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Publisher: Taylor & Francis

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Journal of Natural History

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tnah20>

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Published online: 17 Feb 2007.

To cite this article: David M. Pratt & Virginia H. Anderson (1985) Giraffe social behaviour, Journal of Natural History, 19:4, 771-781, DOI: [10.1080/00222938500770471](https://doi.org/10.1080/00222938500770471)

To link to this article: <http://dx.doi.org/10.1080/00222938500770471>

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Giraffe social behaviour

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(Accepted 9 July 1984)

Many features recommend the giraffe (*Giraffa camelopardalis*) for behavioural study: it is big, abundant, conspicuous, active by day, reasonably trusting of people, deliberate, and the best self-marked animal in existence. Surprisingly, its social behaviour has been largely neglected.

We studied giraffe exclusively for the following periods: February–March, 1975 and January–December, 1977 in the Serengeti National Park, July 1979–June 1980 in the Arusha National Park, and January–October, 1981 in the Tarangire National Park, totalling 3264 hours of observation directed principally to social behaviour. All of these parks are in northern Tanzania.

An earlier paper (Pratt and Anderson 1979) presented the results of a year's investigation of giraffe cow-calf relationships in the Serengeti National Park. That study demonstrated the strength of the cow-calf bond in agreement with the findings of Langman (1977) and described in quantitative fashion the behavioural patterns and interactions of mother and young, especially as related to the calf's nurture, protection, and preparation for adult life. We summarize here our observations of other types of social interactions among giraffe. Some of these were made during our year in the Arusha National Park (Pratt and Anderson 1982); to these have been added data from the Tarangire National Park.

Methods

Individuals were recognized by the markings on their necks. Drawings of both sides of the neck were made at first sighting and the individual was named for a prominent mark and assigned to a sex- and age-class.

Our age classification of giraffes is the same as in our earlier reports (Pratt and Anderson 1979, 1982). A young giraffe is considered a calf as long as it regularly accompanies its mother; when it leaves its mother (usually during its second year of life) it is classed as a juvenile. Upon reaching the size of an adult female, at about five years (Backhaus 1961, Dagg and Foster 1976), it is classed as a cow or a bull. On the basis of admittedly somewhat subjective impressions (of gait, carriage, skin colour, vigour, and firmness of flesh or emaciation) we classified cows as young, middle-aged, or old. Bulls continue to grow until about seven years old. Again subjectively, we distinguish three classes of bulls. The youngest bulls, in Class C, graduate to Class B as they increase in stature, the neck becoming heavier and the horns longer and thicker. Bulls of Class A tend to be larger than Class B bulls, but the more important differences are the stouter neck, the massive horns, and the addition to the skull of bony exostoses and supernumerary horns. This secondary bone growth alters the proportions of the skull so that in very old animals the eye, previously in the upper part of the head, is now mid-way between the forehead and the lower edge of the jaw.

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Results

The numbers of individuals identified in the two populations are shown in table 1.

Table 1. Numbers of known individuals, by age and sex.

	Arusha National Park	Tarangire National Park
Calves		
female	36	17
male	20	15
Juveniles		
female	34	23
male	24	18
Cows	172	139
Bulls	<u>176</u>	<u>128</u>
	462	340

A. Interactions among cows

1. *Bodily contact.* In our ten months in the Tarangire National Park we recorded 112 instances of cow touching cow (nosing, or rubbing with head or neck) plus five instances of mutual touching. In addition we saw a cow bumping another or hitting with the head twelve times, pressing her chest to another cow's rump seven times, mounting once, urine-testing once, and three times cows performing the naso-frontal greeting (Pratt and Anderson 1979). The amount of bodily contact among cows in the Serengeti and Arusha Parks was comparable.

2. *Associations.* A useful definition of a giraffe herd is Foster's (1966): a collection of individuals that are less than a kilometre apart and moving in the same general direction. While giraffe herds are often described as fluid, their membership changing from day-to-day, there is one characteristic grouping of giraffe that has considerable stability. This is a herd composed of one or a few mothers with calves (usually of similar ages) that choose to remain together, with the bonds between the calves providing further cohesion, plus a few juveniles and maybe an additional cow. We have known such groups in the Serengeti, the Arusha Park and Tarangire.

The Tarangire group consisted of an old cow named Canopener and her male calf (estimated age two to 11 months over the period of our observations), a middle-aged cow Two Line Fan and her male calf (4–13 months), two juvenile females, a juvenile male, and a young cow. We observed these animals for ten months. At the end of five months Two Line Fan left the group and thereafter was seldom seen with them, but her calf, recently weaned, remained with the others. In the 109 sightings we had of Canopener, she was never without one other member of this group of eight, she was seen with one member twice, with two 13 times, with three 16 times, with four 20 times, with five 26 times, with six 16 times, and with all seven other members 16 times. In 72% of her sightings, more than half of the group were with Canopener.

The degree of association between individuals in the group has been computed as

$$a = \frac{N}{N + n1 + n2}$$

where a is the index of association, N is the number of times the two individuals were seen together, and $n1$ and $n2$ are the number of their sightings when not together. Thus if two individuals are together in one half of their aggregate sightings, $a = 0.5$. Among the eight individuals in this group there were 28 possible dyads. Over the 10-month period, nine of these possible dyads (32%) were together in more than half of their aggregate sightings and 22 (79%) were together in one-third or more of their sightings. For the first five months, before Two Line Fan's defection, 20 dyads (71%) were together in more than half of their sightings, and 100% were together in one-third or more of the sightings.

3. *Leadership.* As a loose herd of browsing giraffe move along, it is not always easy to identify a leader. At times perhaps there is no leader. At other times one gets the impression that the leader initiates the movement, which then continues in the same direction, all of the animals knowing from previous experience the route that is to be followed.

In 109 sightings of Canopener and members of her group, Canopener was visibly leading 49 times, Two Line Fan five times, and during two of the sightings Canopener and Two Line Fan appeared to alternate in leading. On three occasions Canopener's group stopped to wait for her when she had lagged behind and when she caught up with them she headed off in a new direction and the others followed. But three times the other members of the group did not follow Canopener and in time she rejoined them. When each individual's indices of association with the other seven members of the group are averaged, Canopener's average index (0.584 for the ten months) is higher than any other. This reflects Canopener's central position in the group.

In our experience the leader of a herd of giraffe is almost invariably a middle-aged or old cow, usually with a calf.

B. Interactions among bulls

1. *Sociability.* The sightings of bulls, by age class, alone or associated with other individuals, are shown in table 2. Young bulls spent two-thirds of the time in mixed groups of giraffe (cows and/or immatures and/or other bulls) and more than a quarter of the time in all-bull groups, and they were seldom alone (about 6% of sightings). As

Table 2. Sightings of bulls, by class, alone or associated with other individuals. (Arusha National Park and Tarangire National Park data combined).

	C bulls		B bulls		A bulls	
	sightings	%	sightings	%	sightings	%
Solitary	76	5.7	194	19.1	95	24.9
In all-bull groups	365	27.4	232	22.8	74	19.4
In mixed groups	889	66.8	590	58.1	212	55.6
	1330		1016		381	

χ^2 values: C bulls vs. B bulls, 101.44. Significant at $\alpha = 0.001$.
 C bulls vs. A bulls, 122.66. Significant at $\alpha = 0.001$.
 B bulls vs. A bulls, 6.32. Significant at $\alpha = 0.05$.

they matured, they spent progressively less time in mixed groups or all-bull groups and tended more and more to a solitary state, alone in almost 25% of sightings. (Cows are much more sociable. In 1522 sightings of cows in Tarangire only 3·8% were solitary.)

2. *Sparring and related activities.* Sparring bouts, in which male giraffes stand side-by-side in parallel or reverse parallel position and deliberately swing their heads and necks against each other, have been well described (Innis 1958, Coe 1967, Guggisberg 1969, Dagg and Foster 1976). The blows are almost always delivered gently, in the tempo of a stately dance, there are sometimes long pauses, and when they stop sparring they are likely to browse side-by-side. To previous descriptions we would add from our observations that (1) the participants usually hold their tails drawn forward between their hind legs, (2) normally they swing by turns, not simultaneously, each recoiling from the other's blow before delivering his own, thus reducing the chance of injury, and (3) sparring appears to be a contagious activity. Sometimes additional bulls join a sparring bout and there may be as many as five milling about together. When the participants are quite different in size, which is often the case, it is usually the smaller individual that initiates the bout.

In 164 bouts observed in the Arusha and Tarangire Parks the participants were four male calves, 12 male juveniles, 61 C Class bulls and 15 B Class bulls, but no A bulls. As can be seen in table 3, the frequency of sparring is highest in C Class bulls. In 668 sightings of C bulls in bull groups, 38% of the individuals were sparring, while only 12% of the B bulls were sparring in a total of 359 seen in bull groups. Sparring is an activity that may begin, hesitantly and awkwardly, when the male giraffe is still a calf less than a year old and its frequency peaks when he is a young bull: it is a behaviour characteristic of adolescent males. We saw one instance of sparring between a juvenile male and a juvenile female (initiated by the male), one bout between the same juvenile male and a very young cow (initiated by the latter), and once saw two young cows sparring.

There are three types of behaviour that often accompany sparring. Bulls seldom rub their heads or necks on one another. In 39 out of 50 recorded instances of this, the individual that rubbed was of inferior or equal rank to the other, and the action appeared to be an invitation to spar. A second behaviour associated with sparring is pointing the snout straight up. This is almost exclusively a male behaviour. The snout up attitude adopted by juvenile males and young bulls in connection with sparring resembles a common feeding posture of mature bulls. It seems likely that it—and the browsing posture which it imitates—has the visual effect of maximizing the animal's stature. But we saw no evidence that it was a threat, and on the other hand we cannot agree that it is a sign of submission, as suggested by Backhaus (1961).

Table 3. Frequency of sparring: numbers of A, B, and C Class bulls (in groups of two or more bulls) observed sparring, and not sparring, Arusha and Tarangire National Parks.

	Sparring	Not sparring	% Sparring	χ^2 values for paired classes
A bulls	0	96	0	13·019 75·276
B bulls	44	315	12·3	
C bulls	254	414	38·0	

Both χ^2 values significant at $\alpha=0\cdot001$.

A third activity sometimes seen in sparring bouts is male attempting to mount male. We saw this eight times in the Arusha Park and eight times at Tarangire. In nine of these 16 events, the animal attempting to mount had his penis unsheathed. None of these actions involved an A bull, one mounter was a B bull, one was a juvenile male and the rest were C bulls. In no case did a bull try to mount another male as large as himself. Intent observation and detailed recording of positions and movements failed to show that this act was an expression of dominance (which we initially surmised); we never saw any indications—e.g., behavioural, postural—of submission in bulls mounted. (In one instance, the individual mounted did not visibly react; he just went on browsing.)

3. *Fighting*. Sometimes sparring is vigorous and heavy blows are exchanged. The mechanics of fighting are essentially the same as those used in sparring. The distinction between the two activities is therefore somewhat arbitrary. A fight does not develop, with gradually increasing intensity, from a sparring bout. In a fight, the two bulls approach each other rapidly; with no preliminaries or introductory movements they start slugging each other with maximum force and, reckless of injury, deliver their blows as rapidly as possible and sometimes simultaneously. The encounter ends as abruptly as it began, with one of the contestants clearly vanquished and running away. We witnessed only two such fights. In one, a B Class bull had been ardently courting a young cow for some hours when a bigger B bull appeared and approached the couple; the courting bull immediately attacked him with violent blows in rapid cadence and drove him off. In the other fight no female was involved: with no obvious provocation a B bull furiously attacked a slightly smaller C Class bull and within 20 seconds chased him away.

4. *Dominance*. There is a dominance hierarchy among the bulls in each population, which develops as they mature (Backhaus 1961, Coe 1967, Foster and Dagg 1972, Mejia (in Moss 1975) and Leuthold 1979). Each individual's relative social standing is defined by the outcome of encounters with other bulls: by walking toward him with head held high or sometimes by merely staring hard at him, the dominant individual obliges the inferior to move off. Sometimes when an A Class bull joins a group of giraffe including cows and other bulls, he will single out the B bulls and send them off, disregarding individuals of lower rank. In 129 such displacements that we recorded in the two parks, cows were present in all cases but one. The distribution of the participants by Class is shown in table 4.

The results of these contests were, for the most part, consistent with Class ranking. Higher rank generally entails greater age, size, and experience. Contests between bulls of the same Class were usually decided in favour of the larger bull if there was a difference in size. It should be noted that each bull was assigned to a Class when seen for the first time; their rankings do not reflect the outcome of contests. The advantage of high rank was best demonstrated by a small but evidently old and experienced bull

Table 4. Displacements of bulls, Arusha National Park and Tarangire National Park.

Displaced	Displacing bulls		
	A bulls	B bulls	C bulls
A bulls	8	5	—
B bulls	28	28	1
C bulls	37	17	3
Juvenile males	1	1	—

which, because of the conformation of his head, we had classed as an A bull. This individual's determination and high self-esteem were such that he challenged and drove off two C Class bulls that were bigger than himself and one B bull that was much bigger.

In six of the 129 contests, individuals of inferior rank prevailed (B bulls displaced A's five times, one C bull displaced a B). In three of these instances the same runty but belligerent A bull just mentioned was confronted by a B Class bull who was not only bigger but who also was not disconcerted by the small A bull's aplomb; in each encounter the A bull approached the B in a threatening manner but when about 50 m away he turned abruptly and ran away. In another contest of anomalous outcome a B bull displaced an old and somewhat decrepit A bull. In another, a B bull was bettered by a bull we had classed as a large C bull but with some doubts, in that he was bigger than some individuals we had labelled B's. Thus the unexpected results in five of the six anomalous displacements were related to peculiarities of individuals, and in only one displacement in the 129 were we totally unable to explain the outcome. This means that our ranking of bulls by Class was usually accurate and that hierarchical standing is in fact determined almost entirely by rank and size.

If the 85 displacements of bulls at Tarangire are shown in a diagram in which an arrow connects each bull with the individual he displaced, two of the displacements (involving four bulls) are unrelated to the others. But one sees that all of the remaining 43 animals are interconnected in a continuous web of interactions, i.e., each individual is related to every other individual directly or by a chain of displacements.

In the 129 contests we recorded, 24 between the same individuals were repeated, always with the same result. Furthermore, the outcome of each contest was consistent with the results of all previous displacements to which it could be related by participants in common, i.e., the dominance relationship was never triangular or circular but rigidly linear.

Displacement expresses dominance and is a mark of maturity. In 129 encounters, we saw only three C bulls displacing others, for a total of four displacements. An individual's social status does not become fixed until he is at least a B Class bull.

The linear hierarchy is established through these encounters. When two bulls quite different in size (and therefore in age) meet in the vicinity of cows, almost always the smaller one will immediately defer. In confrontations between bulls about equally matched, often they approach each other, standing very tall and staring hard at one another; when they are 40–80 m apart one bull will suddenly turn and run away while the other pursues at a fast walk. Very rarely they fight.

C. *Interactions between bulls and calves*

All giraffe are curious about young calves and are visibly attracted to them; bulls are no exception. It is typical behaviour for a bull, on approaching a mixed group of giraffe, to go to each small calf and bend down and nose it, usually on the head. Sometimes he will stand for several minutes with his head over a recumbent calf. The calf's responses to these attentions include nosing the bull's head, walking or running away, and (in very young calves) sometimes trying to find a teat.

D. *Interactions between bulls and cows*

1. *Urine-testing.* A typical group of giraffe, numbering up to ten or 15, consists of cows, calves, juveniles and perhaps two or three C Class bulls. Older bulls make casual visits to such a group, arriving alone and going to each cow in search of one in oestrus. This activity occasionally leads to courtship, which may culminate in mating. Giraffe

bulls test the sexual readiness of cows by urine-testing with flehmen. Combining the Arusha Park and Tarangire Park data, we observed 304 such tests. It is remarkable that although a substantial number of these (82) were done by C Class bulls, not once did we see a juvenile male testing a female. Thus our necessarily arbitrary categorization of male age classes reflected an important biological difference. The frequencies of testing of cows by A, B and C Class bulls (table 5) are strongly correlated with age; by highly significant differences A's tested more often than B's, and B's more often than C's.

Urine-testing requires the cooperation of the female: when the bull nuzzles her rump, she must produce a stream of urine if he is to catch some in his mouth and savour it. In the Tarangire National Park we recorded the bulls' attempts to test cows as well as the frequency of successful assays, with the results shown in table 6. In their attempts to assess the sexual readiness of females, older (A and B Class) bulls had significantly higher rates of success than the younger bulls. The C bulls' low success is attributed to their inexperience and the cows' preference for older suitors. Some young bulls appeared inept in their nuzzling of the cow's rump, and sometimes, having induced the cow to urinate, they did not sample the urine. In other cases, young bulls were persistent but unsuccessful in eliciting urine from cows which soon thereafter urinated readily when a big bull appeared and nuzzled them.

In order to see whether bulls had a preference for cows of any particular age group or were equally attracted to cows of all ages, for each group frequency of testing was computed against the number of sightings with bulls present (table 7). The bulls showed

Table 5. Frequency of testing of cows by bulls: numbers of A, B, and C Class bulls (in the company of cows) observed testing, and not testing cows, Arusha and Tarangire National Parks.

	Testing	Not testing	% Testing	χ^2 values for paired classes
A bulls	84	128	39.6	20.911
B bulls	138	455	23.3	
C bulls	82	808	9.2	55.669

Both χ^2 values significant at $\alpha=0.001$.

Table 6. Bulls' attempts to test the sexual readiness of cows, Tarangire National Park.

	Successful	Unsuccessful	% Successful
A bulls	34	22	60.7
B bulls	76	61	55.5
C bulls	45	89	33.6

χ^2 values for paired classes:

A bulls vs. B bulls, 0.444. Not significant.

A bulls vs. C bulls, 11.979. Significant at $\alpha=0.001$.

B bulls vs. C bulls, 13.137. Significant at $\alpha=0.001$.

Table 7. Frequency of testing of females by bulls: numbers of juvenile females, young cows, middle-aged cows, and old cows (in the company of bulls) observed being tested, and not being tested, by bulls, Arusha and Tarangire National Park.

	Tested	Not tested	% Tested
Juvenile females	44	448	9.8
Young cows	176	889	19.8
Middle-aged cows	113	968	10.5
Old cows	30	430	6.5

χ^2 values:

Young cows vs. juveniles, 15.950.	Significant at $\alpha=0.001$.
Young cows vs. middle-aged, 16.979.	Significant at $\alpha=0.001$.
Young cows vs. old, 27.522.	Significant at $\alpha=0.001$.
Juveniles vs. middle-aged, 0.8595.	Not significant.
Juveniles vs. old, 1.947.	Not significant.
Middle-aged vs. old, 5.428.	Significant at $\alpha=0.02$.

a much keener interest in young cows than in juveniles or middle-aged or old cows, and they tested middle-aged cows somewhat more often than old cows. And although they sometimes tested young cows repeatedly in a short time (e.g. 17 times in two hours) they never did so with older cows.

During the time when an A or a B bull temporarily joins a herd of cows and immatures, cows engage in various behaviours that in one way or another suggest a degree of arousal. The commonest of these is the cow rubbing her head and neck on a bull's neck, back, or rump; almost always the bull showed no reaction. Juvenile females and very young cows sometimes urinate if a big bull walks past them even with no contact, and they may point their snouts straight up (a behaviour we never saw in females except in these circumstances). Four times we saw female juveniles or very young cows trying to mount a male calf of 18–20 months. Our records show cows striking bulls on six occasions (but none of bulls striking cows), and seven instances of cows running away on the approach of a bull.

2. *Courtship and mating.* Sometimes when a bull is testing the sexual readiness of cows he singles out one individual and gives her close and protracted attention. Presumably such a cow is in oestrus, a condition that occurs about every two weeks and lasts for one day (Dagg and Foster 1976, 131). Usually the bull stops browsing, he stays at her side or directly behind her, following her closely and trying to steer her away from other giraffes. She keeps moving and browsing. The bull noses her mane, back and rump and repeatedly performs urine-testing. From time to time he presses his chest against her rump while standing very tall. Occasionally his penis is unsheathed, but when the cow walks to another bush and the bull immediately follows, it is quickly retracted as they move about through the thorny shrubs. If other bulls are present, they watch with keen interest but keep out of the way. Active courtship may go on for one or two days, interspersed with hour-long periods in which the participants browse side by side. In time, the bull stands close at her rump, moves his hind feet forward a little, gently swings a stiff foreleg forward to touch her hind leg ('laufs Schlag', Walther 1981) and, sliding his forelegs up along her flanks, he tries to mount. She usually thwarts this attempt by walking forward. At last she may stand for him; he mounts, makes three or

four vigorous thrusts the last of which brings his head and neck into a position so nearly upright that he seems to be about to fall over backwards, and in a moment they have both returned to browsing.

Combining our observations in the Arusha and Tarangire Parks, we saw 46 courtships. The frequency of courtship, relative to sightings of bulls in the company of cows, was significantly greater in A bulls than in B bulls and in B's than in C's (table 8).

We have seen only one mating, which occurred during our year in the Serengeti National Park—one mating witnessed in 3264 hours of observation of giraffe behaviour.

Table 8. Frequency of courting of cows: numbers of A, B, and C Class bulls (in the company of cows) observed courting, and not courting cows, Arusha and Tarangire National Parks.

	Courting	Not courting	% courting	χ^2 values for paired classes
A bulls	17	158	9.7	6.313† 29.300‡
B bulls	25	519	4.6	
C bulls	4	886	0.45	

† Significant at $\alpha = 0.02$.

‡ Significant at $\alpha = 0.001$.

Discussion

Leuthold (1979) reports that interactions among giraffe cows were rare in Tsavo East National Park (Kenya). She recorded a total of six bodily contacts (of the same sorts as the 141 that we noted in the Tarangire Park). Her number of hours of observation is not stated, but the study extended over a period of seven years. We are unable to reconcile her experience with ours.

Leuthold (1979) calculated the degree of association between individual giraffes in Tsavo East. Her equation is such that when two individuals are seen together in one-third of their aggregate sightings, the resulting association index is not 0.33 but 0.5, and when two individuals are together in half of their sightings, 0.67. Even so, she found that 'among adult and subadult giraffes... indices of 0.5 or more are very rare: 0.3% and 0.6% of the total for males and females respectively.' From this it might appear that there is far less group cohesion in the Tsavo population than in the Tarangire. But this is because Leuthold was measuring associations between all members of the population over a period of years, whereas we are here quantifying the associations in a group of the type that shows the greatest cohesion to be found in giraffe herds, over a period of ten months. While the closeness and endurance of cow-calf associations (Langman 1977, Pratt and Anderson 1979) is not surprising, quite often there are, as in the group described here, accessory members that attach themselves like satellites to the nuclear cow-calf dyads with remarkable fidelity. These added members are usually juveniles; one wonders if they are offspring of the cows in the group.

There is competition for mates in both sexes. Among the males, A Class bulls tested females more frequently than B bulls, which in turn tested more frequently than C's. C Class bulls were not as successful as B's or A's in inducing females to show whether they

were in oestrus. Among the females, young cows were much more attractive to males than any other female age class, and middle-aged cows were more attractive than old cows. Thus sexual competition favours older males and younger females.

That the older males are the most solitary and yet are the most active sexually is a paradox. The bulls' preference for young cows may increase the efficiency of their search for oestrus females in that the young cows are presumably less likely to be already pregnant. With a gestation period of 15 months and the resumption of oestrus as little as three weeks after parturition (Dagg and Foster 1976, 131), a cow is least likely to be pregnant in the period immediately after giving birth. It follows that a bull's chances of maximizing his contribution to the following generations would be increased by courting cows with newborn calves. We looked for, but did not find, evidence that bulls favoured the mothers of neonates.

Leuthold (1979) in Tsavo East recognized a senior class of bulls ('old') that were alone in 30–50% of sightings and made no sexual approaches to females. We are not aware of such a category in the Arusha nor the Tarangire Park. Evidently there are senior bulls in Tsavo East that are even more solitary than the bulls we studied. Among the bulls that courted cows in the Arusha and Tarangire Parks there were three that were described on their identification file cards as 'very old.' This leads us to doubt that, in the populations we studied, the life history of the males regularly includes a stage in which they renounce sexual pursuits.

The function of sparring is uncertain, but the most commonly expressed opinion is that it establishes the dominance hierarchy (e.g. Coe 1967, Mejia (in Moss 1975) and Leuthold 1979). A direct causal connection between sparring and social standing seems a highly plausible assumption but we were obliged to abandon it when repeated and detailed observation of the behaviour of the participants did not provide any visible evidence of dominance or submission. The behaviour of both animals suggests play much more than fighting (Leuthold 1979, calls it 'playfighting'). This play provides practice in an activity that may, in later life, be used in fighting to determine the right to breed. Sparring is a habit of young bulls. When they grow up and enter the lists of those eligible to breed they sometimes need, in competition with peers for mates, the skills learned earlier in sparring bouts.

The courtship of giraffe is a highly conspicuous performance, and when the bull has separated his intended from the herd, doggedly follows her and stands at his tallest with chest pressed against her rump, the nature of the activity is obvious, even at a great distance. The prolongation of this performance by the cow for hours or even days serves her interests well: it may attract a more worthy suitor to displace the bull presently wooing her, but the latter's efforts then go unrewarded.

Conclusions

Bodily contact, e.g., nosing, rubbing, bumping, and striking with the head, commonly occurs among giraffe cows. Assemblages of cow-calf dyads plus juveniles and young cows have considerable stability of membership for periods of ten months or more. Leadership is an attribute of an old or middle-aged cow, usually with a calf.

Young bulls are gregarious, in the Arusha and Tarangire National Parks spending only about 6% of the time alone. As they mature they tend toward a solitary state; in these parks old bulls were alone about 25% of the time.

The sparring of males, which occurs even among calves, reaches a peak frequency in young bulls and rapidly decreases with greater age. Most bouts are initiated by the

smaller participant. Sparring is a form of play. It is often accompanied by three other behaviours: (1) rubbing with head and neck (apparently an invitation to spar), (2) snout pointing straight up, which maximizes the individual's height, and (3) mounting. In none of these behaviours did we see any indication of dominance or submission.

Fighting, which is mechanically similar to sparring but at a much higher intensity, is of rare occurrence.

The bulls in a giraffe population are linked in a dominance hierarchy in which each individual's relative standing is determined by his age and size. A bull demonstrates his superior rank by obliging another to move off in the presence of cows. In 129 such displacements there were 24 repeats, with invariable results, and the dominance relationship was never triangular or circular but rigidly linear.

Bulls, like all other giraffes, show a strong interest in calves.

Of 304 tests by males of the sexual readiness of females, none were performed by juveniles, and the older bulls did proportionally more of the testing than the younger bulls. Older bulls were more successful than young ones in inducing cows to urinate. Judged by the relative frequency of testing, bulls showed a preference for young cows over all other female age categories and a preference for middle-aged cows over old cows. Frequency of courtship was correlated with age of bull.

Acknowledgments

We are grateful for permission to work in the National Parks of Tanzania and we particularly thank the men and women of the Tarangire National Park for help at all levels in the problems of living and working in the Park.

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