

# Movements and group structure of giraffe (*Giraffa camelopardalis*) in Lake Manyara National Park, Tanzania

Henk P. van der Jeugd<sup>1,3\*</sup> and Herbert H. T. Prins<sup>2</sup>

<sup>1</sup>Zoological Laboratory, University of Groningen, P.O. Box 14, NL-9750 AA Haren, The Netherlands

<sup>2</sup>Department of Environmental Sciences, Tropical Nature Conservation and Vertebrate Ecology Group, Wageningen Agricultural University, Bornsesteeg 69, NL-6708 PD, Wageningen, The Netherlands

<sup>3</sup>Department of Animal Ecology, Evolutionary Biology Centre, University of Uppsala, Norbyvägen 18D, S-752 36, Uppsala, Sweden

(Accepted 10 June 1999)

## Abstract

Movements and group structure of giraffe *Giraffa camelopardalis* were studied in Lake Manyara National Park, northern Tanzania. The giraffe population in Manyara had increased from 60 to 85 individuals between the early 1980s and 1991. This increase may have been the result of an increase in browse availability as a result of a dramatic decline in elephant numbers, and bush encroachment following a series of anthrax epidemics that killed impala. Giraffe densities in Manyara are high compared to other areas within the Masai ecosystem, and Manyara probably serves as a dry season refuge. Females were found in small, yet unstable groups, while males associated randomly with each other. Neither males nor females were confined to single localities, although home ranges were small compared with studies in areas with low giraffe densities. In one area within the park a more stable group was found, and resident males who were probably defending a temporary harem, engaged in necking contests with immigrant males. A comparison with other studies showed that giraffe density, home-range size, mobility and group stability differ across different habitats. The tendency that more stable groups are found in high density areas might be taken as evidence for the occurrence of resource defence polygyny in such areas.

**Key words:** giraffe, *Giraffa camelopardalis*, group structure, mating strategies, Tanzania

## INTRODUCTION

Giraffe *Giraffa camelopardalis* (L.) are easy to observe as they are large, and the unique pattern of spots on the body allows the easy identification of individuals. Despite several studies observing individual giraffes (Foster & Dagg, 1972; Leuthold, 1979; Pratt & Andersson, 1982, 1985), little is known about their social systems. For example, mating strategies adopted by male giraffe have, to our knowledge, never been adequately described. Male mammals show a diverse array of mating bonds, ranging from obligate monogamy to group polygyny and promiscuity (Clutton-Brock, 1989). Usually, giraffe social organization is described as non-territorial, with the animals moving around in loose, open herds that are constantly changing configuration. Males generally divide their time between feeding and monitoring the reproductive status

of females (Pellew, 1984*a,c*). Males thus appear to be polygynous or promiscuous, probably mating with as many females as possible. However, several studies have shown that mammalian mating strategies may vary between populations or even individuals of the same species (Gosling, 1986; Langbein & Thirgood, 1989; Prins, 1996). Which male strategy is the most viable will largely depend on the availability and distribution of resources, the density of females and/or males, and the degree of breeding synchrony (Emlen & Oring, 1977; Gosling, 1986; Clutton-Brock, 1989; Langbein & Thirgood, 1989). Since giraffe occur over a wide range of habitats, it is therefore not unlikely that differences in the mating strategies of male giraffe exist across different environments.

We studied giraffe in Lake Manyara National Park, Tanzania, to gather information on local densities, home ranges, movements and group structure. We compare our results with similar studies on giraffe carried out in other environments, and show that densities, home-range size, mobility and group stability of both male and female giraffe vary among different habitats.

\*All correspondence to: H. P. van der Jeugd, Department of Animal Ecology, Evolutionary Biology Centre, University of Uppsala, Norbyvägen 18D, S-752 36, Uppsala, Sweden.  
E-mail: henk.van\_der\_jeugd@zoologi.uu.se

## MATERIAL AND METHODS

### Study area

Fieldwork was carried out in Lake Manyara National Park (3°30'S, 35°45'E), northern Tanzania, at about 1000 m a.s.l. The Park is relatively small (*c.* 100 km<sup>2</sup> of land), and most of it is easily accessible by car. It stretches from north to south, bordered by the escarpment of the Rift Valley on the western side, and by Lake Manyara on the eastern side. The Park is only a few km wide, which enables most of its animals to be seen with relative ease.

The vegetation of the Park is described by Greenway & Vesey-Fitzgerald (1969, 1972) and Loth & Prins (1986). Water is available throughout the year because of many perennial rivers running down from the escarpment into the lake. Our study in 1991 took place mainly during the long dry season (June–October), when rain was almost absent. Herbivore biomass was estimated at 177 kg. ha<sup>-1</sup> in the early 1980s, which was one of the highest in the world (Prins & Douglas-Hamilton, 1990). Main herbivores were buffalo, and elephant, which are now reduced to approx. 15% of their original numbers (Prins, van der Jeugd & Beekman, 1994). The number of giraffe remained stable between 1959 and 1984 at about 60 individuals (Prins & Douglas-Hamilton, 1990).

For research purposes, the Park was divided into 2 areas, 1 north of Ndala river (*c.* 43 km<sup>2</sup>; 'the north'), and the other south of it (*c.* 57 km<sup>2</sup>; 'the south'). During the study the north was covered slightly better than the south (58% of all observations were done in 43% of the area). The chances of finding most of the giraffe were higher in the north where there was an extensive road network and better visibility than in the south. Some of the analyses on known individuals are therefore restricted to observations from the north only.

### Methods

Observations on group structure and activities were made almost daily from May to November 1991. When a group was encountered, the number of adult males and females, immature males and females and juveniles in the group was counted. Individuals within 100 m of each other were defined as belonging to 1 group. This was mainly done for practical reasons as group size would otherwise have been underestimated in dense vegetation. Activities were scored as browsing, standing, lying and moving. Activity scores were used to calculate the activity pattern in the course of the day (07:00–19:00). The exact location of each group was assessed to the nearest 100 m using a grid system on a 1:25 000 vegetation map (Loth & Prins, 1986). Observations on individual giraffe were made between 2 August and 19 November. On 53 days within this period, we spent at least part of the day identifying and following individual giraffe. Whenever a previously unidentified giraffe was seen, the pattern of the markings on breast

and lower neck was drawn on an identification card. All other members of the group were also identified. In total, 101 individuals were identified. The number of observations per individual ranged from 1 to 11, the average and median number were 3.6 and 4 for males, and 3.8 and 5 for females. Home ranges were calculated using the periphery method (Leuthold, 1979) for individuals with at least 5 observations.

Associations between individuals were calculated using the simple formula given by Ginsberg & Young (1992):

$$\frac{x}{x + y_{ab} + y_a + y_b}$$

where  $x$  = number of observation periods during which  $a$  and  $b$  are observed together;

$y_a$  = number of observation periods during which only  $a$  is observed;

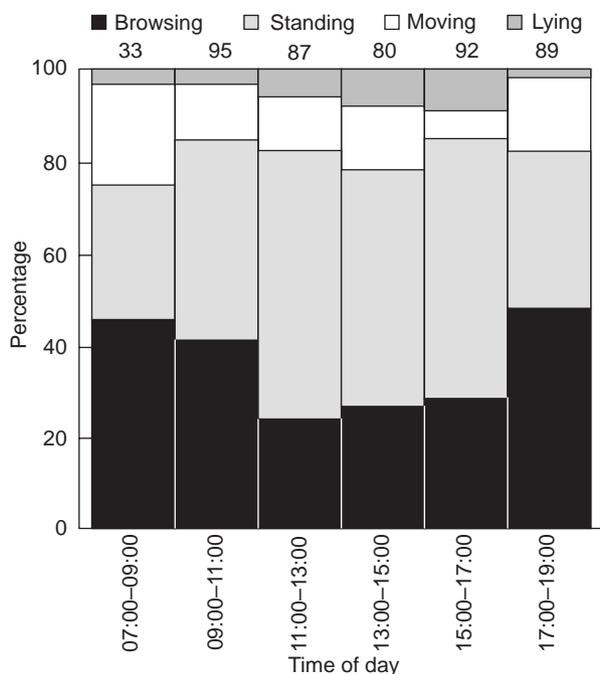
$y_b$  = number of observation periods during which only  $b$  is observed;

$y_{ab}$  = number of observation periods during which  $a$  and  $b$  are both observed in separate groups.

This formula gives a better measure of association than the more commonly used 'twice-weight index' (Ginsberg & Young, 1992). To find out whether associations between animals differed among sex-age categories of giraffe, we compared the observed number of combinations of individuals with the hypothetical number of possible combinations. This measure of association is a minimum estimate, since we could not always identify all individuals in a group.

Although we could not age giraffe exactly, we classified individuals into juveniles (estimated height under 2.5 m, usually accompanied by 1 or more females, age probably < 1 year), immatures (estimated height between 2.5 and 4 m, age probably between 1 and 5 years) and adults (estimated height over 4 m, age probably over 5 years). Of the adult bulls ( $n=45$ ), 8 were very large, and had extra horn-like protuberances on their skulls in addition to the usual 2 horns. Such bulls are probably at least 10 years old (Pellew, 1984c), and comparable to the 'class A bulls' described by Pratt & Anderson (1982, 1985).

Body condition was scored using an index ranging from 1 (ribs visible, skin loose in many folds) to 5 (no skin folds and the animal looking sleek). As we are not aware of any giraffe studies on body condition we constructed the body condition scale using our experience with estimating body condition in buffalo (Prins, 1996), which in turn is based on a body condition score for cattle (Herd & Sprott, 1986). We regularly checked our body condition estimates for inter-observer consistency. Half points were given when the animals condition was in between 2 scores, or when there was disagreement between 2 observers by 1 point. Body condition change was estimated by linear regression of body condition indices of individuals on day number for all individuals for which we had at least 3 body condition scores ranging over at least a 1-month period.



**Fig. 1.** Activity budgets of giraffe in Lake Manyara National Park. Numbers above bars are sample sizes.

## RESULTS

### Activity pattern

Between 07:00 and 19:00 giraffe spent on average 35% of their time browsing. In the morning and late afternoon the percentage of time spent browsing was almost twice as high as during midday (Fig. 1; Kruskal–Wallis,  $\chi^2 = 16.53$ , d.f. = 5,  $P < 0.01$ ). We did not conduct nocturnal observations, but from occasional encounters with giraffe at night we know that they spent at least part of their time browsing. Single males spent more time browsing than males in mixed groups, which in turn spent more time browsing than males in multiple male groups (39.3%, 27.0% and 7.3%, respectively,  $\chi^2 = 10.25$ , d.f. = 2,  $P < 0.01$ ). There were no differences in females for group structure ( $\chi^2 = 1.47$ , d.f. = 2, NS).

### Group size

One hundred and eight male, 39 female, and 94 mixed groups were found (Table 1), with group sizes ranging from one to 32. There was a significant effect of month on group size ( $F_{6,472} = 2.60$ ,  $P < 0.05$ ), but no 2 months differed significantly from each other (Scheffé multiple comparison). The observed differences between months were not clearly a seasonal trend. Male group size distribution differed significantly from female group size distribution in single-sexed groups (Kolmogorov–Smirnov  $Z = 2.490$ ,  $P < 0.001$ ), as well as within mixed groups (Kolmogorov–Smirnov  $Z = 1.896$ ,  $P < 0.005$ ). From counts made from the rim of the escarpment, the

**Table 1.** Mean and modal number of males and females in different group types. Male group, only immature or adult males; female group, only immature or adult females; mixed group, both males and females present; combined, number of males and females in mixed and single-sex groups combined. Total number is always slightly more than the total of males and females because of the presence of juveniles

Group type	n	No. of males		No. of females		Total no.	
		Mean	Modal	Mean	Modal	Mean	Modal
Male	108	1.52	1	–	–	1.58	1
Female	39	–	–	2.64	3	3.23	3
Mixed	94	3.66	6	5.12	7	9.15	12
Combined	241	2.51	4	4.39	7	4.80	10

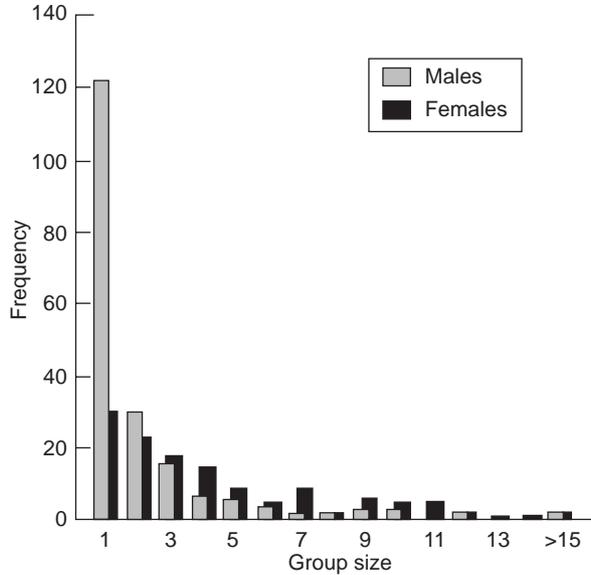
total number of giraffe present in the park at a given moment was estimated to be 85 individuals.

Mean and modal group sizes, i.e. the average group size within which an individual giraffe finds itself, were larger for females than for males in all group types (Table 1). Fisher's logarithmic series distributions were fitted to observed male and female group sizes to investigate whether group sizes were the result of random association between individuals (Pollard, 1977). As a whole, the Fisher's logarithmic series distribution fitted the observed group sizes for males ( $\chi^2 = 21.37$ , d.f. = 12, NS), which suggests a random association between individual males. However, group sizes of one occurred more often than expected ( $\chi^2 = 4.98$ , d.f. = 1,  $P < 0.05$ ; Fig. 2), suggesting that males tend to avoid each other. Female giraffe were more often found in groups of seven, nine and 11 (all  $P < 0.05$ ) and much less often alone than expected ( $\chi^2 = 7.52$ , d.f. = 1,  $P < 0.01$ ; Fig. 2). The model of random association between individuals clearly had to be rejected for females ( $\chi^2 = 35.22$ , d.f. = 12,  $P < 0.001$ ), which suggests a certain amount of association between giraffe cows.

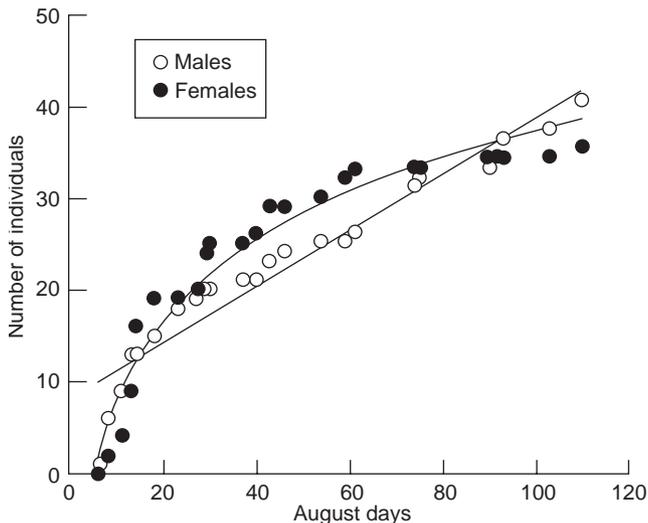
### Movements, group structure and home ranges

In total, 101 individuals were identified: 45 adult males, 44 adult females, two immature males, five immature females and five juveniles. The number of females identified for the first time in the north decreased over time and the cumulative number of identified individuals seemed to reach a plateau. For males, however, after an initial phase, the relationship between time and the cumulative number of identified individuals seemed to be linear, with apparently new males arriving in the area at a more or less constant rate (Fig. 3). As a result, 91.4% of all females found during the whole period were identified when 50% of the identification period had passed, but only 62.5% of all males were ( $\chi^2 = 8.56$ , d.f. = 1,  $P < 0.005$ ).

Mean home-range size was 5.2 km<sup>2</sup> for adult males and 8.6 km<sup>2</sup> for adult females, but variation was large (males range: 0.1–21.5 km<sup>2</sup>; females range: 0.5–27.0 km<sup>2</sup>). An ANOVA model including the factors sex, age-



**Fig. 2.** Group size distribution of male and female giraffe in Lake Manyara National Park. Group size distributions for males and females differ significantly from each other, while male giraffe were associating randomly, whereas female giraffe were not (see text).



**Fig. 3.** Cumulative number of individual giraffes that were identified in Lake Manyara National Park. Lines are fitted second order polynomials.

class and number of observations per individual explained only 26% of this variation, and none of the factors was significant, although home-range size tended to be positively related to the number of observations of a particular individual ( $F_{1,37} = 3.35$ ,  $P = 0.08$ ), and to differ between the sexes ( $F_{1,37} = 2.84$ ,  $P = 0.10$ ) when the number of observations was controlled for. Home ranges were overlapping and no areas were used exclusively by certain individuals. The average distance between two observations of individuals was 3.4 km ( $n = 123$ ,  $SD = 4.3$ ) for males (mean interval = 17 days)

**Table 2.** Number of observed and number of potentially possible dyads among different categories of giraffe. Giraffes observed only once were excluded from the analysis. A 'class A-male' is defined as a fully mature, adult male giraffe (see Methods). Juv, juvenile; imm, immature

Category	Observed	Possible	%
Male-male	152	780	19.5
'A male'-'A male'	4	28	14.3
Other male-other male	104	496	21.0
'A male'-other male	44	256	17.2
Female-female	162	528	30.6
Male-female	226	1320	17.1
Juv/imm-male	76	360	21.1
Juv/imm-female	82	297	27.6
Juv/imm-juv/imm	14	36	38.9
Overall/total	712	3321	21.4

and 3.2 km ( $n = 146$ ,  $SD = 3.6$ ) for females (mean interval = 16 days) (sex difference: Wilcoxon two-sample test,  $\chi^2 = 1.02$ , NS).

The number of observed associations between two individuals in relation to the total number of possible combinations differed significantly between sex-age categories (Table 2;  $G$ -test for independence  $G = 53.69$ ,  $d.f. = 5$ ,  $P < 0.001$ ). Subsequent unplanned  $G$ -tests (Sokal & Rohlf, 1994) revealed that associations among females occurred significantly more often than all other associations ( $G = 29.68$ ,  $d.f. = 1$ ,  $P < 0.001$ ) and associations between males and females significantly less often ( $G = 24.77$ ,  $d.f. = 1$ ,  $P < 0.001$ ). Associations between males tended to be less common ( $G = 2.34$ ,  $d.f. = 1$ ,  $P = 0.13$ ). Within males, associations between A-bulls were rare as compared to those between other bulls (Table 1), but this difference was not significant ( $G = 0.54$ ,  $d.f. = 1$ , NS), probably due to the low sample size.

Only in 22 instances was the level of association higher than 0.5. Again, there were differences among different sex-age categories ( $G = 16.30$ ,  $d.f. = 3$ ,  $P < 0.001$ ). Females tended to associate more often with females than expected ( $G = 2.82$ ,  $d.f. = 1$ ,  $P < 0.1$ ), and associations between males and females at this high level were very rare ( $G = 13.93$ ,  $d.f. = 1$ ,  $P < 0.0005$ ). Most of the associations higher than 0.5 were between individuals in a group of at least 17 individuals (eight adult males, four adult females, three immature females, two juveniles) that were seen regularly at the same places in the north. In the rest of the park no such large and stable groups were encountered. Males in this group were seen to engage in aggressive encounters with newly identified males on five occasions, but never with resident males in the group. Such behaviour was never observed outside this group. This 'necking or sparring behaviour' (Innis, 1958; Coe, 1967) usually continued for several hours and appeared to be quite harmless to the contestants.

### Body condition

Body condition indices ranged from 1.0 (very poor) to 4.0 (good) for both males and females and the

**Table 3.** Numbers and density/per km<sup>2</sup> of giraffe in the Masai ecosystem; all figures refer to the dry season (September or October). GCAs, game controlled areas surrounding Tarangire National Park. Densities in other areas are given for comparison

Area	Year	<i>n</i>	Size (km <sup>2</sup> )	Density ( <i>n</i> /km <sup>2</sup> )	Source
<b>Masai Ecosystem</b>					
Manyara National Park	1984	60	100	0.60	Prins & Douglas-Hamilton, 1990
	1991	85	100	0.85	This study
Tarangire + GCAs	1990	1041	6140	0.17	Campbell & Huish, 1991
	1990	1377	8359	0.17	Campbell & Huish, 1991
Serengeti National Park	1972	–	–	0.76	Sinclair, 1972
Masai Ecosystem	1991	2–3000	35.000	0.07	This study
<b>Other areas</b>					
Tsavo East National Park	1970–74	–	–	0.1–0.3	Leuthold, 1979
Nairobi National Park	1970	86	114	0.75	Foster & Dagg, 1972
Arusha National Park	1979	471	119	3.96	Pratt & Anderson, 1982

distribution of the indices was equal for both sexes ( $\chi^2 = 7.35$ , d.f. = 5, NS). Body condition indices were not correlated with day number (Spearman rank:  $r = -0.10$ , NS). Body condition change of individuals (see Methods) tended to be mostly negative for females (Wilcoxon signed rank =  $-31.5$ ,  $P = 0.11$ ), but did not show any trend in males (Wilcoxon signed rank =  $2.5$ , NS).

There were no significant differences in the body condition indices of giraffe that were identified for the first time in a given month compared with those of giraffe already present in the park. However, in November, at the end of the dry season, newly identified males had significantly lower body condition indices than males that were already present before November (Wilcoxon two-sample test,  $\chi^2 = 4.04$ ,  $P < 0.05$ ). Males in mixed groups had a somewhat lower body condition than single males, or males in multi-male groups. (Wilcoxon two-sample test,  $\chi^2 = 4.15$ , d.f. = 1,  $P < 0.05$ ). For females there were no differences in body condition with group structure (Wilcoxon two-sample test,  $\chi^2 = 1.37$ , d.f. = 2, NS).

## DISCUSSION

Lake Manyara National Park forms a part of the Masai ecosystem, and ungulates use the area around Lake Manyara as part of their annual migration through this ecosystem. Within the Masai ecosystem there are two clear foci that act as dry season refuges, Tarangire National Park *c.* 50 km east of Manyara and Lake Manyara National Park. Although the giraffe population of Lake Manyara National Park is small compared to the total numbers in the Masai ecosystem, the density here is much higher (Table 3), and it seems that the Park forms a local optimum for giraffe. This also applies to elephant, buffalo and other species (Drent & Prins, 1987). As condition loss during the dry season was negligible in Manyara, and giraffe spent only 35.3% of daylight hours browsing compared with 55.4% (males) to 72.4% (females) in the Serengeti (Pellew, 1984b), it seems that either habitat effectiveness or food intake rate is higher in Manyara than in the Serengeti.

The population estimate of 85 giraffe represented an increase from the 60 individuals that were present in the same area during the earlier three decades (Prins & Douglas-Hamilton, 1990). This increase may have been caused by the increase in the available amount of browse because of a dramatic decline in the number of elephants (Prins & Douglas-Hamilton, 1990; Prins *et al.*, 1994). Simultaneously, there was an increase in browse availability as a result of bush encroachment (Prins & van der Jeugd, 1993). The number of individual giraffe (101) that were identified was clearly higher than the maximum number counted in the Park, suggesting that the population was not closed, and that movements between Manyara and surrounding areas were common. A similar discrepancy between numbers counted and numbers identified was found in Nairobi National Park by Foster & Dagg (1972).

Our results on the accumulative identification of giraffe in Manyara show that the females form a more-or-less resident population in the Park, but males are immigrating and emigrating (Fig. 2). Our data show that, at the end of the dry season, newly arriving males were in a lower body condition than males that were already present in Manyara. There are two explanations for this finding. First, Manyara might act as a dry-season refuge for male giraffe, who are better off than are males outside the Park. Second, immigrant males may be low status males, wandering around in search of better opportunities.

Home ranges were small compared to the ones given by Leuthold (1979) in Tsavo East and Foster & Dagg (1972) in Nairobi National Park, but probably comparable with the ones in Arusha National Park, which can be inferred from data published by Pratt & Anderson (1982). These differences in home-range size might be explained by both Manyara and especially Arusha National Park being relatively heavily vegetated compared to Tsavo and Nairobi, and thus offering more food per unit area. Since the number of observations per individual was rather low, home-range sizes were probably underestimated in our study, particularly for males, who were found to immigrate and emigrate and whose home range might be partly outside our study area. Home ranges were overlapping and no clear

indications of territoriality were found. Females were not associating randomly, but were found more often in small groups (56% of all observations, Fig. 1), although most groups were continuously changing composition. More or less stable female groups were also observed in Arusha National Park by Pratt & Anderson (1985). Males, on the other hand associated randomly, and were mainly found alone (60% of all observations, Fig. 1). The situation in Manyara contrasted with the situation in Arusha National Park, where giraffe were strongly segregated into sub-populations with very little exchange (Pratt & Anderson, 1982, 1985), something that is not reported in any other giraffe study.

Males in mixed groups had a lower body condition, which might suggest that they spent relatively more time inspecting and guarding females at the expense of time spent browsing. In red deer *Cervus elaphus*, for example, stags hardly eat during the rut, and body weight rapidly declines at this time (Clutton-Brock, Guinness & Albon, 1982). However, male giraffes in mixed groups did devote a substantial proportion of their time to browsing, which does not support this hypothesis, while hardly any browsing was observed in multi-male groups. Most browsing was observed when males were alone, and one of the reasons that males are often found alone might thus be to replenish body reserves, as was found for buffalo (Prins, 1996).

Only one fairly stable group of giraffes was present in Manyara, in which association levels between individuals were higher than between other individuals. Adult bulls belonging to this group engaged in necking contests with newly arriving males, but never with resident males. Necking has been observed at different intensities ranging from 'sparring' or 'friendly encounters, chiefly between sub-adult males' (Innis, 1958; Leuthold, 1979), to violent fights between adults, rarely leading to injury or death (Coe, 1967; Simmons & Scheepers, 1996). Innis (1958), Coe (1967) and Simmons & Scheepers (1996) state that necking, at least between adult bulls, seems to be associated with dominance over females, and is observed when a male 'intruder' approaches a group of females accompanied by one or more males. The contests in Manyara never escalated into fights and fitted best the description of 'high intensity necking' (Coe, 1967), but they were always between an adult resident male and a newly arriving adult male from outside the Park. Our interpretation is that males in this group were defending a, probably temporary, harem against intruding males. It seemed that there was a dominance hierarchy within the resident group of giraffe in Manyara making necking unnecessary, but new males arriving into this group were challenged by resident males. Stable dominance hierarchies among male giraffe were found by Coe (1967), Foster & Dagg (1972) and Leuthold (1979).

Densities of giraffe differ widely across different habitats (Table 3). Not surprisingly, highest densities, as well as smallest home ranges, low mobility and most stable groups were found in the most vegetated areas (Foster & Dagg, 1972; Leuthold, 1979; Pratt &

Anderson, 1982, 1985). Manyara seemed to take an intermediate position. For animals that do not have a clearly defined short breeding season like the giraffe (Leuthold, 1979; Pratt & Anderson, 1982, 1985, pers. obs.; Pellew, 1984c), there exists a trade-off between maximizing food intake and maximizing female encounter rate (Emlen & Oring, 1977; Gosling 1986; Andersson, 1994). High levels of continuously distributed resources and high female densities promote male defence of an area that holds valuable resources for females (Emlen & Oring, 1977; Gosling, 1986). When resources are scattered and female densities low, males usually follow females on their foraging routes (Gosling, 1986; Clutton-Brock, 1989). Intermediary systems exist, for example where one or several males defend a group of females against other males (harem systems). Given the large variation in habitat types it is not unlikely that giraffe adopt different mating strategies across different habitats. The tendency for more stable groups, confined to single locations, to be found in high-density areas might be taken as evidence for the occurrence of resource defence polygyny in such areas, although clearly more work is needed to confirm this. The fact that differences in ecological circumstances can create variability in mating strategies should be taken into account in future studies on giraffe social systems.

### Acknowledgements

Permission to conduct fieldwork in Lake Manyara National Park and to use the Ndala Research Camp by the Tanzania National Council for Science and Technology and the Serengeti Wildlife Research Institute is gratefully acknowledged. Tanzania National Parks, and in particular its director Mr G. Sabuni, was always helpful and supportive. Shombe Hassan and Shabani Swalleh helped during fieldwork. Petr Komers, Rob Simmons, David Stenström and two anonymous referees gave comments on earlier versions of the manuscript. Herman van Oeveren is acknowledged for his help preparing the manuscript. Financial support was given by the Royal Netherlands Academy of Arts and Sciences and the Treub Maatschappij. This is an SWRI publication.

### REFERENCES

- Andersson, M. (1994). *Sexual selection*. Princeton, NJ: Princeton University Press.
- Campbell, K. L. I. & Huish, S. A. (1991). *Wildlife census Tarangire 1990*. Arusha: Tanzania Wildlife Conservation.
- Clutton-Brock, T. H. (1989). Mammalian mating systems. *Proc. R. Soc. Lond. B Biol. Sci.* **236**: 339–372.
- Clutton-Brock, T. H., Guinness, F. E. & Albon, S. D. (1982). *Red deer: behaviour and ecology of two sexes*. Chicago: Chicago University Press.
- Coe, M. J. (1967). Necking behaviour in the giraffe. *J. Zool. (Lond.)* **151**: 313–321.

- Drent, R. H. & Prins, H. H. T. (1987). The herbivore as prisoner of its food supply. In *Disturbance in grasslands: species and population responses*: 133–149. van Andel, J., Bakker, J. P. & Snaydon, R. W. (Eds). Dordrecht: Junk.
- Emlen, S. T. & Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science* **197**: 215–223.
- Foster, J. B. & Dagg, A. I. (1972). Notes on the biology of the giraffe. *East Afr. Wildl. J.* **10**: 1–16.
- Ginsberg, J. R. & Young, T. P. (1992). Measuring association between individuals or groups in behavioural studies. *Anim. Behav.* **44**: 377–379.
- Gosling, L. M. (1986). The evolution of mating strategies in male antelopes. In *Ecological aspects of social evolution*: 244–281. Rubenstein, D. I. & Wrangham, R. W. (Ed.). Princeton: Princeton University Press.
- Greenway, P. J. & Vesey-Fitzgerald, D. F. (1969). The vegetation of Lake Manyara National Park. *J. Ecol.* **57**: 127–149.
- Greenway, P. J. & Vesey-Fitzgerald, D. F. (1972). Annotated check-list of plants occurring in Lake Manyara National Park. *J. East Afr. Nat. Hist. Soc. natl Mus.* **28**: 1–29.
- Herd, D. B. & Sprott, L. R. (1986). *Body condition, nutrition and reproduction of beef cows*. Texas Agricultural Extension Service B-1526, Texas A & M University.
- Innis, A. C. (1958). The behaviour of the giraffe, *Giraffa camelopardalis*, in the eastern transvaal. *Proc. zool. Soc. Lond.* **131**: 245–278.
- Langbein, J. & Thirgood, S. J. (1989). Variation in mating systems of fallow deer (*Dama dama*) in relation to ecology. *Ethology* **83**: 195–214.
- Leuthold, W. (1979). Social organization and behaviour of giraffe in Tsavo East National Park. *Afr. J. Ecol.* **17**: 19–34.
- Loth, P. E. & Prins, H. H. T. (1986). Spatial patterns of the landscape and vegetation of Lake Manyara National Park. *ITC (Int. Inst. Aerosp. Surv. Earth Sci) J.* **2**: 115–130.
- Pellew, R. A. (1984a). Food consumption and energy budgets of the Giraffe. *J. appl. Ecol.* **21**: 141–159.
- Pellew, R. A. (1984b). The feeding ecology of a selective browser, the giraffe (*Giraffa camelopardalis tippelskirchi*). *J. Zool. (Lond.)* **202**: 57–81.
- Pellew, R. A. (1984c). Giraffe & okapi. In *The encyclopaedia of mammals*: 534–541. Macdonald, D. (Ed.). London: Allen & Unwin.
- Pollard, J. H. (1977). *A handbook of numerical and statistical techniques, with examples mainly from the life sciences*. Cambridge: Cambridge University Press.
- Pratt, D. M. & Anderson, V. H. (1982). Population, distribution, and behaviour of giraffe in the Arusha National Park, Tanzania. *J. Nat. Hist.* **16**: 481–489.
- Pratt, D. M. & Anderson, V. H. (1985). Giraffe social behaviour. *J. Nat. Hist.* **19**: 771–781.
- Prins, H. H. T. (1996). *Ecology and behaviour of the African buffalo: social inequality and decision making*. London: Chapman & Hall.
- Prins, H. H. T. & Douglas-Hamilton, I. (1990). Stability in a multi-species assemblage of large herbivores in East Africa. *Oecologia (Berl.)* **83**: 392–400.
- Prins, H. H. T. & van der Jeugd, H. P. (1993). Herbivore crashes and woodland structure in East Africa. *J. Ecol.* **81**: 305–314.
- Prins, H. H. T., van der Jeugd, H. P. & Beekman, J. H. (1994). Elephant decline in Lake Manyara National Park, Tanzania. *Afr. J. Ecol.* **32**: 185–191.
- Simmons, R. E. & Scheepers, L. (1996). Winning by a neck: sexual selection in the evolution of giraffe. *Am. Nat.* **148**: 771–786.
- Sinclair, A. R. E. (1972). Long term monitoring of mammal populations in the Serengeti: census of non-migratory ungulates, 1971. *East Afr. Wildl. J.* **10**: 287–297.
- Sokal, R. R. & Rohlf, F. J. (1995). *Biometry*. New York: Freeman.