7036

whether or not dominance plays a role in the migratory process. However, since males tend to segregate themselves from females by migrating shorter distances, it is clearly possible that dominance may be involved. The marked relationship between size and the time spent observing the winter (pine–oak) habitat in the present study suggests that dominance may be important in the expression of winter-habitat preference. Perhaps these results will help to explain the winter latitudinal distribution of this species as described by Ketterson & Nolan (1976, 1979). In conclusion, while the development of a preference for summer breeding habitats [illegible] advancing photoperiod is a uniform [illegible] among the juncos studied, the prefer[illegible] winter habitats appears to be a function [illegible] photoperiod and dominance [illegible]

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7036

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SOCIAL DOMINANCE AND FEEDING PATTERNS OF SPOTTED HYAENAS

BY RONALD L. TILSON*† & WILLIAM J. HAMILTON III‡ 1984
Desert Ecological Research Unit, Gobabeb, Namibia
and
‡*Institute of Ecology, University of California, Davis, CA 95616, U.S.A.*

Abstract. In some parts of East Africa, spotted hyaenas (*Crocuta crocuta*) live in large groups and at high population densities, and scramble competition among clan members during feeding at large carcasses is reported. By contrast, spotted hyaenas in the Namib Desert of southwestern Africa live in small groups and at low densities. When assembled at carcasses, Namib Desert spotted hyaenas show linear dominance hierarchies. Adult females outrank adult males and usually feed one at a time or with their dependent offspring. Feeding rates at small carcasses in the Namib Desert are approximately equal to those reported in East Africa, but at large carcasses Namib Desert spotted hyaenas feed significantly more slowly. Thus lower-ranking individuals eventually gain access to large carcasses but are excluded from smaller ones. We relate these patterns of food consumption to possible evolutionary pathways to social hunting by spotted hyaenas.

Linear dominance hierarchies characterize many mammalian groups (Wittenberger 1981). One consequence of a hierarchical social organization is that high-ranking individuals may sequester defensible resources. Challenges to the validity (Rowell 1974) and/or utility (Bernstein 1976; Popp & DeVore 1979; Harding 1980) of the concept of dominance hierarchies, especially for highly social species, suggest that the circumstances determining the expression of dominance hierarchies in natural environments may be of special interest. Here we relate evidence concerning hierarchy-like behaviour for one such species, the spotted hyaena, *Crocuta crocuta*.

Here we make comparisons between a Namib Desert spotted hyaena population studied by us and the East African spotted hyaena populations studied by Kruuk (1972). Feeding behaviour in the small Namib Desert spotted hyaena groups contrasts strongly with the rapid feeding and gorging reported for large groups of the same species in East Africa (van Lawick & van Lawick-Goodall 1970; Kruuk 1972). We suggest that differing patterns of prey consumption in the Namib Desert and in East Africa can be correlated with the differing predator and prey densities characteristic of these areas.

Materials and Methods

Study Area

Our study area includes 3080 km² within the Namib-Naukluft Park, Namibia, where the Kuiseb River has incised a deep, narrow canyon 115 km long across the Namib Desert. South of the Kuiseb River Canyon lies a vast tract of sand dunes lacking any free water. Resident mammalian species there relevant to this study include a population of gemsbok (*Oryx gazella*) living throughout this dunes system, which feeds upon perennial and annual grasses, tubers and bulbs (Hamilton et al. 1977), and small herds of springbok, *Antidorcas marsupialis*, which extend into the fringe areas of the dunes following sporadic rains and subsequent grass flushes. Rocky, sparse grasslands north of the canyon are the preferred habitat of mountain zebra, *Equus zebra*, another important spotted hyaena prey species.

Annual rainfall at Gobabeb (23°34′S, 15°03′E) on the edge of the study area, has averaged 1.8 cm for the past 18 years (range=0–12.5 cm, Desert Ecological Research Unit Meterological Records). Heavier austral summer rains in the central highlands 400 km to the east produce a temporary and unpredictable summer surface water flow through the Kuiseb Canyon. Mountain zebras descend nightly into the narrow confines of the canyon, where water is available throughout the year in small, isolated pools. Down-river from the canyon there is a decreasing gradient of water but an increasing gradient of food resources for herbivores, extending from marginal to abundant (Hamilton & Tilson 1982). During prolonged drought, a regular condition, growth of the perennial grasses away from the canyon slows and the food supply for these

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Present address: Minnesota Zoological Garden, Apple Valley, Minnesota 55124, U.S.A.

herbivores throughout the Namib Desert declines. Under these conditions gemsbok descend to the canyon floor to drink at pools and, during extreme drought, leave the dunes altogether to reside in the Kuiseb Canyon until rains come again or until they die (Hamilton et al. 1977; Tilson 1980; Tilson et al. 1980).

Study Animals

Namib Desert spotted hyaenas forage and feed in small, dispersed social groups, probably extended family units comparable to the 'clans' described by Kruuk (1972) in East Africa. We identified three such groups along a 75-km section of the Kuiseb River Canyon. The groups consist of from three to eight individuals, including one to two resident adult females, their cubs, and two or three subadult and adult males. The adult males may not be close relatives of other group members, since limited evidence (Kruuk 1972; ... observations suggests that they transfer

into matriarchal clans. The 21 months of concentrated data collection upon which this report is based (see below) followed several preliminary months of habituation and identification of individuals and groups. Each group foraged within areas estimated to extend over 570 km² in extent (Fig. 1; Tilson & Henschel, in preparation). These areas did not have contiguous borders. Thus inter-group conflict and competition for carcasses, as described by Kruuk (1972) for East African hyaenas, were not observed. We suspect these groups do not express territorial behaviour because of the low density of groups and the consequent low probability of their ranges overlapping.

We observed hyaenas from a vehicle parked ~20 m from carcasses. All individuals were photographed and identified by their conspicuous and distinctive spot patterns. Adult females were distinguished from males by their association with young individuals at dens and by enlarged
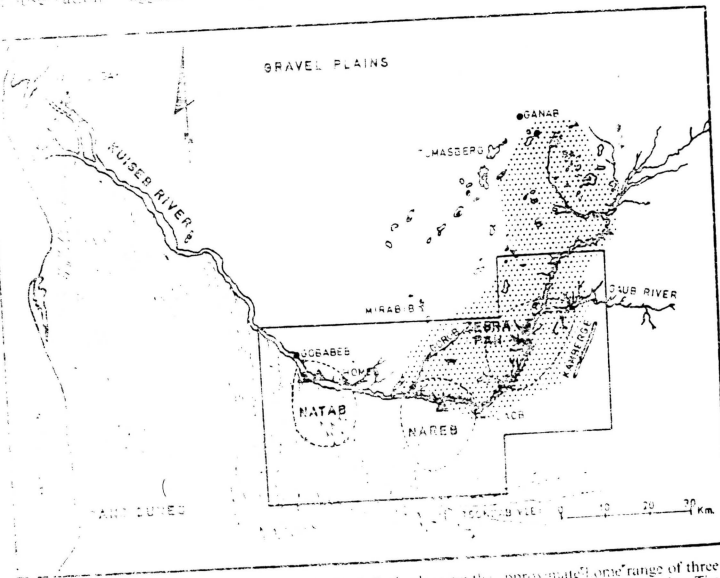
nipples, which develop following pregnancy and parturition. The age of cubs was known from long-term observations of their development at the Natab dens.

Observations of dominance focused on, but were not limited to, the Natab group of two adult females (Ns and Np), two males (Nr and Hc), and an unsexed subadult (Gr) who associated with them for varying intervals. One female (Ns) gave birth to two cubs (Ro and Re) in November 1977; the other female (Np) bore a single cub (Az) in April 1978. The Nareb group of three adults lived 35 km upriver from Natab. Another 45 km upriver from Natab (Fig. 1) lived the Zebra Pan group of seven individuals: five adults and two cubs, presumably siblings, 12–18 months old. No cubs were born to either of these groups during the study.

Namib Desert spotted hyaenas feed mainly on gemsbok, remains of which were present in 79.6% of 595 scat samples, and mountain zebra (present in 12.7% of all scat samples). The remains of smaller antelope species, springbok, steenbok (*Raphicerus campestris*) and klipspringer (*Oreotragus oreotragus*), were present in 2.2% of the hyaena scats (Tilson et al. 1980). Because there are no large predators present in the Namib Desert other than spotted hyaenas, all ungulate deaths by predation can be attributed to them. The only other resident predator is the black-backed jackal (*Canis mesomelas*), which does not prey on large ungulates. Even when hyaenas left carcasses unattended (e.g. in daylight hours and during periodic absences at night) jackals seldom fed upon them, nor did lappet-faced (*Torgos tracheliotus*) or Cape vultures (*Gyps coprotheres*), which were also present. An independent study of jackal food preferences in the Namib shows that gemsbok were present in only 8.5% of 405 scat samples (Stuart 1976). This unusual situation may be in part related to the low population densities of these scavengers, and in part to other factors not identified by our study.

Carcasses were found by back-tracking hyaena spoors from den areas or by searching the area by vehicle. Of 56 carcasses (29 gemsbok, 26 mountain zebra) found in this way, 27 were fresh kills and had only been fed on for one night; 25 carcasses had been partially or almost totally consumed, so that we could not establish how the animal died; and the remaining four animals died from causes other than predation (Tilson et al. 1980). In addition, we set out four large carcasses and three small carcasses to test the

effects of satiation and hierarchical behaviour on feeding rates (see Results, below).

Behavioural Measurements

Namib Desert spotted hyaenas were present at carcasses only during the night. Individuals emerged from day-time lairs near sundown, congregated at den areas and usually left within the hour to feed. Groups left carcasses just before sunrise. To avoid the disruptive effects of artificial lights (Bearder 1977; Whateley & Brooks 1978), we made observations only during the three to four nights before and after full moon. Data presented here summarize all possible observations for this necessarily limited monthly interval during the 21-month study period. Feeding and dominance data are from 67 nights (about 12 h, from sunset to sunrise) during which hyaenas were observed for 676 h at 18 different carcasses: 31 nights (356 h) at Natab, 21 nights (180 h) at Nareb, and 15 nights (140 h) at Zebra Pan. Large carcasses refer to gemsbok ($\cong 150$ kg) and mountain zebra ($\cong 250$ kg); springbok ($\cong 35$ kg) and provisioned domestic goats ($\cong 35$ kg) are considered small.

The large prey species for East Africa hyaenas (in Ngorongoro Crater and Serengeti Plains) are wildebeest, *Connachaetes taurinus* ($\cong 175$ kg) and plains zebra, *Equus burchelli* ($\cong 250$ kg). The predominant small species there is the Thomson's gazelle, *Gazella thomsoni* ($\cong 25$ kg). The biomass density of all relevant spotted hyaena prey species in the Namib Desert averages 130 kg/km². At East African sites prey biomass density averages about 7100 kg/km² in the Serengeti Plains and 19 200 kg/km² at the Ngorongoro Crater. Hyaena densities at these localities are proportional to prey densities: 12 and 170 hyaenas/100 km² in Serengeti and Ngorongoro, respectively (Kruuk 1972), and 0.5 hyaenas/100 km² in the Namib Desert (Tilson et al. 1980).

A feeding bout is defined here as an uninterrupted interval of feeding at a carcass. Departure from a carcass defines the termination of the feeding bout. The interval, to the nearest minute, during which each hyaena fed on a carcass was recorded during 36 nights. Total feeding time is defined here as the number of minutes an individual fed on a carcass per night. When an individual stopped feeding temporarily while at a carcass, this non-feeding time was subtracted from total feeding time. Time at carcass is defined as the total minutes per night spent by an individual in the proximity (30–50 m) of a carcass while not feeding, regardless of its

Figure 1. The study area within the Namib-Naukluft Park, showing the approximate home range of three spotted hyaena groups at Natab, Nareb and Zebra Pan. Dens and lairs are indicated by triangles. The stippled area represents the observed distribution of mountain zebra, gemsbok are found throughout the area with larger concentrations south of the Kuiseb ... (Tilson et al. 1980).

activity and whether or not other individuals were feeding. Data are included only for the first three or four nights of feeding following the appearance of a fresh carcass. After the fourth night, carcasses became dismembered and small fragments were carried away and either consumed, abandoned or transported to the den (see Henschel et al. 1979). By this time most flesh was gone and feeding was limited to bone consumption. Caching of food, which apparently occurs occasionally in the Ngorongoro hyaena population (Kruuk 1972), was never observed in the Namib hyaena population (Henschel et al. 1979).

On 12 of the 36 observation nights we weighed carcasses before and after hyaena feeding. The difference in carcass weight before and after a night, divided by the time spent feeding, gives group carcass consumption rates, from which average individual food consumption rates were estimated. Feeding rates were based on individual time budgets and assumed equal consumption rates per unit feeding time per adult.

The assessment of dominance relationships was based on 234 supplantings at carcasses. A typical supplanting action involves retreat of the subordinate and approach to and utilization of the carcass by the dominant. Such events also include one or more of the following behavioural components: rapid approach of the dominant while holding the head and shoulder high; cocking the ears; erecting the mane; holding the tail vertical; and growling. Subordinates responded by holding the ears and mane flat, curling the tail under the belly, squealing; and retreating, as reported by Kruuk (1972). Supplanters sometimes bit opponents on the neck, in a manner similar to that described for brown hyaenas, *Hyaena brunnea* (Owens & Owens 1978) but not as persistent. Passive replacements of an individual abandoning a carcass without interacting in the manner described above were not scored as supplantings. It was not possible to assess rank order away from carcasses, because males were not allowed to approach den areas, the only other site where social interactions were observed.

Results

Feeding Dominance

The hierarchical structure of Namib Desert spotted hyaenas, as determined by supplanting at carcasses, was nearly linear. Supplanting occurred on the average 10.1 times per group per night. Adult females won almost all observed encounters. High female status at carcasses was extended to their accompanying offspring, who were subordinate to other adult females but supplanted the subadult and adult males (Table I).

Although cubs were considerably smaller than the males they challenged, proximity to their mothers gave them access to carcasses. Two cubs (Ro and Re) of the top-ranking female (Ns) in the Natab clan first started feeding at carcasses when they were 3 months old, or about one-quarter of the body size of adult males. Together, they successfully challenged the lower-ranking hyaenas (Hc and Gr) the first night they were observed at a carcass. Subsequently, they fed at every carcass we observed and rarely had to challenge those individuals, as well as a third male (Nr). Of the 21 combined supplantings by Ro and Re, 17 (81%) occurred during the first three nights they were observed at carcasses. Thus access to carcasses became as uncontested for the cubs as for their mothers. An even more extreme case was female Np's cub. Az. Az accompanied the group to carcasses when it was 6 weeks old, despite Np's attempts to carry it back to the den 2–3 km away. At a carcass it repeatedly challenged and supplanted larger hyaenas. The single dominance reversal between the adult females (Np > Ns) occurred on the first night Az was observed at a carcass with Np (Table I). These observations emphasize the importance of long-term and, if possible, continuous observations. Once status is established, a prolonged period of observation can pass without any observable expression of status-determining or maintaining behaviour.

Feeding Characteristics

Previous descriptions of spotted hyaenas feeding at carcasses emphasize frenzied gorging by all group members until carcasses are completely consumed, usually in a matter of minutes (Deane 1962; van Lawick & van Lawick-Goodall 1970; Bearder 1977). Kruuk (1972) describes the complete dismemberment and consumption of two zebras, a mare and a colt, together weighing about 370 kg, by 35 spotted hyaenas in 36 min.

In contrast to the reports of 30 or more East African hyaenas eating side by side at carcasses (van Lawick & van Lawick-Goodall 1970; Kruuk 1972), Namib Desert hyaenas most frequently fed one at a time. Combined data from the three groups show that during 53% of 657 observed feeding bouts when two or more individuals were present at a carcass, only one individual fed (Table II). Most simultaneous feeding bouts of two (28%), three (15%) and four (4%) hyaenas were combinations of mothers and their offspring. Although up to seven hyaenas assembled at a carcass (Zebra Pan group), the largest number of individuals observed feeding simultaneously was five (5 of 657 bouts). Simultaneous feeding bouts at a carcass by two or more adult hyaenas were less frequent than solitary feeding bouts (Table II). Thus individual access is limited in small groups of spotted hyaenas assembling at large carcasses in the Namib Desert.

Individuals usually replaced one another at large carcasses throughout the night. During 67 observation nights, an average of 4.0 (range 1–7) hyaenas attended each carcass per night, taking an average of 5 days (range 3–9, $N = 12$ carcasses) to consume it completely. Skulls and other large bones were often left behind, but may subsequently have been consumed or carried off to den sites (Henschel et al. 1979).

Each individual fed for an average total of 69.8 min during 5.3 feeding bouts per night for the 36 observation nights. Intervals between bouts averaged 57.4 min. Feeding bouts lasted an average of 12.2 min (Table II). Between feeding bouts, non-feeding individuals rested or interacted with other group members for an average of 270 min per night.

Although the expression of hierarchical behaviour gave certain individuals priority of access to carcasses, it did not exclude subordinate individuals from sustained feeding at large carcasses. Average nightly feeding times at large carcasses were nearly equal for most individuals in the group, regardless of sex, age or status (Table III). Only the lowest-ranking individuals, Hc and Gr, showed significantly shorter feeding periods at large carcasses, about half as long as for the rest of the group.

Hyaenas were not present at carcasses throughout the entire night. Group movements were coordinated. The group would sometimes leave for several hours, travelling to water-holes where other collaborating observers saw them. All group members left the carcass and returned to it together. Rather than remain behind and feed unmolested, subordinate members chose to accompany the group. Carcasses were aban-

Table I. Dominance Matrix for the Natab Clan of Spotted Hyaenas, *Crocuta crocuta*, in the Namib Desert, Namibia

Species	Ns	Np	Az	Ro	Re	Nr	Hc	Gr	Wins	Losses
Ns (adult)							48	26	82	1
Np (adult)						3	52		15	2
Az (juvenile)						3	10		15	0
Ro (juvenile)				9	3				12	3
Re (juvenile)										2
Nr (adult)				9	3		23	23	29	
Hc (adult)					9		3	31		46
Gr (subadult)	6			3			41			125

The sex of the ... , most of ... in ... of ranks, see ...

Table II. Number of Feeding Bouts of Different Durations and Involving Different Numbers of Participants (Bouts in which only adults participated are in parentheses)

Duration (min)	Number of hyaenas feeding				
	1	2	3	4	5
1–5	187 (119)	136 (46)	80 (6)	20 (0)	2 (0)
6–10	74 (35)	27 (11)	15 (0)	4 (0)	2 (0)
11–15	38 (34)	5 (5)	1 (0)	1 (0)	1 (0)
16–20	18 (17)	3 (0)	1 (0)	0	0
21–25	17 (12)	3 (2)	0	0	0
> 25	18 (18)	8 (8)	0	0	0
Total	347 (235)	182 (72)	97 (6)	26 (0)	5 (0)
Percentage	52.8 (75.1)	27.7 (23.0)	14.8 (1.9)	4.0 (0)	0.1 (0)

Table III. Total Feeding Time (min) for Individual Spotted Hyaenas at Large Carcasses

Date	Ns	Np	Nr	Hc	Gr	Ro	Re	Time (min)	Amount* (kg)
Feb 3	110	—	95	—	—			205	(—)
Mar 30	114	110	84	—	—	76	75	459	(35)
Mar 31	40	102	101	—	61			304	(36)
Apr 1	44	76	110	—	60	63	64	417	(23)
Apr 27	132	113	96	—		180	181	702	(57)
Apr 28	67	79	87	—		64	87	384	(36)
Apr 29	89	23	61			63	92	328	(23)
May 22	104	—			26	36	49	215	(16)
May 23	111	86	—		39	107	117	460	(34)
May 24	117	116	—		56	119	164	572	(25)
June 17	23	27		18		21	20	109	(—)
June 18	67	100		58		107	105	437	(—)
June 19	75	69				93	85	375	(—)
x̄	84	82	91	43	48	84	94	382	(32)

*Estimated total amount of food consumed per night by the group.

...ned altogether during daylight hours. Thus group association seemed to be more important to subordinates than enhanced access to carcasses.

Under conditions of scramble competition as reported by Kruuk (1972), East African spotted hyaenas rapidly devoured carcasses at an average rate of 434 kg per h, or 18 kg per h per individual hyaena (Table IV). Under these conditions feeding success depended upon each individual's ability to tear apart and consume a carcass. For our study population, observed group feeding rates were much lower on larger carcasses. Group feeding rates at four large carcasses averaged 8 kg per h, or 6 kg per h per individual hyaena (Table IV). Carcass consumption rates for groups in East Africa were significantly higher (Mann–Whitney U-test, $P < 0.001$), averaging 54 times the rate observed by us.

Namib Desert spotted hyaenas fed significantly faster at small carcasses than at large carcasses (Mann–Whitney U-test, $P < 0.01$). Individual feeding rates at small carcasses were also higher (Mann–Whitney U-test, $P < 0.01$), averaging twice the rates observed at large carcasses. Both group and individual feeding rates at small carcasses in the Namib Desert and in East Africa were nearly equal (Mann–Whitney U-test, NS), and in some cases values for the Namib Desert exceeded those for East Africa (Table IV).

Individual feeding rates for Namib Desert spotted hyaenas at large carcasses were on the average relatively varied, ranging from 2.6 to 7.1 kg per h (Table V). Differences in total feeding times on successive nights at large carcasses were not significant (Mann–Whitney U-test, NS). On the average, Namib Desert hyaena groups consume large carcasses at a rate of 26.1 kg per night (SD = 11.0, N = 16 nights).

Discussion

The relationship of dominance hierarchies to the behaviour of social carnivores in general is complicated by reports that hierarchies for some species are poorly defined (e.g. wolves, Canis lupus: Haber 1977). In other species, hierarchies were not reported by earlier observers (e.g. wild dogs, Lycaon pictus: Kühme 1965; Estes & Goddard 1967; Schaller 1972) but were recognized in later studies (Frame et al. 1979; Malcolm & Marten 1982). One possible explanation for this situation is that hierarchies in social species, and especially in family groups, may be determined during early development or during infrequent contests and later reinforced by subtle signals, avoidance or concession. Another possibility is that selection against the expression of hierarchy may follow the development of social hunting as an adaptation for facilitating the benefits of cooperative hunting. It is also probable that hierarchies develop in some groups of social hunters, but are expressed only under special environmental circumstances, as reported here for spotted hyaenas.

Hierarchical relationships within spotted hyaena social groups are in some cases an important determinant of individual access to large

Table IV. Average Feeding Rates of Spotted Hyaenas at Different Localities (Summated means for group and individual feeding rates are in parentheses)

Carcass type	Feeding data Weight (kg)	Amount (kg)	Time (min)	Total no. of hyaenas	Group feeding rate (kg/h/group)	Individual feeding rate (kg/h/hyaena)	Source
East Africa (high-density)							
Large:							
Zebra	370	370	36	35	616.7	17.6	Kruuk 1972
Wildebeest	100	100	13	21	461.5	21.9	Kruuk 1972
Wildebeest	185	185	50	14	222.9 (434)	15.9 (18)	Kruuk 1972
Small:							
Gazelle	20	14.5	45	1	19.3	19.3	Kruuk 1972
Impala (S. Africa)	50	45	80	2	34.6 (27)	17.3 (18)	Bearder 1977
Namib Desert (low-density)							
Large:							
Gemsbok	132	116	689	4	10.1	5.5	This study
Mountain zebra	178	132	921	5	8.6	7.1	This study
Gemsbok	125	94	808	4.5	6.7	5.4	This study
Gemsbok	137	75	673	4	7.7 (8.0)	4.7 (5.7)	This study
Small:							
Goat	36	36	199	4	10.9	7.9	This study
Goat	35	35	33	3	63.6	39.8	This study
Goat	30	30	50	2	36.0 (37)	25.0 (24)	This study

Table V. Group and Individual Feeding Rates of Spotted Hyaenas on Consecutive Nights

Carcass	Day no.	Carcass weight, kg*	No. of hyaenas	Group feeding rate (kg/h/group)	Average individual feeding rate (kg/h/hyaena)
Gemsbok A	1	125 (35)	4	9.6	4.5
	2	89 (36)	4	7.7	7.1
	3	52 (23)	4	4.5	3.3
Gemsbok B	1	132 (57)	4	11.6	4.9
	2	75 (36)	4	9.8	5.6
	3	39 (23)	4	7.9	4.2
Gemsbok C	1	107 (16)	3	6.4	4.5
	2	89 (34)	4	7.9	4.4
	3	54 (25)	4	5.6	2.6
Mountain zebra	1–5	204 (91)†	6	9.5†	4.9†
	6	113 (23)	5	7.9	5.8
	7	90 (18)	3	6.2	4.5

*Values in parentheses represent the amount consumed per night.
†These values represent the summation of five consecutive nights.

carcasses (van Lawick & van Lawick-Goodall 1970; Kruuk 1972), their principal food (Deane 1962; Eloff 1964; van Lawick & van Lawick-Goodall 1970; Kruuk 1972; Bearder 1977; Tilson et al. 1980). If a high-ranking individual is able to supplant one or more other individuals it may gain uncontested access to meat, then feed to satiation and abandon the carcass. Thus, the larger the carcass, the greater the number of individuals it will accommodate, and the greater the number of individuals that will be profitably rewarded by participation in a hunt to produce such a carcass. It follows that larger social groups with persistent membership will be accommo-

dated only if relatively large carcasses regularly become available. At some lower limit of prey or carcass size and frequency of kills, social hunting may become unprofitable to some or all subordinate individuals.

Our observations show that subordinate adult males do feed at large carcasses (Table III) and thus profit from participating in social hunts for large prey, although they are completely excluded from small carcasses and partially from large ones. A comparable situation has been reported for lions, *Panthera leo*. Adult lionesses as a class are subordinate to adult males, but under most circumstances they are the primary hunters. They gain access to large prey in scramble competition with males, or feed after the males have fed to satiation (Bertram 1976).

For spotted hyaenas we assume that during the evolutionary development of social hunting family members were retained as group members to enhance the effectiveness of hunts for larger prey. Observations of the Namib Desert population emphasize the females and their young form family units that probably endure until cubs can participate in social hunts. The relationship of males to these groups requires further study. We assume that males join the spotted hyaena groups and that they are not close relatives of the females who dominate them. For small family groups, such as those observed here, family members may obtain exclusive access to small carcasses at the expense of unrelated subordinates, and even possibly at the expense of their father.

If hierarchical limitations were expressed by the evolutionary precursors of present-day social carnivores, one necessary feature of coordinated hunting is that enough kills of prey large enough to satisfy the needs of all the hunters must be made if subordinates are to continue as members of the group. This suggestion is supported by a comparison of the prey of spotted hyaenas with that of brown and striped hyaenas (*Hyaena hyaena*), which hunt prey or scavenge at carcasses which, on the average, are considerably smaller than those taken by spotted hyaenas. These related species do not hunt socially, though brown hyaenas may assemble at carcasses and also feed in hierarchical order (Owens & Owens 1978). Female brown hyaenas also remain in their natal clans, which gives support to the suggestion that expanded matriarchal family groups are a forerunner of contemporary spotted hyaena social organization. Such a social grouping may have led to the evolution of social hunt-

ing by spotted hyaenas, contemporary populations of which also feed on carrion, fruit and a variety of other small, discovered carcasses (reviewed by Mills 1978). Both brown (Skinner 1976; Mills 1977; Owens & Owens 1978) and striped hyaenas (Kruuk 1976; Macdonald 1978; Skinner & Ilani 1979) forage alone and scavenge together only at large carcasses left by other predators.

By contrast, spotted hyaenas hunt socially and eat primarily at large carcasses, most of which they kill themselves (Deane 1962; Eloff 1964; Pienaar 1969; van Lawick & van Lawick-Goodall 1970; Kruuk 1972; Tilson et al. 1980). Spotted hyaenas may nevertheless scavenge most of their food where lions are numerous and leave surpluses, such as at giraffe (*Giraffa camelopardalis*) carcasses (Bearder 1977).

The possible relationship of hierarchical behaviour to group size has not been previously reported and may be one of several mechanisms balancing group size to prey availability. Caraco & Wolf (1975) for lions, and Zimen (1975) and Nudds (1978) for wolves, suggested that hunting-group size should be balanced to prey size to provide a yield per hunter per unit effort, a suggestion for which we find no support. These authors also identified the importance of a threshold food yield per hunting individual, a requirement with which we agree. Social hunters living in a seasonally fluctuating environment or depending upon a migratory prey resource may fragment and rejoin to satisfy this condition. Thus the average hunting-group size for social carnivores may vary geographically according to the spectrum of size, density and availability of prey and scavengeable carcasses.

Where conspecifics are tolerated at central denning sites, many individuals may join in feeding aggregations, including some that have not participated in the hunt. Kruuk's (1972) observations show that when large groups of individuals assemble at a kill, it may not be defensible by any of them, regardless of rank or potential rank, making unfeasible any expression of individual status. We view scramble contests at carcasses as a potential response of spotted hyaena social groups to high concentrations of food.

An alternative explanation for the above observations of scramble competition at carcasses may be related to local densities of competing large carnivores, such as lions. Where lions are numerous they often usurp hyaena kills (Kruuk 1972; Schaller 1972; Bertram 1976). Thus hyaenas may concentrate on consuming

the kill as fast as possible, sharing it with as many potential kin or clan-members as possible before the lions can arrive and usurp the carcass. By consuming the carcass 72 times faster than at rates observed under hierarchical conditions, hyaenas are assured of the bulk of the carcass. In the Namib, where there are no lions, hyaenas can feed slower, and to satiation. This explanation, however, fails to explain why hyaenas in East Africa feed so slowly at small carcasses, which presumably are as susceptible to lion usurpation as are large carcasses.

Some features of social hunting by spotted hyaenas may have developed in arid environments occupied at lower densities by smaller groups of individuals, rather than in prey-rich environments of contemporary East African parks. There remains a need for extensive observations of the behaviour of social carnivore species living in various environments. These species are probably highly flexible in their social organization and structure (Rowell 1979), according to variations in the environment.

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BEHAVIOUR OF COLONIAL AND SOLITARY SPIDERS OF THE THERIDIID SPECIES *ANELOSIMUS EXIMIUS*

BY TERRY E. CHRISTENSON

Department of Psychology, Tulane University, New Orleans, LA 70118, U.S.A.

and

Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Panama

Abstract. Most *Anelosimus eximius* live in colonies, but a few females emigrate short distances and establish small, individual webs. Field studies were conducted on one colony and nearby smaller webs in order to describe communal activities and division of labour, and to note costs and benefits of remaining in the parental colony and emigrating. Adult and juvenile females repaired the web and captured prey. Adult females, rather than juveniles, cared for egg sacs and fed young. When colonial egg sacs were abundant, females moved from sac to sac. Several colonial females regurgitated food to spiderlings which had recently emerged from a particular sac. In smaller webs inhabited by two or three females, the mother cared for the sac but all females fed the young by regurgitation. Males rarely participated in communal activities. Advantages of colony living include protection from predators, the availability of large prey and, in the event of a female's death, the care of her egg sac and feeding of her young. Cannibalism of the egg sac is a potential cost of coloniality, affecting about 10–20% of colonial sacs. Cannibalism was not observed in the smaller webs. However, the costs of emigrating are very high: most of the solitary females disappeared, leading to interspecific predation on their eggs and young.

Adults of the vast majority of spider species are solitary, with the male occasionally maintaining proximity to the female for mating purposes. There are, however, a few notable exceptions, in which adults remain together in a communal web throughout their lifetime. Buskirk (1981) and Burgess & Uetz (1982) have reviewed the behaviour of such species.

Anelosimus eximius is an interesting New World communal species because it demonstrates relatively complicated social processes (Kullmann 1972). Thousands of individuals of more than one generation inhabit a single web. Many adult females and juveniles in a colony repair and clean the web, and more than one will attack a prey item at one time and then transport it to a leaf retreat for consumption (Simon 1891; Brach 1975; Tapia & de Vries 1980; Vollrath & Rohde-Arndt 1983). Adult males do not appear to participate in these activities.

There are few details available concerning reproduction. Some females of a colony mate and some do not (Vollrath & Rohde-Arndt 1983), with the likelihood of mating related to feeding success. According to Simon (1891) and Stejskal (1976), females care for their own egg sacs, but Brach (1975) and Tapia & de Vries (1980) suggest that females are indiscriminate in their care. Colony egg sacs are also subject to cannibalism (Vollrath, personal communication), but its frequency of occurrence and causes are not known. Females apear to feed the spiderlings by regurgitation soon after emergence (Vollrath, personal communication), but it is not known how many females feed the young of a particular sac.

Anelosimus also lends itself to the comparative study of social behaviour. First, female *An. eximius* may either inhabit colonies or emigrate and inhabit solitary webs (Brach 1975; Vollrath 1982). Vollrath observed naturally occurring solitary webs and those of females released in suitable areas, and found that most webs were inhabited for only a few days. He concluded that the costs of emigration were high. Second, within the genus there is between-species diversity in social behaviour, as *An. studiosus* females inhabit solitary webs (Brach 1977). Third, excellent taxonomic revisions of the genus are available to the behaviourist (Levi 1956, 1963, 1972).

I conducted field observations on an *An. eximius* colony and neighbouring individually constructed webs in order to describe the degree to which colony activities can be considered communal, to describe the division of labour of colony activities, and to outline the costs and benefits of remaining in the colony or emigrating.

Methods

Study Area

The study was conducted along a roadside in the moist rainforest on Cerro Galera. The site