sup>Creel, S., Creel, N.M., 2002. “The African Wild Dog. Behavior, Ecology, and Conservation.” Princeton University Press, Princeton.

<sup>j</sup>Lindeque, M., 1981. “Reproduction in the spotted hyaena, *Crocuta crocuta* (Erxleben).” D. Phil. Thesis, University of Pretoria.

<sup>k</sup>Mills, M.G.L., 1985b. Hyaena survey of Kruger National Park: August–October 1984. *IUCN/SSC Hyaena Specialist Group Newsletter*. 2, 15–25.

<sup>l</sup>Skinner, J.D., van Aarde, R.J., 1991. The distribution and ecology of the brown hyaena *Hyaena brunnea* and spotted hyaena *Crocuta crocuta* in the central Namib desert. *Madoqua* 12, 231–239.

<sup>m</sup>Henschel, J.R., Tilson, R.L., 1988. How much does a spotted hyaena eat? Perspective from the Namib Desert. *African J. Ecol.* 26, 247–255.

<sup>n</sup>Bearder, S.K., 1975. Inter-relationship between hyaenas and their competitors in the Transvaal Lowveld. *Publikasie Universitaet Nuwe Reeks*, 97, 39–48.

<sup>o</sup>Bearder, S.K., Randall, R.M., 1978. The use of fecal marking sites by spotted hyaenas and civets. *Carnivore* 1, 32–48.

<sup>p</sup>Graf, J.A., Somers, M.J., Szykman Gunther, M., Slotow, R., 2009. Heterogeneity in the density of spotted hyaenas in Hluhluwe-iMfolozi Park, South Africa. *Acta Theriologica*, 54, 333–343.

<sup>q</sup>Whately, A.M., 1980. Comparative body measurements of male and female spotted hyaenas from Natal. *Lammergeyer*, 26, 44–52.

## A. CLAN STRUCTURE

Throughout the species' range, spotted hyenas live in complex social groups, called clans (Kruuk, 1972; Smith et al., 2008). Clans are fission–fusion societies in which individual members travel, rest, and forage in subgroups that frequently change composition (Kruuk, 1972; Mills, 1990; Smith et al., 2008). Clan members all recognize one another individually (Hofer and East, 1993a; Holekamp et al., 1999a; Kruuk, 1972), and they rear their cubs together at a communal den (White, 2006), although clan members do not cooperate in rearing young (Mills 1985a). The core of any spotted hyena clan includes one to several matrilineal kin groups, each composed of closely related adult females and their offspring. Individuals from up to four different generations may be present concurrently within the clan. The lifespan of a wild spotted hyena can exceed 18 years (Drea and Frank, 2003).

Hyena clans are rigidly structured by stable, linear rank relationships that determine priority of access to food during competition at kills with other clan members (Frank, 1986b; Henschel and Skinner, 1987; Tilson and Hamilton, 1984). All members of a particular matriline usually occupy adjacent rank positions in the clan's dominance hierarchy. As they grow up in their natal clans, youngsters of both sexes assume rank positions immediately below those of their mothers, and females maintain their maternal ranks throughout their lives. Males also usually maintain their maternal ranks as long as they remain in the natal clan (Smale et al., 1993, 1997), but they assume a subordinate status at dispersal or, in those rare cases when males fail to disperse, when they start breeding (East and Hofer, 2001).

In addition to matrilineal kin groups, each clan also typically contains one to several immigrant males who join the group as adults. Thus, a clan contains both male and female natal animals born in the clan, and male immigrants that were born elsewhere. All natal hyenas are socially dominant to all immigrants (Kruuk, 1972; Smale et al., 1993). This means that adult females and their immature offspring, even very young ones, can displace adult immigrant males from food and other critical resources. Although all adult female clan-members breed, they do so at rates that increase with social rank (Frank et al., 1995; Hofer and East, 2003; Holekamp et al., 1996).

## B. DISPERSAL AND REPRODUCTION

Females usually spend their entire lives in their natal clans (Frank, 1986b), but nearly all males emigrate between the ages of two and six years (Fig. 1), and attempt to join a new clan after dispersal (Smale et al.,

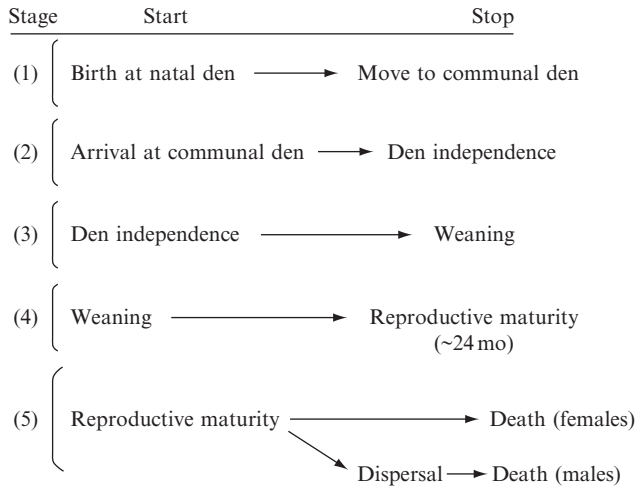


FIG. 1. Life history patterns characteristic of spotted hyenas throughout their range. Each life history stage starts and ends with observable milestones. No sexual dimorphism in these patterns appears until the final (fifth) stage. Although the relative lengths and sequence of the stages do not vary across the species' range, the timing of all life history milestones except age at reproductive maturity vary considerably among study populations.

1997; [Boydston et al., 2005](#); [Höner et al., 2007](#); [Van Horn et al., 2008](#)). Although virtually all males disperse from their natal clans, only a fraction of these males successfully immigrate into a new clan after dispersal. If a male manages to become successfully integrated into a new clan, he may eventually be able to breed there. Some successful immigrant males in most study populations later disperse again to join at least one other new clan in their lifetimes ([Van Horn et al., 2003](#)).

Dispersing males adopt a behavioral strategy that bears a striking resemblance to that seen in the submissive behavior of cubs living at the natal den. That is, males outside their natal territories always appease any new hyena encountered, regardless of the other animal's relative body size, and regardless of whether or not the other animal behaves aggressively ([Smale et al., 1997](#)). We suspect that males may find it difficult or impossible to become socially integrated into a new clan after dispersal unless they adopt this pattern of highly obsequious behavior. Interestingly, emigration represents the point during ontogenetic development at which females come to dominate males ([Smale et al., 1993](#)). In fact, because emigrating males even initiate their social interactions with small cubs in neighboring clans by appeasing them, all natal animals can dominate all immigrants.

The mating system of the spotted hyena is polygynandrous. There are usually more adult females than adult males in a clan, and each breeding male mates with multiple females (East et al., 2003; Engh et al., 2002). However, females also often mate with multiple males, and they frequently produce offspring fathered by multiple males in a single litter. In many gregarious carnivores, including most social mongooses and canids, there is only a single breeding female per group. By contrast, all adult female members of a spotted hyena clan produce offspring. Females can bear young at all times of year, although many populations exhibit a moderate degree of seasonality, with birth troughs and peaks that most likely reflect responses to variation in local energy availability (Cooper, 1993; Frank, 1986a; Holekamp et al., 1999b; Kruuk, 1972; Lindeque and Skinner, 1982; Mills, 1990; Smithers, 1966).

The female copulates and gives birth through her pseudopenis. When spotted hyenas mate, the male must insert his erect phallus into the female's flaccid one, which is difficult because the female's pseudopenis points forward (Cunha et al., 2003; Drea et al., 2002). Therefore, during copulation the male must squat behind the female and hop around while thrusting blindly upward and backward until he achieves intromission. Inside the female's body, her reproductive tract contains a uterus and ovaries like those of other mammals, but instead of the vaginal canal exiting the body under the tail as occurs in other carnivores, it makes a hairpin turn there and exits the body ventrally through the pseudopenis. Due to the odd "masculinized" genitalia characteristic of females in this species, throughout the species' range female spotted hyenas have complete control over which males mate with them.

Hyenas of both sexes are physiologically competent to breed by 24 months of age, but most delay their first reproduction by several months or years after puberty. The gestation period in this species throughout its range appears to be 110 days (Schneider, 1926). Female spotted hyenas bear litters of one, two, or rarely three cubs in isolated natal dens (East et al., 1989). In fact, litter size is another parameter that varies remarkably little among study populations. Modal litter size is two when cubs are first observed above ground in all wild populations for which such information is reported. Mean litter size was 1.62 when cubs were first observed above ground in 10 independent estimates made in eight different wild study populations (Table II). Litter sizes at first emergence in all these studies ranged only from 1.43 to 1.91, so litter size is small in this species across the hyena's natural range. In fact, litter size does not differ between wild and captive populations (Table II). The mean litter size at birth is 1.86 in four captive populations, and it is 1.91 when measured *in utero* in both wild and captive populations.



TABLE II  
LITTER SIZES REPORTED FOR *Crocuta crocuta*

Study site <sup>a</sup>	Number of litters	Mean litter size	When counted	Source
Captive, Berkeley	27	1.93	<i>In utero</i>	Wahaj et al. (2007)
Kalahari Desert	19	1.9	<i>In utero</i>	Mills (1990)
Masai Mara NR, Kenya	22	1.91	<i>In utero</i>	Wahaj et al. (2007)
Captive, Zoo	17	1.94	Birth	Schneider (1926)
Captive, Zoo	5	2.2	Birth	Pournelle (1965)
Captive, Zoo	7	2	Birth	Crandall (1964)
Captive, Berkeley	32	1.31	Birth	Wahaj et al. (2007)
Ngorongoro CA, Tanzania	45	1.87	Emergence from den	Kruuk (1972)
Kalahari Desert	20	1.7	Emergence from den	Mills (1990)
Serengeti NP, Tanzania	735	1.53	Emergence from den	Hofer and East (2008) <sup>b</sup>
Chobe NP, Botswana	22	1.91	Emergence from den	Cooper (1993)
Ngorongoro CA, Tanzania	28	1.43	Emergence from den	Wachter et al. (2002)
Hwange NP, Zimbabwe	35	1.57	Emergence from den	Salnicki (2004)
Amboseli NP, Kenya	53	1.68	Emergence from den	Watts and Holekamp (2008)
Masai Mara NR, Kenya	106	1.44	Emergence from den	Holekamp et al. (1996)
Masai Mara NR, Kenya	55	1.56	Emergence from den	Watts and Holekamp (2008)
Masai Mara NR, Kenya	18	1.5	Emergence from den	Wahaj et al. (2007)

<sup>a</sup>CA, Conservation Area; NP, National Park; NR, National Reserve.

<sup>b</sup>Hofer, H. East, M.L., 2008. Siblicide in Serengeti spotted hyenas: a long-term study of maternal input and cub survival. *Behav. Ecol. Sociobiol.* 62, 341–351.

Male hyenas do not participate at all in parental care. Females shelter their young in either rocky caves or earthen dens; the latter are usually originally excavated by other species (Boydston et al., 2006; East et al., 1989; Hill, 1980). The entrances of most dens are too small to permit adults or lions to enter, and adults generally rest on the surface near the den, or take shelter in thickets. However, cubs spend much time underground in dens during the first several months of their lives.

Cubs generally spend their first few weeks of life at an isolated natal den (East et al., 1989; Kruuk, 1972), but they are then carried by their mother to the clan's communal den (Fig. 1). Except for those still sheltered at natal dens, all cubs less than 8–9 months of age concurrently alive in the clan reside together at the communal den. Although female spotted hyenas breed asynchronously throughout the year, all the members of a clan rear their cubs together at the clan's communal den. In the fission–fusion

societies characteristic of spotted hyenas throughout their range, the communal den represents the social center of a clan's territory; it offers a place where members can reliably find each other again after having been separated, where clan mates can reaffirm their relationships, and where groups can form for activities such as hunting or patrolling territory boundaries (Holekamp et al., 2000). The den also offers daily opportunities for youngsters to meet their clan mates, and facilitates the integration of the cubs into the group (Cooper, 1993; White, 2006).

Females invest extremely heavily in each litter for an unusually long time relative to maternal investment in most other fissiped carnivores (Watts et al., 2009). The basic elements of maternal care vary little throughout the species' range. These include attendance at dens to nurse and groom cubs, vigilance and defense of cubs against danger, intervention on behalf of offspring in disputes with clan-mates, providing cubs with exceptionally rich milk (Hofer and East, 1996) for many months and, rarely, provisioning of den-dwelling cubs with solid food brought from ungulate kills (Holekamp and Smale, 1990). Weaning occurs very late in this species compared to most other fissiped carnivores (Watts et al., 2009). It appears that prolonged and intensive maternal investment by female spotted hyenas has evolved in response to the unusually protracted development of the skull in offspring. Adult spotted hyenas have massive skulls highly specialized for bone-cracking, but development of this feeding apparatus during ontogeny is not complete until the hyena reaches 35 months of age, which is over one year after reproductive maturity and multiple years after weaning (Tanner et al., 2010). Evidently, protracted development of the feeding apparatus handicaps young hyenas with respect to feeding speed during competition with adults at kills, and this has led to selection for extended and intensive maternal care by females to enhance survival of their young after weaning (Watts et al., 2009).

### C. FEMALE DOMINANCE AND RANK-RELATED MATERNAL EFFECTS

In all populations studied to date, females are socially dominant to males among adults. Recent evidence suggests that the evolution of female dominance has been shaped in spotted hyenas, but not in other bone-cracking hyenas or other carnivore species, by the unique coupling of two sets of extreme conditions (Watts et al., 2009). That is, it appears that female dominance has been favored in this species by the intensive feeding competition among conspecifics characteristic of modern spotted hyenas, occurring in conjunction with protracted development of a feeding apparatus specialized for bone-cracking, as retained from a carrion-feeding ancestor. The feeding apparatus is not fully developed in spotted hyenas until

35 months of age, and this affects their feeding performance (Tanner et al., 2010). Thus, young spotted hyenas cannot consume a fresh goat femur as quickly as can older adults until they are 36 months old (Tanner, 2007). In fact, youngsters are handicapped relative to adults even when consuming soft foods. For example, their ability to consume a 30 g dog biscuit made of compressed cereal does not match that of older adults until they are 34 months old (Tanner, 2007). Because hyenas reach reproductive maturity at 24 months, this means that they can produce their own offspring well before their feeding apparatus is fully developed. Thus, the feeding performance of young hyenas remains inferior to that of adults for an exceptionally long time relative to patterns of development in most other mammalian carnivores (Tanner, 2007; Watts et al., 2009).

Protracted development of the skull in young hyenas apparently leads to selection for increased aggressiveness in females as a compensatory mechanism for mothers to secure food access for their young after weaning. The period between weaning and completed skull development is particularly challenging for young hyenas, as indicated by high mortality during this stage of their life. In addition, both maternal rank and maternal presence between weaning and full skull maturity are important determinants of offspring survival (Watts et al., 2009).

Virtually every aspect of the life of a spotted hyena is strongly affected by its position in the clan's dominance hierarchy. A hyena's social rank is not determined by its fighting ability or size (Engh et al., 2000), but rather rank is learned in a fashion nearly identical to the associative learning process in primates that has been dubbed "maternal rank inheritance" by primatologists (Frank, 1986b; Holekamp and Smale, 1991, 1993; Maestripieri, 2009; Smale et al., 1993). Thus, a key maternal effect in spotted hyenas throughout their range is the nongenetic transmission of maternal rank to offspring.

Status-related maternal effects and their mediating mechanisms have been intensively studied in spotted hyenas, and have been found to be critical influences on offspring phenotype (Dloniak et al., 2006; Hofer and East, 2003; Holekamp and Dloniak, 2009). Many aspects of a hyena's behavioral phenotype are strongly affected by maternal rank, and evidence for this appears very early in life. For example, neonatal spotted hyenas often fight vigorously with their siblings during the first days or weeks after birth (Frank et al., 1991; Smale et al., 1999; Wachter et al., 2002; Wahaj and Holekamp, 2006), and the rates and intensities at which siblings fight decrease with increasing maternal rank (Golla et al., 1999; Smale et al., 1999). An adult's social status determines its priority of access to food, so rank has profound effects on hyenas' intake of calories and nutrients. The time budgets of high- and low-ranking hyenas differ (Kolowski et al., 2007),

and low-ranking adults are obliged to hunt at higher hourly rates than are dominants, presumably because their priority of access to kills made by other clan members is so low (Holekamp et al., 1997). If a low-ranking hyena kills an antelope, it can usually feed on the carcass for at least a few minutes before being displaced when clan-mates detect the kill (Smith et al., 2008), and a hungry adult hyena can consume roughly 1.3 kg of meat and bone per minute (Kruuk, 1972). It is presumably to provide themselves with at least a few minutes of solitary feeding that low-ranking hyenas are more likely to hunt alone than are their higher-ranking counterparts.

High-ranking cubs enjoy a superior ability to win in contests with conspecifics over resources, especially when their mothers or other allies are nearby to help them out in these contests. After cubs leave the den, dominant mothers are more successful than subordinate females at helping their young gain access to ungulate carcasses (Holekamp and Smale, 1990). This rank-related variation in cubs' ability to access food has striking effects on cub growth rates, with high-ranking cubs growing much faster than their low-ranking peers (Hofer and East, 1996, 2003).

The age at which females first bear young is strongly correlated with maternal rank, with daughters of high-ranking females experiencing their first parturition years earlier than daughters of the lowest-ranking females (Hofer and East, 2003; Holekamp et al., 1996). Although rank does not affect litter size in hyenas, interlitter intervals are much shorter in dominant than subordinate females, and dominants are more frequently able to support pregnancy and lactation concurrently, so the annual rate of cub production is substantially higher among high- than low-ranking females (Holekamp et al., 1996). Maternal rank affects the likelihood that cubs will survive to reproductive maturity, and it also has a pronounced effect on longevity among adult females (Watts, 2007).

Because high-ranking females start breeding earlier, live longer, and produce more surviving cubs per unit time, as much as a fivefold difference in lifetime reproductive success can occur between the highest and lowest-ranking females in a particular study population (Holekamp and Smale, 2000). Thus, these maternal effects have enormously important fitness consequences (Watts et al., 2009). Because survivorship among dominant animals is so much better than that among subordinate hyenas (Watts et al., 2009), dominants tend to have many more surviving kin in the population at any given time than do subordinates, and thus they enjoy a much larger network of potential allies (Van Horn et al., 2004; Smith et al., 2010). Dominant females are also able to wean their cubs at much younger ages than can subordinate females (Frank et al., 1995; Holekamp et al., 1996). Also, dominant females are much more attractive to males as prospective

mates than are subordinate females (Szykman et al., 2001), presumably because their offspring are so much more likely to survive to adulthood, and to live longer as adults (Watts et al., 2009).

#### D. CONCLUSIONS

To summarize, certain aspects of the behavioral ecology of spotted hyenas vary remarkably little among diverse study areas. These include female dominance over males, fission–fusion sociality, male dispersal, female philopatry, the hierarchical organization of individual clans, and the rank-related maternal effects that ensue from this hierarchical organization. Other phenomena that appear to be invariant, but have not yet been widely studied, include basic patterns of cub rearing and protracted development of a feeding apparatus specialized for durophagy. Recent work by Watts et al. (2009) suggests that hyena traits associated with clan structure and maternal rank effects, which appear not to vary across the species' range, were favored by selection for enhanced female aggressiveness to permit their young to feed at carcasses. Even long after puberty, young hyenas are handicapped during competitive feeding because constrained development of the feeding apparatus causes them to ingest both hard and soft foods more slowly than adults (Tanner et al., 2010; Watts et al., 2009).

### III. INTRASPECIFIC VARIATION IN THE BEHAVIORAL ECOLOGY OF SPOTTED HYENAS

We now turn our attention to those aspects of the behavioral ecology of spotted hyenas in which substantial variation has been documented among study populations. The aspects of the hyena's behavioral ecology that appear most variable include the temporal patterning of their activity, patterns of space utilization, territorial behavior, diet and foraging behavior, clan size, and the timing of their transitions between life history stages.

#### A. TEMPORAL PATTERNING OF ACTIVITY

Spotted hyenas may be active at any time during the 24-h cycle, and in fact they are often observed foraging in broad daylight (e.g., Child and Robbel, 1975; Rainy and Rainy, 1989; Stelzner and Strier, 1981). However, they are more commonly active at night, and around dawn and dusk, than during the heat of mid-day (Hayward and Hayward, 2006; Kolowski et al., 2007; Kruuk, 1972; Mills, 1990), when they generally prefer to lie up in shady thickets or other safe places. In the Masai Mara National Reserve in

Kenya (henceforth “the Mara”), where we have studied spotted hyenas since the late 1980s, the daily pattern of hyena activity is crepuscular and nocturnal, but there are no clear peaks in activity throughout the night (Kolowski et al., 2007). In other parts of Africa, peaks of activity are common around dawn and dusk (Kolowski et al., 2007; Kruuk, 1972). Although hyenas in Serengeti National Park and Ngorongoro Crater in Tanzania are also generally inactive around mid-day, their nocturnal activity tends to peak in the first half of the night (Kruuk, 1972). In marked contrast to Mara hyenas, spotted hyenas in Addo Elephant National Park in South Africa exhibit peak activity during the hours surrounding midnight, and these animals are completely inactive in the middle of the day (Hayward and Hayward, 2006). Across the African continent, in arid regions where daytime temperatures are high, spotted hyenas generally tend to restrict their activity to hours of darkness, as do individuals living in areas in which humans are frequently abroad during daylight hours (Kolowski et al., 2007). Shifting the timing of their activity appears to be one of the first responses to anthropogenic disturbance documented among spotted hyenas; that is they become substantially more nocturnal (Boydston et al., 2003a; Kolowski and Holekamp, 2009).

Like other large carnivores, spotted hyenas spend much of each day resting. Hyena activity occurs in bouts separated by periods of rest. There is much individual variation in the timing and length of bouts of activity, and in the total amount of time spent active, but males tend to spend more time active than females (Kolowski et al., 2007). During an average 24-h day, Mara hyenas spend  $31.5 \pm 2.7\%$  of their time active (traveling, socializing, foraging, etc). Similarly, of each 24-h period Kalahari hyenas spend roughly 31% active (Mills, 1990), and Kruger hyenas spend 27.5% active (Henschel, 1986), but spotted hyenas in Ngorongoro Crater spend only 16% active (Kruuk, 1972). At the other extreme, Addo hyenas spend  $42 \pm 14\%$  of the 24-h day active (Hayward and Hayward, 2006).

## B. TERRITORIALITY AND SPACE USE PATTERNS

The territorial behavior exhibited by spotted hyenas varies dramatically among study populations. Clan members in most areas use a common territory, but they may or may not actively advertise and defend it against intrusions by alien hyenas (Boydston et al., 2001; Henschel and Skinner, 1991; Kruuk, 1972). Alien hyenas discovered within the clan's home range are often viciously attacked in some areas (Smale et al., 1997), but they are ignored in others (Hofer and East, 1993c). Territory size ranges from 20 to 30 km<sup>2</sup> in the tightly packed clans of Ngorongoro Crater and Kenya's Amboseli National Park (Honer et al., 2002, 2005; Watts and Holekamp, 2008) to over

1000 km<sup>2</sup> in the Kalahari Desert (Mills, 1984). Vigorous and frequent territorial behavior by spotted hyenas appears to occur where hyena density is high and intrusion pressure is intense (Henschel and Skinner, 1991; Kruuk, 1972). For example, territories of spotted hyenas on the prey-rich plains of the Mara–Serengeti ecosystem form an uninterrupted mosaic (Hofer and East, 1993a; Kruuk, 1972). Under these circumstances, clans advertise their communal territories through vocal displays (East and Hofer, 1991), scent marking (called “pasting”; Gorman and Mills, 1984), and border patrols (Kruuk, 1972), and clan members cooperate to defend territories during boundary disputes with neighboring clans, which Kruuk (1972) called “clan wars.”

By contrast, in parts of Africa characterized by very low hyena density, clans occupy exclusive ranges but there is little evidence of intrusion pressure or contested carcasses in border areas. In these habitats, both clan wars and border patrols tend to be rare, or they are not observed at all (Tilson and Henschel, 1986). For example, in the Namib Desert, conflicts between neighboring clans are not observed (Tilson and Hamilton, 1984), and clan ranges neither overlap nor abut one another. Instead, territories of adjacent clans may be separated by up to 15 km (Tilson and Henschel, 1986). Whereas scent-marking occurs at unusually high rates along territory borders in east African hyenas (e.g., Boydston et al., 2001), this is not the case among the desert-dwelling hyenas of southern Africa; there scent-marking is concentrated in core use areas, including the vicinity of the communal den, and on paths that fan out from core areas (Tilson and Henschel, 1986).

Trinkel et al. (2004) studied a clan of spotted hyenas inhabiting Etosha National Park, Namibia, and found that their spatial organization changed markedly between dry and wet seasons. The Etosha clan occupies a territory of 160 km<sup>2</sup> in the dry season, but territory size increases to 320 km<sup>2</sup> during the wet season. The dry season territory contains a low density (1 animal per square kilometer) of resident herbivores, and a higher density of migratory species (12 animals per square kilometer), the latter being the main prey of Etosha hyenas. In response to ungulate movements at the start of the wet season, the hyenas shift the focus of their activities to the new grazing area used by the migratory herbivores during that time. Trinkel et al. (2004) found a strong relationship between densities of the hyenas and their migratory prey in both the dry and wet season. They suggest that the considerable enlargement of the hyenas’ territory during the wet season occurs in response to both the migratory movements of prey and an increase in the dispersion of prey.

Trinkel et al. (2006) evaluated the territorial behavior of spotted hyenas in eight different African ecosystems for which data were available on per capita prey availability, which ranges among seasons and habitats from 0.5 to 37.4 herbivores/hyena. These authors found that some clans inhabit

areas where most prey are resident herbivores such that prey numbers are generally constant over time. In areas characterized by constant and relatively high prey abundance, they found that hyenas show no temporal variation in their territorial behavior, and these clans maintain permanent territories with boundaries that shift very little among years. In contrast, in such areas as Etosha National Park (Trinkel et al., 2004) and the Serengeti (Hofer and East, 1993a,b), seasonal migration of herbivores causes enormous seasonal changes in per capita prey abundance, and the resident hyenas in these areas exhibit foraging and land-use strategies that vary considerably over time.

Associated with variable territory size among spotted hyena populations is variable ranging behavior among individual hyenas. In areas where prey are abundant (60–95 antelope per square kilometer) and easily found due to the open structure of the habitat, hyenas travel only 10–12 km/day (Kolowski et al., 2007; Kruuk, 1972). By contrast, in the Kalahari desert or Kruger National Park in South Africa, where prey are thinly distributed (11–12 antelope per square kilometer, Mills, 1984), hyenas travel 23–27 km/day (Henschel and Skinner, 1987; Mills, 1990). Thus, it appears that variation in prey density among habitats generates corresponding variation in territoriality and space-use patterns among resident spotted hyenas (Trinkel et al., 2006).

### C. FEEDING AND FORAGING

The foraging behavior of spotted hyenas is remarkably flexible. First, these animals can obtain food either by hunting live animals or by scavenging carcasses of dead ones. On average, across 10 study populations in which the relative proportions of hunted and scavenged foods have been documented, 66.5% of the diet of spotted hyenas is derived from kills they make themselves, and only 33.5% from scavenged food items (Cooper, 1990; Cooper et al., 1999; Gasaway et al., 1991; Henschel and Skinner, 1990a; Höner et al., 2002; Kruuk, 1972; Mills, 1990; Sillero-Zubiri and Gottelli, 1992; Tilson et al., 1980). However, the percentage of the diet derived from kills the hyenas make themselves ranges among habitats from 43% to 95%. Spotted hyenas in most localities hunt the majority of their own food, primarily medium- and large-bodied ungulates (Holekamp et al., 1997; Kruuk, 1972; Mills, 1990). In addition, spotted hyenas exhibit extraordinary plasticity with respect to their prey preferences, both within and between clans. Hyenas can derive energy and nutrients from a vast and diverse array of prey, ranging from small insects to the largest herbivores. Indeed, it is largely this astonishing versatility in foraging behavior that



permits spotted hyenas to survive in such a broad array of African habitat types, and to persist in areas where other large carnivores have become locally extinct.

In our Masai Mara study population, we have observed spotted hyenas ingesting at least 43 different animal species ranging from crayfish to elephants. When flying termites emerge after a heavy rain, we frequently see hyenas snapping them out of the air, and we once arrived at the den to find all the hyenas there engaged in what appeared to be grazing behavior; upon closer inspection we found that they were licking up caterpillars that were abundant on the ground. Although Mara hyenas do not appear to care for catfish, [Stevenson-Hamilton \(1954\)](#) describes a hyena actively engaged in fishing behavior. In the forests of Aberdare National Park in Kenya, spotted hyenas consume many buffalo (*Syncerus caffer*) and bushbuck (*Tragelephus scriptus*), but they have also been observed eating moths and quail (*Coturnix* spp.) ([Prickett, 1977](#); [Sillero-Zubiri and Gottelli, 1992](#)). Thus, on the one hand, these animals are extreme opportunists, able to exploit a vast array of potential prey types. On the other hand, in most parts of Africa, spotted hyenas derive the large majority of their food intake from only a small subset of the prey species available to them locally. Specifically, spotted hyenas focus on the medium and large-sized ungulates in their local environment whose capture yields the greatest caloric return while demanding the least effort and the fewest risks ([Cooper et al., 1999](#); [Holekamp et al., 1997](#)).

In Timbavati and in Kruger National Park, South Africa, spotted hyenas prey most frequently on impala (*Aepyceros melampus*; [Owen-Smith and Mills, 2008](#); [Pienaar, 1969](#); [Smuts, 1978](#)). In the Namib Desert, they feed mainly on gemsbok (*Oryx gazella*; [Skinner et al., 1992](#); [Tilson et al., 1980](#)). In the Acholi region of northern Uganda, spotted hyenas prey mainly on Uganda Kob (*Kobus kob thomasi*) and Jackson's hartebeest (*Alcelaphus buselaphus*; [Kingdon, 1977](#)). In the Serengeti, they prey most commonly on wildebeest (*Connochaetes taurinus*), gazelles, and zebra (*Equus quagga*; [Hofer and East, 1993a](#); [Höner et al., 2002](#); [Kruuk, 1972](#)). In Cameroon the staple in their diet is Buffon's kob (*Kobus kob kob*; [Breuer, 2005](#)). In our Mara study population, spotted hyenas feed mainly on topi (*Damaliscus lunatus*) and Thompson's gazelles (*Eudorcas thomsonii*) during most of the year, but they switch to feeding primarily on wildebeest and zebra as soon as the migratory herds of these species arrive in our study area from the Serengeti ([Cooper et al., 1999](#); [Holekamp et al., 1997](#)). In virtually every study population for which prey preferences are known, spotted hyenas prey most heavily on herbivores weighing 15–250 kg. Lone hyenas in the Mara regularly bring down topi and wildebeest, which each weigh roughly

three times the hunter's body mass; we once even saw a lone hyena kill an adult zebra. Thus, contrary to the beliefs of many people, spotted hyenas are very effective predators.

#### D. CLAN SIZE

Clan size is one of the most variable traits in the biology of the spotted hyena (Table III). Clans range in size from tiny groups found in the deserts of southern Africa, which may contain as few as four or five members (Gasaway et al., 1989; Mills, 1990; Tilson and Henschel, 1986), to the large groups in eastern Africa, which may contain over 90 members (Frank, 1986a,b; Hofer and East, 1993a; Holekamp et al., 1993; Kruuk, 1972). Across 19 study populations in which all individual members were known for one or more clans, the mean clan size is 28.8 hyenas, but this ranges from 3 to 67 (Table III). Clan size varies with local prey density, suggesting that the number of animals in a spotted hyena clan may be limited by food availability (Mills, 1990). Indeed, larger clans tend to occur in areas inhabited by higher concentrations of prey animals. However, habitat type also appears to affect clan size independently of prey availability. The mean clan size is 47 in savanna habitats, 9 in desert habitats, and 12 in thorn scrub or woodland habitats. Surprisingly, the only study done in the montane forest habitat of the Aberdare Mountains in Kenya reported an average clan size of 47 (Sillero-Zubiri and Gottelli, 1992). The small clans found in the deserts of southern Africa usually contain only one or two matriline (Mills, 1990), whereas the large clans in the prey-rich plains of eastern Africa may contain several different matriline (Frank, 1986a,b).

#### E. TIMING OF LIFE HISTORY MILESTONES

The life history of a spotted hyena takes place in five discrete stages, each of which begins and ends with observable milestones (Fig. 1). These five stages vary greatly in duration, with stage length increasing as the hyena matures (Holekamp and Smale, 1998). In the second stage of the life history, the length of time individual cubs spend living at the communal den varies quite a bit among habitats, and this can also be quite variable even within clans (e.g., White, 2006). In our own study populations, we determine that a cub has "graduated" from the communal den when that cub is found away from the den during four consecutive observation sessions (Boydston et al., 2005). In the Masai Mara and Amboseli, cubs leave the communal den at  $8.60 \pm 1.44$  months ( $N = 49$  litters) and  $8.69 \pm 0.12$  months ( $N = 33$  litters) of age, respectively (Watts, 2007). Male and female cubs do not differ in our study populations regarding the

TABLE III  
REPORTED CLAN SIZES FOR *Crocuta crocuta*

Location <sup>a</sup>	Years	Prey base <sup>b</sup>	Number of clans studied	Hyena density <sup>c</sup>	Mean clan size <sup>d</sup>	Home range size <sup>e</sup>	Source
Ngorongoro CA, Tanzania	1965–1967	R	7	1.54	67	27.6	Kruuk (1972)
Ngorongoro CA, Tanzania	1996–2003	R	8	0.59	22.3	23.8	Honer et al. (2002, 2005)
Kalahari Desert	1979–1984	–	6	0.009	8	1095	Mills (1990)
Masai Mara NR, Kenya	1979–1987	R, M	1	0.86	52	60	Frank (1986a)
Serengeti NP, Tanzania	1987–present	M	7	0.17	47	55	Hofer and East (1993a)
Masai Mara NR, Kenya	1988–present	R, M	3	0.94	57	62	Watts and Holekamp (2008)
Amboseli NP, Kenya	2002–2005	R	2	1.65	45	27	Watts and Holekamp (2008)
Aberdare NP, Kenya	1986–1987	R	2	1.34	47	32	Sillero-Zubiri and Gottelli (1992)
Etosha NP, Namibia	1982–1986	R, M	3	0.05	15	360	Gasaway et al. (1989)
Etosha NP, Namibia	2000–2001	M	3	0.02	15	240	Trinkel and Kastberger (2005)
Kruger NP, South Africa	1982–1984	R	1	0.13	17	130	Henschel and Skinner (1987)
Naukluft NP, Namibia	1977–1979	–	3	0.0085	6	570	Tilson and Henschel (1986)
Chobe NP, Botswana	1986–1988	R, M	5	0.44	49.2	101	Cooper (1989)
Umfolozi NP, South Africa	1979–1981	R	1	0.36	14	39	Whateley (1981)
Hluhluwe NP, South Africa	1975–1977	R	3	0.46	9	13	Whateley and Brooks (1978)
Timbavati, South Africa	1973–1975	R, M	1	0.48	12	25	Bearder (1977)
Mkuzi GR, South Africa	1989	R	1	0.13	6.5	–	Skinner et al. (1992)
Hwange NP, Zimbabwe	1999–2003	R	4	0.07	11.3	110	Salnicki (2004)
Masai Mara NR, Kenya	2008–2010	R, M	3	0.60	46	76	Holekamp unpublished <sup>f</sup>
Total			<i>N</i> = 63		Mean = 28.8	Mean = 175	

<sup>a</sup>CA, Conservation Area; NP, National Park; NR, National Reserve; GR, Game Reserve.

<sup>b</sup>R, resident; M, migratory.

<sup>c</sup>Hyena density is reported as number of individuals per square kilometer.

<sup>d</sup>Mean clan size is based on the total number of individuals.

<sup>e</sup>Home range size is reported as square kilometers.

<sup>f</sup>These 3 clans inhabit the Mara Conservancy, whereas the 3 clans studied by Watts and Holekamp (2008) live in the eastern Mara.

age at which they leave the communal den (Boydston et al., 2005). Serengeti cubs, and those in Hwange National Park, Zimbabwe, generally live at the communal den until they are approximately 12 months of age (Hofer and East, 1993c; Salnicki, 2004). Kalahari cubs remain at the den until they are 12–15 months of age (Mills, 1990). Thus, it appears that cubs stay longer at communal dens in habitats characterized by more difficult and challenging ecological conditions than in places like Amboseli or the Mara, where life is usually relatively easy for spotted hyenas because of the year-round presence of abundant prey in these areas.

Challenges to young spotted hyenas imposed by local ecological conditions also appear to generate variation in mean weaning ages among populations. Although there is much intraclan variation in this measure due to maternal rank, on average cubs are weaned at 11 months in Amboseli, 13.5 months in the Masai Mara, 12–16 months in Kalahari, and 14–16 months in the Serengeti (Hofer and East, 1995; Mills, 1990; Watts and Holekamp, 2008). Mean age at first parturition and interbirth intervals are other life history parameters that vary considerably among study populations. Mean age at first parturition ranges from  $37 \pm 2$  to  $46 \pm 7$  months, but surprisingly here the smallest value was obtained in the Kalahari (Mills, 1990) and the largest in the Serengeti (Hofer and East, 2003). Similarly, mean interbirth intervals following litters in which at least one cub survives to weaning range from 14–15 months in Amboseli and the Mara to 19–21 months in both the Kalahari and the Serengeti (Frank, 1986a,b; Hofer and East, 1995; Mills, 1990; Watts, 2007).

## F. CONCLUSIONS

To summarize, a great deal of variation has been documented throughout the range of spotted hyenas with respect to their temporal patterning of activity, clan size, diet, territorial defense, patterns of space use, intrusion pressure, and the timing of life history milestones. Variation in some aspects of the behavioral ecology of these animals is most likely attributable to corresponding spatial or temporal variation in per capita prey abundance among study sites. Aspects of the behavioral ecology of spotted hyenas that appear to vary most dramatically with local prey abundance include clan size, territorial defense, patterns of space use, and intrusion pressure. However, variation in other aspects of the behavioral biology of spotted hyenas may be causally related to factors other than per capita prey abundance. These other factors most likely include habitat structure, availability of suitable den sites, feeding competition with sympatric carnivores, and intraguild predation. For example, from our own comparisons of hyenas in the Mara and Amboseli, we know that local density ratios of hyenas to lions

affect food availability to hyenas via kleptoparasitism from lions; the extra energy female hyenas can sequester via kleptoparasitism in areas with low lion density permits substantial increases in reproductive output by females (Watts and Holekamp, 2008). Furthermore, we would expect temporal patterning of activity to be strongly affected by variation in ambient temperature and vegetative cover. The timing of life history milestones, such as age at transfer to the communal den or age at den independence, should theoretically be affected not only by local prey abundance, but also by substrate characteristics affecting the nature and availability of den sites. Finally, age at den independence should also theoretically be affected by density of lions, as these represent an important mortality source for young hyenas (Watts and Holekamp, 2008).

#### IV. COMPARISON BETWEEN SERENGETI AND MARA HYENAS

##### A. HISTORY AND ECOLOGY OF THE STUDY AREAS

Much of the available data documenting the behavioral ecology of the spotted hyena has come from research conducted in two long-term studies of these animals in the Mara–Serengeti ecosystem of Tanzania and Kenya (Fig. 2). The Serengeti study, centered on clans inhabiting the Seronera area in Figure 2, was initiated in the late 1960s by Hans Kruuk (1972), but after a hiatus of several years, has been headed by Heribert Hofer and Marion East since 1987. The Serengeti study population lives mainly on the plains, so we include a caveat here that hyenas inhabiting the woodlands in the western Serengeti have not been well studied, and might differ substantially in their behavioral biology from plains-dwelling hyenas. Mara hyenas occupy habitat that is primarily grassland, as is the area around Seronera.

The Mara study originally focused on hyenas inhabiting the Talek area (Fig. 2). The Mara study was initiated in 1979 by Laurence Frank (1986a,b), but has been managed since 1988 by Kay Holekamp, Laura Smale, and their students. Whereas the Serengeti project focused from the outset on multiple clans, our Mara study focused initially on only a single large clan, and we did not incorporate other Mara clans into the study until 2001. Data collection in the Serengeti study has thus focused more on population level phenomena, whereas ours has focused more intensively on detailed analysis of individual behavior. Both study areas lie between one and three degrees south of the equator, and their flora and fauna are virtually identical. However, ecological conditions differ markedly between these two study

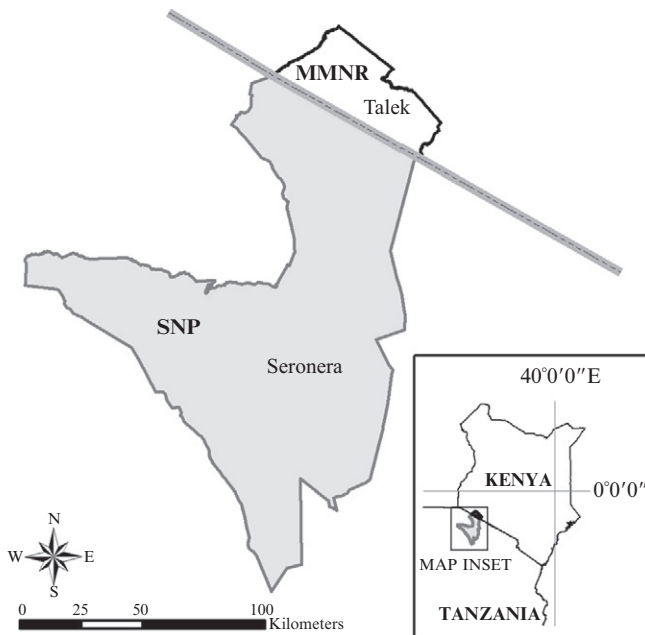


FIG. 2. The Mara-Serengeti ecosystem, which straddles the border between Kenya and Tanzania, is home to the two longest-running continuous studies of spotted hyenas. The Mara project is focused on multiple hyena clans living inside the Masai Mara National Reserve (MMNR), with the largest data set available for one large clan near Talek. The Serengeti project is located within the Serengeti National Park (SNP), and is focused on hyenas inhabiting the plains near Seronera.

areas, and these ecological differences generate striking differences between the resident hyena populations with respect to their space-use patterns, feeding ecology, life history patterns, and demography.

The Mara-Serengeti ecosystem is defined by the annual migration, from the southern Serengeti plains to the Mara and back, of 200,000–600,000 zebras and up to 1,300,000 wildebeest (Sinclair, 1979; Thirgood et al., 2004). The large-scale movements of these two ungulate species also engender smaller-scale movements of many Thompson's gazelles and other antelope. The annual migration of these herbivores is driven by latitudinal variation in rainfall patterns and the ensuing patterns of vegetative growth.

The hyena study area near Seronera in the Serengeti, centered at roughly 2°25' S latitude, typically has a single, long rainy season that stimulates grass growth from November to May (McNaughton, 1979). The migratory ungulates are present on the southernmost plains in the Serengeti during

this rainy season, but during the long dry season only a few warthogs, topi, and gazelles remain there. By contrast, the Mara study area, centered near Talek at roughly at  $1^{\circ}40'$  S latitude, has two rainy seasons; the short rains occur in October–November and the long rains in March–May, and these two rainy seasons are separated by dry periods. The Mara also has irregular, but sometimes substantial, rainfall throughout the dry seasons. Average annual rainfall in the Mara is often twice that of the Serengeti plains, so grazed grass is replenished during most of the year. This has two important implications: the spotted hyenas in the Masai Mara enjoy a much higher resident prey availability throughout the year, and they also usually experience a superabundance of prey between July and September, when the migratory herds of zebra and wildebeest are typically concentrated in and around the Mara (Ogutu et al., 2008). By contrast, Serengeti hyenas typically experience “feast or famine” conditions in their territories, that is they enjoy a superabundance of prey during months when the migratory ungulates are grazing in or near their territories, but a paucity of prey in other months. The overall mean year-round density of resident ungulates in the territories of Serengeti hyenas is 7.2 animals per square kilometer, but when both resident and migratory herbivores are present, prey densities jump to 239 animals per square kilometer (Hofer and East, 1993a). The mean year-round prey density in the eastern Mara is 225.3 animals per square kilometer. Interestingly, despite the large differences between these two study areas with respect to their rainfall and herbivore densities, the elevation, habitat, and hyena densities in the two areas are all virtually identical. Hyena density in the Mara is  $0.86/\text{km}^2$  (Frank, 1986a,b), and  $0.82/\text{km}^2$  in the Serengeti (Hofer and East, 1993a).

## B. FORAGING AND TERRITORIAL BEHAVIOR

The most conspicuous way in which the behaviors of Mara and Serengeti hyenas differ relates to foraging. Whereas Mara hyenas feed mainly within their defended territories throughout the year, hyenas in the Serengeti have feeding ranges that are often separated in space from their defended group territories. Serengeti hyenas exhibit a unique pattern of ranging and foraging behavior that combines a residential existence in stable clans in defended group territories with regular extensive movements outside the territories to feed on the nearest large herds of migratory herbivores (Hofer and East, 1993a). This system of “commuting” is used by spotted hyenas inhabiting the central part of the Serengeti, where on average, clans containing 47 hyenas defend territories covering a mean area of  $56 \text{ km}^2$  (Hofer and East, 1993a,b). Although Serengeti territories contain only low concentrations of resident prey, the large herds of migratory antelope can

generally be found year-round within 100 km of these territories, and sometimes they occur within clan territories. During the wet season, spotted hyenas from the central Serengeti commute to the wildebeest calving grounds in the southeast, and during the dry season, they commute to wildebeest aggregations in the northwest. The mean commuting distance for individual hyenas is 40 km, but some trips can be much longer (Hofer and East, 1993b). By contrast, the average Mara hyena travels less than 13 km to forage (Kolowski et al., 2007).

All the hyenas from one Serengeti clan do not necessarily travel to the same place to forage, but individual hyenas from many different Serengeti clans commute to forage in the area where the density of prey animals is currently highest. Adult males and females with no den-dwelling cubs make 15–18 commuting trips per year, each trip lasting 6–10 days (Hofer and East, 1993c). As a result, these individuals travel at least 1010 km per year while commuting. Adult females with den-dwelling cubs must frequently return to their territories to nurse their young, so the commuting effort of these females exceeds that of other adults at least by 2.6-fold (Hofer and East, 1993c). Females with den-dwelling cubs make 42–51 commuting trips per year, each trip lasting 3 or 4 days (Hofer and East, 1993c). Thus, these individuals travel at least 2880 km per year while commuting.

Foraging conditions are much more challenging for Serengeti than Mara hyenas. Roughly 69% of the diet consumed by Serengeti hyenas is comprised of wildebeest and Thompson's gazelles (Hofer and East, 1993a), whereas only 52% of the Mara diet is comprised of these two antelope (Cooper et al., 1999). In addition to wildebeest and Thompson's gazelles, the main dietary staples of Mara hyenas are zebra (21.8%) and topi (16.8%). Thus the Mara hyenas generally have more prey species from which to choose than do their counterparts in the Serengeti. It appears that Serengeti hyenas must also depend more heavily on carrion as a component of the diet than do Mara hyenas. Estimates of the percentage of the diet derived from kills the hyenas have made themselves range from 43% to 69% for Serengeti hyenas (Höner et al., 2002; Kruuk, 1972), but hover around 95% for Mara hyenas (Cooper et al., 1999). Estimates of daily food consumption are 3 kg/day/hyena in the Serengeti (Kruuk, 1972) but 6.4 kg/day/hyena in the Mara (Smith et al., 2008).

The commuting behavior of Serengeti hyenas effectively allows them to separate their feeding ranges from their defended territories, which are retained for breeding and for foraging during the few months each year when migratory ungulates happen to be present there (Hofer and East, 1993a). The flexible foraging behavior of Serengeti hyenas allows them to live at densities higher than the carrying capacities of their individual territories estimated from resident herbivore densities alone. Thus,



Serengeti hyenas, in contrast to many other carnivores including most populations of spotted hyenas, are not limited by resources on their territories, and their feeding ranges are effectively decoupled from their defended territories.

### C. DEMOGRAPHY

The average sex ratio among adults in Serengeti clans is 1.17 females to 1 male (Hofer and East, 1993a), whereas the adult sex ratio in the Mara is 1.8 females to 1 male (Watts, 2007). Accordingly, we would expect male–male competition for mates to be more intense in Serengeti than in the Mara. Mortality among juvenile spotted hyenas is essentially the same in the Mara as in the Serengeti; roughly half of all cubs born in both areas fail to survive to puberty (Hofer and East, 1995; Watts et al., 2009). However, the juvenile mortality rate (53%) for the Serengeti is probably an underestimate because most Serengeti cubs are first observed after their arrival at the communal den, whereas we usually see cubs first at natal dens in the Mara (Hofer and East, 1995). We expect juvenile mortality to be higher in the Serengeti than in the Mara, given that seasonal fluctuations in prey abundance are much greater in the Serengeti (Sinclair and Norton-Griffiths, 1979), and mothers in the Serengeti must often commute long distances from the communal den to forage, resulting in reduced cub growth and survival (Hofer and East, 1993c). Mortality rates among juveniles increase after den independence and after weaning in our Masai Mara study population (Watts et al., 2009). In contrast, Hofer and East (1995) found no increase in mortality after weaning in Serengeti hyenas, and they suggested this is because weaning is more gradual in spotted hyenas than in other carnivores. Regardless of whether or not it is gradual, weaning should be a very challenging process for young spotted hyenas throughout their range. Juvenile spotted hyenas in the Mara are not yet competent hunters (Holekamp et al., 1997), they have not yet reached full adult body size (Mills, 1990), and they are far less efficient at processing food than are the adults with whom they compete at kills (Binder and Van Valkenburgh, 2000; Tanner et al., 2010). As we would not expect Serengeti youngsters to develop faster than those in the Mara, if Serengeti cubs are not severely challenged by weaning, their mothers must be working even harder than Mara females to help their young survive the transition to nutritional independence.

### D. REPRODUCTIVE SUCCESS

Lifetime reproductive success (LRS) has now been calculated for female spotted hyenas living in both the Mara and the Serengeti. To calculate LRS, we measure annual reproductive success as the number of offspring

produced each year that survive to reproductive maturity (24 months of age), and multiply this number by the mean number of years during which a female who survives to puberty can be expected to breed. [Watts and Holekamp \(2008\)](#) found that the mean lifetime reproductive success among Mara females was 2.9 offspring. [Hofer and East \(1996, 2003\)](#) performed the same calculations to estimate the mean lifetime reproductive success among Serengeti females, which was 2.36 offspring. Thus, despite the fact that the mean estimated reproductive lifespan among Serengeti females who survive to puberty is substantially longer than that among Mara females (7.48 vs. 4.7 years), Serengeti females achieve a mean lifetime reproductive success 19% lower than that among Mara females. This is consistent with the notion that the “feast or famine” conditions typical of the Serengeti are more challenging for female hyenas than are the more constant resource conditions found in the Mara.

[East et al. \(2009\)](#) describe 13 cases of cub adoption by free-living female hyenas in the Serengeti and Ngorongoro Crater. Although spotted hyenas have been studied in many other parts of Africa, adoption has never been observed in other African ecosystems and we have never seen it in the Mara. In three of the adoption cases described by [East et al. \(2009\)](#), the surrogate mothers were closely related to the genetic mothers of the adopted cubs, but in all other cases the surrogate mothers were very distantly related or unrelated to the mothers of adopted cubs. Given the immense parental effort made by female spotted hyenas, and the enormous apparent fitness costs associated with nursing adoptive offspring for many months, it is not at all clear why a female hyena might adopt the offspring of a nonrelative. Surprisingly, [East et al. \(2009\)](#) suggest no explanations for adoption among their study animals. These adoptions are particularly unexpected because female spotted hyenas in other well-studied populations will rarely even tolerate brief nursing attempts by infants other than their own (e.g., [Mills, 1985a](#)). In fact, it was previously reported that even Serengeti females suckle only their own offspring ([East et al., 1989](#)). As spotted hyenas are capable of recognizing individuals, and discriminating clan-mates from nonclan-mates and kin from nonkin ([Van Horn et al., 2003](#); [Wahaj et al., 2007](#)), it seems very unlikely that Serengeti hyena mothers that adopt unrelated cubs are merely making mistakes in offspring recognition. Furthermore, we can rule out explanations for adoption that involve the unusual commuting system in Serengeti, or its more generally harsh ecological conditions, because half the adoptions documented by [East et al. \(2009\)](#) took place in Ngorongoro Crater, where the conditions confronted by resident spotted hyenas are very much like those in the Mara. Perhaps socioecological conditions that prevailed when adoptions occurred favored females with large networks of allies, whether related to them genetically or

not, and thus allowed adoption of nonrelatives to offset costs with long-delayed direct benefits. If so, this should become apparent through comparison of adoptive and nonadoptive females once adoptive offspring have become adults. Otherwise, given that rearing the cub of an unrelated female to adulthood represents a huge loss of both direct and inclusive fitness, adoption behavior would appear highly maladaptive.

#### E. CONCLUSIONS

Our comparison of Mara and Serengeti hyenas clearly reveals that one need not travel very far to find evidence of the immense plasticity characteristic of the behavioral ecology of spotted hyenas. Mara hyenas lead lives very different from those of hyenas in Serengeti, and the ecological conditions with which the latter must contend make their survival and reproduction extremely challenging. This burden might be expected to affect females more strongly than males, because males do not participate at all in parental care. Indeed, if females bear a disproportionately large burden imposed by dependence on migratory prey, this might contribute to the relatively even sex ratios among adults reported for Serengeti clans. In any case, comparison of Mara and Serengeti hyenas makes clear that natural environmental variation within a single ecosystem can have significant effects on the behavior and demography of resident spotted hyenas.

#### V. EFFECTS OF HUMAN ACTIVITY ON SPOTTED HYENAS

The data reviewed in the previous sections show that natural variation in the environment can have significant effects on the behavioral ecology of spotted hyenas. In general, spotted hyenas are a very successful species and show remarkable behavioral plasticity in response to variation in energy availability. However, like most other members of the large carnivore guild in Africa, spotted hyenas are facing encroachment, habitat loss, and direct persecution from humans, as well as an increasingly uncertain future due to the potential effects of climate change. Although these animals are not yet listed by IUCN as Threatened or Endangered ([Mills and Hofer, 1998](#)), to conserve viable populations of spotted hyenas in the future, it will be necessary to understand how these animals are affected by each of these anthropogenic variables so that management strategies can be developed to mitigate their effects. Threats recently imposed by humans will certainly test just how flexible hyenas can be, and unfortunately we may soon have answers to questions about the limits of their plasticity, as indicated by local extinctions of entire hyena populations.

Human population density is increasing rapidly throughout much of tropical Africa, and large carnivore populations are declining apace (e.g., Brashares, 2003; Wittemyer et al., 2008; Woodroffe and Ginsberg, 1998). Studying how humans are affecting spotted hyenas may ultimately teach us a great deal about how best to protect, not only hyenas, but also sympatric carnivore species exhibiting relatively little behavioral plasticity. Compared to other large African carnivores, spotted hyenas are abundant, and their behavior, physiology, and demography are fairly easy to monitor in many areas. The extraordinary behavioral plasticity exhibited by spotted hyenas may in fact allow them to serve as conservative indicators of how other large carnivores might be expected to respond to anthropogenic disturbance.

Currently in many parts of Africa hyenas and other large carnivores are subject to direct predation by humans, but they are also vulnerable to indirect or “risk” effects induced by anthropogenic activity. Risk effects arise when animals alter their behavior in response to predators, and these responses carry costs (Creel and Christiansen, 2007). Humans are now the primary predators of many African carnivores. Interestingly, both Serengeti and Mara hyenas currently face direct threats from humans, but the nature of the threat differs between the two study areas. Serengeti hyenas evidently pose no threats to livestock, so they experience little active persecution from humans, but they frequently blunder into snares and poison laid out by game-meat hunters in the western Serengeti (Hofer and East, 1995; Hofer et al., 1993). Hofer et al. (1993) estimated that roughly 8% of their adult study animals are killed by game-meat poachers each year. By contrast, Mara hyenas seldom venture into areas where game-meat poaching is a serious problem, but our study animals are often killed by humans because of the threat they pose to livestock.

As in many protected areas worldwide (e.g., Joppa et al., 2009; Wittemyer et al., 2008), the human population along the border of the Mara has grown rapidly in recent years, and carnivores there are confronted with declining prey availability and increasing rates of conflict with local people and livestock (Ogutu et al., 2009). Our recent research with the spotted hyena clans defending territories just inside the northern border of the Mara has shown that conflicts are now common between hyenas and livestock both inside and outside of the Reserve (Kolowski and Holekamp, 2006). In our Mara study area, rates of conflict are high because of the dense human population abutting the reserve, illegal livestock grazing inside the reserve, and poor livestock husbandry. Monthly rates of hyena attacks on livestock are correlated positively with rainfall and negatively with natural prey abundance (Kolowski and Holekamp, 2006).

In response to attacks on livestock, hyenas and other Mara carnivores are actively persecuted by local pastoralists armed with spears, snares, and poisons. Although spearing and snaring mainly target individual hyenas, when adult females with dependent cubs are killed, their cubs usually also perish, as there is no alloparental care in this species. We have in fact observed many cases of this among hyenas inhabiting the Talek region of the Mara. Spotted hyenas are also particularly susceptible to poisoning for two reasons. First, hyenas are opportunistic scavengers, so they are attracted to livestock carcasses as they are to carcasses of wild ungulates. The typical method of poisoning hyenas around the Mara is to lace a cow or goat carcass with pesticide, and leave it in an area frequented by hyenas. Any hyena that comes across the carcass is likely to feed, so poison saturating the carcass of a large cow can thus kill a great number of hyenas. Secondly, because all of the cubs from a clan usually occupy a single communal den, if meat laced with poison is left close to the den, an entire generation can be wiped out overnight. Although the main source of mortality among Mara hyenas has historically been lions, in recent years, this has changed such that humans are now responsible for most hyena deaths in those cases where cause of death can be determined with a high degree of certainty (Fig. 3; see also [Pangle and Holekamp, 2010](#)).

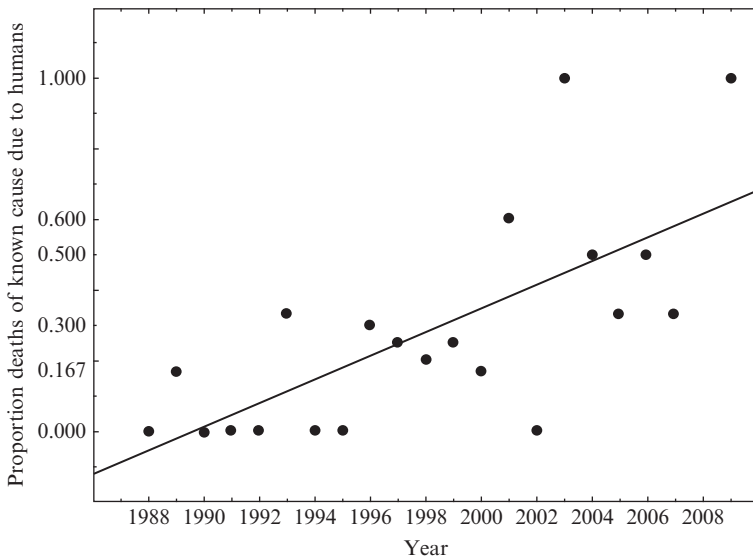


FIG. 3. Percent of all hyena deaths of known causes that were attributable to humans in the eastern Masai Mara from 1988 to 2009.

In addition to the obvious direct effects on mortality, poisoning can also have indirect effects on social dynamics within local hyena clans. For example, because high-ranking hyenas enjoy priority of access to food, members of top matrilineal may ingest a disproportionately large share of the poison, and these matrilineal may be decimated as a result. Furthermore, the first of two large-scale clan fission events witnessed in the Mara since 1988 was due to the poisoning of an entire neighboring clan (Holekamp and Smale, 1992); this left an undefended territory into which several low-ranking Talek hyenas moved together in 1989 (Holekamp et al., 1993). Interestingly, in the late 1990s, we witnessed a second and much more gradual clan fission event that, although apparently also caused by human activity, had a different etiology from the first one. That is, in the mid 1990s, when local pastoralists began daily herding of several hundred cattle into the Reserve from villages just across the Talek River from the territory defended by the original Talek study clan, the resident hyenas started concentrating their activity in portions of the territory farthest from the cattle transit route (Fig. 4). Numbers of cattle being herded back and forth

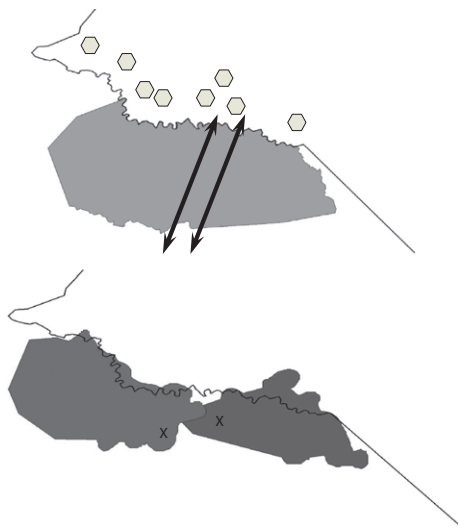


FIG. 4. Clan fission event documented in 1998–2001 during which the original Talek study clan split into two new clans, Talek East and Talek West. The original territory is roughly 10 km long and 6 km wide. This fission event occurred gradually, as cattle grazing became more and more intense in the southern central portion of the original territory. Light solid lines indicate the Reserve boundary, which is comprised mainly of the Talek River in this region. Pentagons represent clusters of pastoralist villages just outside the Reserve and arrows indicate major routes by which herders take their cattle into the Reserve every day. Crosses indicate sites of clan wars observed after clan fission was complete.

each day continued to increase each year, and by the late 1990s, association patterns among the Talek hyenas had changed such that they formed two distinct clusters on either side of the main cattle transit route (Boydston et al., 2003a,b), and individuals began to move between these two clusters less and less frequently. By 2001, the two clusters had become two separate clans, and we started seeing clan wars along the original cattle transit route between members of eastern and western clusters (Fig. 4). Thus, once again, anthropogenic activity had drastically altered the social dynamics of the resident hyenas.

The changes in social dynamics that we observed in temporal conjunction with increasing anthropogenic activity prompted us to inquire specifically which human activities were affecting the hyenas, and then to quantify the effects of these activities. Boydston et al. (2003a,b) used a historical analysis to compare the behavior of Talek hyenas between the late 1980s and the late 1990s. In this study we found that female hyenas in the late 1990s were located farther from dens, but closer to dense vegetation and to the edges of their territory, than in the late 1980s, and that females in the late 1990s also had larger home ranges, occurred in smaller groups, traveled farther between consecutive sightings, and were more nocturnal than in the late 1980s. We next attempted to explain differences observed between time periods by testing predictions of hypotheses invoking prey abundance, climate change, interactions with lions, tourism and livestock grazing. Our data were consistent only with the hypothesis that increased reliance on the Reserve for livestock grazing was responsible for observed changes.

Kolowski et al. (2007) used long-term “follows” of radio-collared hyenas from three Mara clans to document the extent to which human disturbance influenced hyena activity patterns, movement rates, and timing of den use. Female hyenas in territories characterized by daily livestock grazing and high tourist visitation rates showed lower activity and den use than hyenas in an undisturbed territory during the times of day when human activity coincided with potential hyena activity. Furthermore, the specific times of day when hyena activity was reduced indicated that livestock grazing, but not tourist activity, was responsible for observed shifts in activity. Hyenas inhabiting areas grazed heavily by livestock were again found to be much more exclusively nocturnal than those in undisturbed areas.

Kolowski and Holekamp (2009) then compared hyena space use between two Mara clans that differed dramatically in exposure to livestock grazing. By this time, the Talek clan territory was being grazed daily by thousands of cattle, but another clan only 6 km away, but far from Reserve borders, was never exposed to any livestock grazing. Logistic regression modeling indicated that space use in the absence of livestock was most strongly influenced by the location of the clan’s communal den, but hyenas also preferred bushy

areas, areas of high prey density, and proximity to seasonal streams. Movements of hyenas exposed to livestock grazing were most profoundly influenced by vegetation type, with a strong avoidance of open grass plains. Den location and prey density had significantly less influence on space use decisions in the disturbed than the undisturbed clan. Surprisingly, livestock distribution did not directly influence hyena movements either during daytime, when livestock were present, or at night after livestock had left the Reserve. It appeared that direct livestock avoidance by the hyenas was obviated by their increased use of vegetative cover, but that the presence of livestock was energetically costly to the hyenas because they were forced to commute further from dens and prey to find safe refuges from humans. Our results suggested that reduced vegetative cover, as is often found outside protected areas, may result in more dramatic modifications of hyena movements in the presence of livestock than those we observed inside the Mara. Thus, as in other areas with high levels of anthropogenic activity (Gill and Sutherland, 2000), it appears that the responses to human disturbance shown by Mara hyenas represent trade-offs between optimal resource use and decreased risk of persecution.

Using both longitudinal data from the Talek clan, and cross-sectional data from other clans located in the Mara and in Amboseli National Park, Van Meter et al. (2009) measured fecal glucocorticoids (fGC) to inquire whether anthropogenic disturbance is chronically stressful to spotted hyenas. Longitudinal data from adult members of the Talek clan revealed that anthropogenic disturbance in the form of pastoralist activity, but not tourism, influenced fGC concentrations among adult male hyenas; rising concentrations of fGC among males over 12 years of our study were significantly correlated with increasing human population density along the northern edge of the Talek territory. We next compared fGC concentrations among current Talek hyenas with those obtained concurrently from hyenas living in three other groups undisturbed by pastoralist activity, one deep in the Mara and two others in Amboseli. We found that fGC concentrations from the undisturbed groups were significantly lower than those in the disturbed group, and we were able to rule out tourism and ecological stressors as sources of variation in fGC among the populations. Thus, it appears that anthropogenic disturbance elevates fGC concentrations, and represents a stressor for wild spotted hyenas.

Overall we have found remarkable consistency among data sets documenting anthropogenic effects on hyena behavior, physiology, and demography. Human activity is clearly altering use of space and time by hyenas as well as their social dynamics, energetics, mortality sources, and stress physiology. The changes we have documented have been engendered by pastoralist activity including grazing of livestock, but not by tourist



visitation, which represents another potential source of disturbance to Mara wildlife. We suspect that the effects of pastoralist activity are profound on the hyenas, while the effects of tourist activity are negligible, because the tourists never carry weapons nor do they usually exit their vehicles. By contrast, pastoralists travel with their herds on foot, and they are always armed with spears and throwing sticks ("*rungus*"), with which they commonly persecute any hyenas that fail to keep well clear of them.

Interestingly, the behavioral and physiological changes documented in our study animals have preceded detectable changes in mortality sources by a few years. Thus, detection of such behavioral and physiological changes might eventually permit us to anticipate and avoid demographic changes in hyena populations before they occur. We are currently attempting to determine whether the types of "early warnings" apparent in hyena behavior and physiology also allow us to anticipate demographic changes in sympatric predator and prey species. If a species with as much behavioral plasticity as the spotted hyena is showing the clear-cut responses to human activity described here, then we fear that many sympatric species may be faring even worse.

To the best of our knowledge, the effects of anthropogenic disturbance on spotted hyenas have not been studied elsewhere. Similarly we know of no studies investigating the effects of climate change on these or other tropical carnivores. As spotted hyenas often den near seasonal or permanent watercourses, more severe and unseasonal rainstorms might increase cub mortality due to den flooding. More severe or frequent droughts are likely to increase grazing pressure from livestock inside protected areas, with all the attendant consequences described above. It is also likely that climate change will result in altered distributions of herbivores in space and time (e.g., [Boone et al., 2006](#); [Ogutu et al., 2008](#)), and these in turn may have strong negative consequences for resident hyenas in many areas. Long-term studies examining both natural conditions and the effects of anthropogenic disturbance and climate change will be very important for determining how best to adaptively manage these fascinating animals.

## VI. CONCLUSIONS

It is clear from this review that spotted hyenas are remarkably flexible predators, and that they readily adjust many aspects of their behavior and life history to their immediate environmental conditions. Particularly remarkable is the fact that the behavioral ecology of hyenas in the Mara differs in so many respects from that of hyenas inhabiting the Serengeti plains. These differences are striking despite the fact that the areas occupied by these two groups of hyenas are situated less than 100 km apart as

the crow flies, and the two areas appear superficially to be very similar. However, in light of the fact that energy intake mediates reproductive success among female spotted hyenas (Holekamp et al., 1996), many differences between Mara and Serengeti hyenas can be explained directly by the fact that the latter experience many months each year when their territories contain very few prey animals. By contrast, Mara hyenas enjoy easy access year-round to relatively dense prey concentrations.

Spotted hyenas are clearly able to adapt to the presence of humans in many ways. Indeed the adaptive behavioral responses to natural and human-induced environmental variation exhibited by spotted hyenas suggest that the behavioral plasticity typical of these animals may be largely responsible for the numerical and distributional success of this species; their behavioral plasticity may also generally protect them from extinction. Nonetheless, certain inflexible aspects of the hyena's behavioral repertoire leave them particularly vulnerable to threats associated with humans. Because spotted hyenas hunt and kill other animals, conflict with humans and their livestock is inevitable anywhere humans and hyenas coexist. When livestock depredation occurs, pastoralists often retaliate with large-scale campaigns of poisoning that may result in local extinctions of entire hyena populations. Fortunately, we may be able to develop widely applicable schemes for noninvasively monitoring behavior and physiology of spotted hyenas. Because both behavioral changes and changes in stress physiology predict demographic changes in hyena populations, we may be able to use these traits as informative sentinels years before populations start to decline, and thereby conserve one of the most interesting and unusual creatures in tropical Africa.

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