Anim. Behav., 1989, 38, 309–317

Physiological costs of behavioural strategies for male cheetahs

T. M. CARO*†, C. D. FITZGIBBON†‡ & M. E. HOLT§
* Evolution and Human Behavior Program, Rackham Building, University of Michigan, Ann Arbor, MI 48109-1070, U.S.A.
† Serengeti Wildlife Research Institute, P.O. Box 661, Arusha, Tanzania
‡ Sub-Department of Animal Behaviour, University of Cambridge, Madingley, Cambridge CB3 8AA, U.K.
§ Department of Clinical Veterinary Medicine, University of Cambridge, Madingley Road, Cambridge CB3 0ES, U.K.

Abstract. In adult cheetahs, *Acinonyx jubatus*, some males compete fiercely for access to territories, become residents and encounter females within territories, while others seek out females in the course of a nomadic existence. This study shows that non-resident male cheetahs are in poor health compared to resident males based on examination of their body condition and haematological measures. Non-residents are both behaviourally and physiologically stressed compared to residents. They not only spend a lower per cent of time in exposed resting places and more time alert than residents, but they also have raised cortisol levels, suggesting behavioural differences associated with their status may contribute to their poor physical condition.

Amongst certain species of mammals, males use qualitatively different forms of behaviour (strategies) to secure access to females and further their reproductive success (e.g. elephant seals, *Mirounga angustirostris*, LeBoeuf 1974; mountain gorillas, *Gorilla gorilla beringei*, Harcourt & Stewart 1981; waterbuck, *Kobus ellipsirymnus*, Wirtz 1982; gelada baboons, *Theropithecus gelada*, Dunbar 1984; bighorn sheep, *Ovis canadensis*, Hogg 1984; and stoats, *Mustela erminea*, Sandell 1986; see Maynard Smith 1982). On casual observation, the time, energy and survivorship costs of different forms of behaviour in many of these species appear so different that it is generally assumed that the reproductive pay-offs of different strategies will probably be unequal (Davies 1982; Caro & Bateson 1986). However, only a few studies have attempted to measure any costs to breeding in male mammals. These have shown that males expend considerable energy (e.g. golden-manteled ground squirrels, *Spermophilus saturatus*, Kenagy 1987), and that they lost both condition (e.g. *Antechinus stuartii*, Lee & Cockburn 1985) and weight over the course of the breeding season (e.g. red deer, *Cervus elaphus*, Clutton-Brock et al. 1982; grey seals, *Halichoerus grypus*, Anderson & Fedak 1985). Unfortunately, no study has yet attempted to compare the costs of different strategies within a species of mammal, or to indicate how differential costs might influence fitness.

In contrast, amongst birds there is some evidence to show that non-territorial males have lower survivorship than territorial individuals (e.g. song sparrows, *Melospiza melodia*, Arcese & Smith 1985; red grouse, *Lagopus lagopus*, Watson 1985) and that nematode infestations and viral diseases may mediate these differences in mortality (Moss & Watson 1985; Hudson 1986). This study sets out to demonstrate that, in mammals, different strategies are associated with important differences in physical condition as has been shown for birds.

Female cheetahs, *Acinonyx jubatus*, in the Serengeti National Park, Tanzania have extremely large home ranges (ca. 800 km^2) with considerable overlap (Frame & Frame 1981; Caro, in press) compared to other similar-sized felids (ca. 25–240 km^2, from Gittleman & Harvey 1982). These ranges reflect the movements of their main migratory prey, Thomson's gazelles, *Gazella thomsoni* (Schaller 1972; Durant et al. 1988). Between 1980 and 1985, 30% ($N=110$) of individually recognizable males occupied, scent marked and defended territories centred on these female cheetah concentrations for periods as long as 6 years (Caro & Collins 1987a). These residents were young adults or adults and were often members of permanent coalitions of two or three males (Caro & Collins 1986; 1987a, b). Other males, non-residents, ranged over wide areas

0003-3472/89/080309+09 $03.00/0

:he Park for their whole lives, sought out females
i rarely scent marked (rates of scent marking
·h: $\bar{X}\pm$SE$=1{\cdot}00\pm0{\cdot}13$, $N=19$, and $\bar{X}\pm$SE$=$
5$\pm0{\cdot}02$, $N=20$, respectively; Caro & Collins
i7a; Durant et al. 1988). The majority of non-idents were also young adults or adults but luded a minority of recently independent adoles-ts not considered here (Caro & Collins 1987a). ew non-residents subsequently became residents r this study was completed.

Competition over territories was severe. Males e been observed to kill each other in territorial outes (Kuenkel 1978; Caro & Collins 1987a). eed, all of the eight radio collars so far overed from dead telemetred males have been nd inside territories. Lastly, 12 of the 17 male ups observed closely for more than 20 h con-ed a member with injuries apparently incurred ng intraspecific fighting; males were rarely seen be wounded in hunting or in interspecific petition. Such mortality may, in part, contri-: to the female-dominanted adult sex ratio id in all cheetah populations (McVittie)).

erritorial males probably secured enhanced ing access to females because females were e often sighted within territories than outside ı during the wet season which spans the ths of peak conception (December–March) in population; however non-residents were also in the company of females (Caro & Collins a, b). Nevertheless, the precise reproductive equences of territoriality are difficult to deter-: because: (1) mating has been observed only times in the wild despite extended observa-· (Frame & Frame 1981; Caro & Collins a); (2) females ranged through several male ories during the course of a year (Frame); and (3) estimating paternity using genetic ers is problematic in this homozygous species rien et al. 1983, 1987).

ven the marked differences in behaviour n by males of this species, the high costs of specific combat, and the probable differences productive pay-offs of the two strategies, it ed likely that there would be strong differences e physiological costs associated with each gy. The purpose of this study was to docu-these costs, determine how differences in viour might be responsible for these costs, and hether the costs might be of sufficient severity ect individuals' reproductive success.

METHODS

Physiological Measures

Twenty-one adult male cheetahs that could be approached closely because they were not shy of the observers' vehicle were anaesthetized as part of a radio telemetry programme. A dart containing 1–1·5 ml of tiletamine hydrochloride and zolazepam hydrochloride mixture (200 mg/ml) was dispatched from a hand-held blowpipe from the vehicle 5–15 m away (see Caro et al. 1987; Wildt et al. 1987 for details). Within 10 min, the animal became recumbant. A 20-ml blood sample was immediately taken from the cephalic vein of 16 of the individuals. Half the blood was mixed with EDTA while the remainder was allowed to clot; samples were stored at 0°C. Individuals were then weighed, measured and given a physical examination during which three measures of body condition were scored. (1) The ease with which spinous processes of vertebrae could be palpated was recorded on a 3-point scale. (2) The extent of sarcoptic mange on each ear was recorded on a 6-point scale. (3) The coat quality was noted as soft or coarse. Observers then retreated to the vehicle and waited until the cheetah had recovered sufficiently to avoid lions, *Panthera leo*, and spotted hyaenas, *Crocuta crocuta*.

In the laboratory, total red and white cell numbers were counted by standard techniques using a Neubauer counting chamber; packed cell volumes and haemoglobin concentrations were measured using Microcompur minicentrifuges. Blood smears were made, air dried, fixed in methanol, stained with Giesma stain, and a differential white cell count was performed. Blood cell counts were very consistent across individuals sampled twice and differential white cell counts were consistent between observers (see Caro et al. 1987).

In a parallel electro-ejaculation study, cortisol concentrations were used as an index of adrenal activity to compare resident and non-resident males (Wildt et al. 1984, 1987). The first eight males that could be approached close enough to anaesthetize were subjected to repeated blood sampling. All of these males were handled in the same way and were unconscious and unaware of their surroundings at this time. For all eight males, the first blood sample (10 ml) was obtained when the darted animal was tractable, usually 2–3 min before the plane of anaesthesia was suitable for electro-ejaculation. Subsequent samples were collected

after each of the three electro-ejaculation stimulus series, an average of 11, 19 and 26 min after the first blood sample. Subsequent samples were collected 15, 30, 45 and 60 min after the last electrical stimulus (see Wildt et al. 1987 for details).

Serum was collected and stored at −20°C until assayed for cortisol; assays were performed using duplicate series aliquots. Adrenal activity was evaluated on the basis of cortisol concentrations measured using an ^{125}I RIA kit (RIANEN™, New England Nuclear, No. Billerica, Massachusetts). This assay employed a cortisol antiserum complex solution containing rabbit cortisol antibody pre-reacted with an antiserum to rabbit gamma globulin in phosphate buffer. The rabbit cortisol antibody had previously been determined to have the following cross-reactivities: 100% with cortisol; 38·9% with prednisolone; 26·4% with corticosterone; 7·4% with aldosterone; 5·9% with 11-deoxycortisol; 3·5% with 17α-hydroxyprogesterone; 2% or less with progesterone, testosterone, dihydrotestosterone and estradiol-17β. Inter-assay and intra-assay coefficients of variation were 9·5% ($N=8$) and 8·7% ($N=6$), respectively, and minimum assay sensitivity was 0·2 ng/tube.

Behavioural Measures

The behaviour of most of these males and others was compared by following males for 1–10 days (each for 12 or more h; 1207 h in total), during which time their activity was noted every 15 min during daylight hours. Between 0930 and 1700 hours, outside the main hunting period (Schaller 1972), we observed males for 3 h during which time we recorded vigilance and posture every 5 min. Postures scored were: 'lying flat out', lying prone with head on the ground; 'lying out', lying prone with head raised; 'lying alert', lying with flank and hindquarters on the ground but forelegs tucked under the body; and 'sitting up', sitting on backlegs with forelegs vertically supporting the body. An observation period was terminated if a hunt began or any male was recorded as walking for three consecutive 5-min scans. If such termination occurred, only data from previous whole 1/2-h blocks were used in the analysis. After a hunt had ended or when cheetahs had settled again, a new observation period was started until 3 h of undisturbed observation had been made that day. These stringent criteria were used to ensure that cheetahs were only sampled when relatively relaxed. The per cent of 5-min samples in which each male was in each posture was calculated for each unbroken observation period, then for each day, and finally for all days the individual was followed, to yield one figure for each male.

To measure ranging patterns, locations of 30 individual males seen three or more times, obtained from sightings on the ground and aerial fixes of radio-collared animals, were plotted on a map composed of grid squares measuring 500 m × 500 m. The square root of the sum of squared vertical and horizontal displacements between consecutive sightings was then calculated. Rate of movement was determined from distance moved between consecutive sightings divided by the number of days between them; later, an average of these rates was taken. Only consecutive sightings that were less than 100 days apart were used in order to reduce the possibility that short distances interspersed by a long period of circuitous travel would be included in analysis.

Hunger level was appraised by scoring belly size on a scale from 1, representing near starvation, to 14, where the cheetah appeared to have swallowed a basketball; cheetahs would voluntarily leave a kill while there was still meat on it at size 14. Belly size scores were taken from non-consecutive days and then averaged for each of those 36 males for whom there were three or more sightings. Belly size estimates are employed routinely in carnivore studies (e.g. Bertram 1978; Frame & Frame 1981; Packer 1986) and showed high inter-observer reliability (Caro 1987).

Analysis

Log transformations were applied to dependent variables that were not found to be normal; if such variables could not be normalized in this way, non-parametric statistics were used. Measures were checked using ANOVAs to see whether coalition members were significantly more similar to each other than to other males. Males in coalitions were no more similar to each other than to other males on any physiological measure, so these variables were compared with residency status for individuals. On those few behavioural measures and belly size estimates where coalition members showed similarity, mean values for coalition members were calculated and used in the analysis.

ɔle I. Status and condition of non-resident (Non-Res) and resident (Res) adult male cheetahs

tus	DPV*	Mange†	Coat	Condition
ı-Res	—	—	Coarse?	Mouth and throat ulcerated; otherwise no data taken
ı-Res	1·0	2·0	Coarse	Hair loss on chest, back, right thigh (dermatitis). Upper canines broken with nerves exposed, one remaining incisor broken at gum level; gums inflamed; right side mouth infected; one tick; lymph nodes swollen
ı-Res	1·5	4·0	Coarse	Hair loss on chest (exchloriation or mange) with circular erythomatous red lesions. Encrustations on all paws, limbjoints, ears (also ulcerated). Mange around anus; exudate in groin. Ulcerative gingivitis with papules under tongue, gums inflamed on one side, three lower incisors missing; waxy discharge from ears; 37 ticks; lymph nodes swollen
-Res	2·0	0	Soft	Hair loss at elbow. Inflamed gums on one side. Old scar on right thigh; 16 ticks
-Res	2·0	0·5	Soft	Yellow sebaceous discharge in groin; lesion on left rump; 12 ticks
-Res‡	2·0	3·5	Coarse	Tongue tip missing; two upper and one lower incisor missing. Callouses on elbows; tear in left ear
-Res	2·0	0	Soft	Callouses on elbows; one tick
-Res	2·0	5·0	Soft	Osteomyelitis or abcess in swollen left front paw with excudate. Cranial nipples encrusted and enlarged; all legs encrusted on plantar aspects. Callouses on elbows, shoulder, carpus rump. Two upper incisors missing. Waxy discharge from ears, 43 ticks, lymph nodes swollen
Res	—	—	—	Hair loss on chest, elbows, shoulder and base of tail; extensive mange and ticks
Res	3·0	0	Soft	Waxy discharge from ears; 47 ticks including around eyes and penis
Res	2·0	1·0	—	10 ticks
Res‡	2·0	1·0	Coarse	Callouses on elbows; 15 ticks; scar on right flank
Res‡	1·0	2·0	Coarse	Callouses on elbows; four ticks; two wounds on foreleg
	—	—	—	No data taken
	3·0	1·0	Soft	Four ticks; small scar on knee; one popliteal lymph node slightly enlarged
	—	—	—	No data taken. (Vestigial pendulous dewclaws on hindlimbs.)
	—	—	—	No data taken
	3·0	0	Soft	Right ear missing. Scar measuring 5 × 3·5 cm on flank but flesh hardened, scar on jaw. Left ear waxy; eight ticks
	3·0	0	Soft	38 ticks
	3·0	0	Soft	Scars on two right paws; upper two incisors missing; slight waxy discharge from ears; 50 ticks
	3·0	0	Soft	Two upper and one lower incisor missing; 32 ticks

ɜ stated, pelage, eyes, mouth, teeth, ears and lymph nodes were examined; absence of mention below signifies no ɱality was detected.

ɜal processes of vertebrae: 1, vertebrae easily palpable; 2, palpable with pressure; 3, thick muscle, difficult to ɜte.

ge: average of independent score for each ear, 0 none; 5 entire pinna covered with sarcoptic infestation.

equently became a resident.

ntrol for possible effects of coalition member- single males and coalitions were entered ıtely into a two-way ANOVA comparing ɜsidents with residents, but for all the statisti- ɩts reported here except one, there were no ɔant effects of being in a coalition. Residents ɔn-residents were therefore compared with using pooled estimates of variance after for homogeneity of variance.

RESULTS

Physiological Differences

Non-resident males were in poor physical condition compared to resident males (Table I). They had significantly thinner vertebral musculature (median scores 2·0, 3·0, $N=11,5$, Mann–Whitney U-test, $U=2{\cdot}5$, $P<0{\cdot}01$); the mange on their ears was more extensive (median scores 1·0, 0, $N=11,5$, $U=11$, $P<0{\cdot}1$), and several had coarse coats, whereas all of the residents had soft coats, although this difference was not significant (Fisher exact probability test, $P>0{\cdot}1$). Table I shows that in contrast to residents, many non-residents had ulcerated mouths and gingivitis, sebaceous exudate on the chest and groin, extensive hair loss and mange, a waxy discharge from their ears, and swollen lymph nodes; one individual had severe dermatitis, another erythomatous lesions, and a third either osteomyelitis or an abscess in its foot.

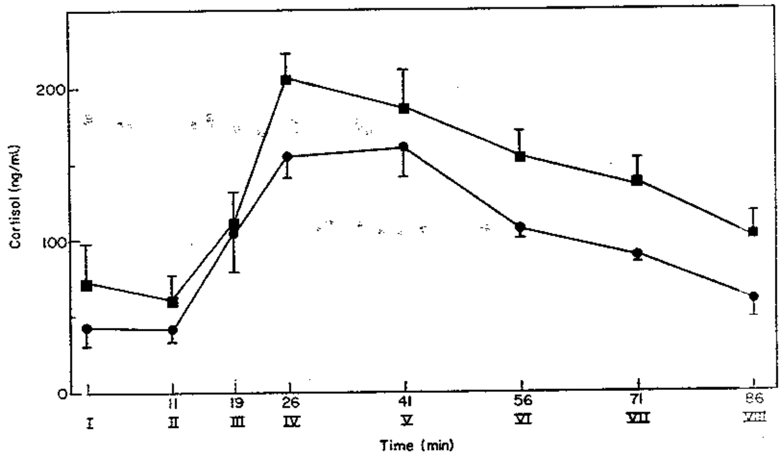

Figure 1. Mean and SE serum cortisol concentrations (ng/ml) for four non-resident (■) and four resident (●) male cheetahs. Figures along the X-axis denote the number of min following the first blood sample when subsequent samples were taken. Cheetahs were serially bled before (I), during (II, III, IV) and after (V, VI, VII, VIII) electro-ejaculation. I: $t=-1{\cdot}23$, $P>0{\cdot}2$; II: $t=-1{\cdot}41$, $P>0{\cdot}2$; III: $t=-0{\cdot}24$, $P>0{\cdot}8$; IV: $t=-2{\cdot}53$, $P=0{\cdot}045$; V: $t=-0{\cdot}88$, $P>0{\cdot}4$; VI: $t=-2{\cdot}63$, $P=0{\cdot}039$; VII: ($N=3$ non-residents) $t=-3{\cdot}16$, $P=0{\cdot}025$; VIII: ($N=3$ non-residents) $t=-2{\cdot}11$, $P=0{\cdot}089$; see Wildt et al. 1984, 1987 for details.

The differences found in external condition were reflected in non-residents males' higher white blood cell counts compared to residents ($\bar{X}\pm\text{SE}=14{\cdot}74\pm2{\cdot}17$, $N=8$; $\bar{X}\pm\text{SE}=9{\cdot}58\pm1{\cdot}43$, $N=5$; $t=1{\cdot}92$, $P=0{\cdot}080$; including three non-residents that subsequently became territorial: $\bar{X}\pm\text{SE}=13{\cdot}57\pm1.67$, $N=11$; $t=1{\cdot}74$, $P=0{\cdot}103$), possibly suggesting a higher level of chronic bacterial infection. Non-residents also had significantly raised eosinophil levels ($\bar{X}\pm\text{SE}=1{\cdot}13\pm0{\cdot}22$, $N=8$; $\bar{X}\pm\text{SE}=0{\cdot}33\pm0.11$, $N=5$; $t=3{\cdot}30$, $P=0{\cdot}007$; including three non-residents that subsequently became territorial: $\bar{X}\pm\text{SE}=1{\cdot}17\pm0{\cdot}20$, $N=11$; $t=3{\cdot}26$, $P=0{\cdot}006$). This is a diagnostic feature of a broad range of parasitic infections and allergic respiratory diseases (Schalm et al. 1985; Duncan & Praise 1986). Haemoglobin concentrations, red blood cell counts, packed cell volumes and mean cell volumes did not differ significantly between the two samples, regardless of whether non-residents that subsequently became territorial were included or not.

Differences in condition were mirrored by further physiological differences in the two types of male. Non-residents appeared more stressed than residents as reflected in their tendency towards elevated serum resting cortisol concentrations before and during a standardized electro-ejaculation procedure (Fig. 1). Non-residents had significantly higher acute adrenal responses following electro-ejaculation up to an hour after the last stimulus (see Fig. 1).

Behavioural Differences

By definition, non-residents ranged more extensively than residents (mean of median number of grid squares covered per day, 1·15 and 0·61, respectively, $N=18,12$, $t=2{\cdot}55$, $P<0{\cdot}02$, though

Table II. Mean (±SE) per cent of 5-min scans non-resident ($N=9$) and resident ($N=13$) male cheetahs spent in different body postures during the daytime rest period

Body posture	Non-resident males	Resident males	*t*-value	*P*
Lying flat out	20·0 (3·7)	29·8 (2·1)	−2·32	0·031
Lying out	45·9 (5·3)	46·3 (2·3)	−0·09	0·932
Lying alert	22·9 (3·1)	15·6 1·8)	2·15	0·044
Sitting up	10·4 (2·3)	5·2 (0·9)	1·99	0·060

usually at night); no differences were found in the per cent of the daytime spent moving ($\bar{X}=9·0$, 10·5%, $F_{1,20}=0·032$, $P>0·5$). However there were additional differences in the behaviour of the two sorts of male. Non-residents were often located in tall vegetation. They rarely rested on exposed rocky outcrops above ground level where they might be visible to resident cheetahs who would often attack them on sight (per cent of daytime rest period spent above ground level for non-residents and residents, respectively, $\bar{X}=4·8$ and 12·2%, Mann–Whitney *U*-test, $N=15,15$, $z=-2·08$, $P<0·04$). Moreoever, they appeared less relaxed han residents as reflected in their body posture. Table II shows that non-residents spent a significantly lower per cent of their daytime rest period lying flat out, and a significantly greater amount of ime lying alert and sitting up than did residents.

In contrast to these behavioural measures, residents and non-residents did not differ significantly n weight or in any of their linear measurements chest girth, head and body, tail, hindfoot and canine lengths), although residents were usually slightly larger. Non-residents had significantly smaller belly sizes than residents ($\bar{X}$ belly size 5·9 and 6·8, respectively, $N=17,19$, $t=-2·09$, $P=0·044$); however, female cheetahs with cubs had even smaller bellies ($\bar{X}\pm\text{SE}=5·2\pm0·2$, $N=33$) than non-resident males.

DISCUSSION

When cheetah males were given a careful physical examination, it was found that non-resident males were in poor condition compared to residents and that they suffered from a greater extent and variety of infections. Comparison of blood cell parameters revealed that non-residents had higher white blood cell counts and were more eosinophilic than residents. Respectively, these measures can reflect chronic bacterial infection and a wide spectrum of parasitic infections, and they provide further strong support for non-residents being in poor health compared to resident males.

Three factors can be probably dismissed as accounting for these differences in condition. First, there was no evidence of differential exposure to pathogenic organisms, as there were no geographically distinct sub-populations within the study area; indeed, non-residents passed through residents' territories (Durant et al. 1988). Second, it appeared improbable that differences in condition resulted from differences in adult nutrition. Although residents had larger belly sizes than non-residents, female cheetahs had smaller bellies still. If lack of food contributed to the poor condition of non-residents, females might also be expected to be in poor condition, yet females showed very few symptoms of ill health (Caro et al. 1987). Third, possible differences in juvenile nutrition were unlikely to have accounted for differences in condition. This is because linear dimensions, which are sensitive indicators of juvenile nutrition in many mammals (e.g. Schinkel & Short 1961; Suttie 1980), did not differ significantly between the two sorts of male. Nevertheless, the importance of nutrition in amplifying differences in health needs further work in this species.

Non-resident males showed elevated plasma cortisol levels compared to residents, particularly following electro-ejaculation. Cortisol concentrations closely reflect increasing levels of experimentally induced stress in both domestic animals (e.g. rats, *Rattus norvegicus*, Sakellaris & Vernikos-Danellis 1975; and sheep, *Ovis aries*, McNatty & Thurley 1973; Harlow et al. 1987a) and in wild species (e.g. bighorn sheep, *Ovis canadensis*, Harlow et al. 1987b; and rhesus monkeys, *Macaca mulatta*, Mason et al. 1957). It is also known that the pituitary–adrenal system is hypersensitive to additional stimuli in chronically stressed individuals (e.g. Sakellaris & Vernikos-Daniellis 1975). These comparative studies imply that non-resident cheetah males were physiologically stressed compared to residents. This was supported by data showing that non-resident males spent less time exposed above ground level and in relaxed postures and more time lying alert and sitting up than did residents. Female cheetahs whose cubs had been killed by lions spent an increased proportion of time lying alert after these attacks, and this posture appears to be a measure of unease in cheetahs (Caro 1987).

It is difficult to ascertain why non-resident males were more stressed than residents because few encounters have been seen between unfamiliar males of any status. Non-residents might not have held territories for three reasons. First, they may have attempted and failed to take over territories in the past; second, they might have assessed the probability of winning a fight with territorial animals and decided against trying; or third, they might be waiting for demographic conditions or factors such as personal body size to change and make the probability of winning a contest more likely. Whatever the case, their inability to be successful in intraspecific combat would probably make them afraid of being located by residents. Characteristically, we found non-residents were difficult to locate, and they made their extensive movements under the cover of darkness.

Laboratory studies have shown that both stress (Jensen & Rasmussen 1970) and chronically raised levels of blood cortisol (Hudson 1973) can compromise an individual's immune system and ability to combat disease, and socially induced stress has been associated with parasite burdens in free-living populations (Hausfater & Watson 1976). These, and many other studies (Martin 1987), suggest that the behavioural and physiological stress experienced by non-resident males could well have been responsible for their ill health. The extensive ranging and unease shown by non-residents in this study are more likely to be contributory factors to poor condition rather than its consequence because animals in poor health might be expected to prefer resting rather than move large distances. Certainly, such behaviour is likely to exacerbate the poor condition of non-resident animals. At present then, the data suggest that differences in physical condition associated with the two strategies result from behavioural differences in lifestyle.

There is little doubt that ill health of non-residents will reduce their chances of survival based on the severity of some of the infections, but our sample is still too small to be able to make this comparison at present. It is tempting to speculate that the genetic monomorphism of this species makes non-residents particularly susceptible to infection but this cannot be assessed until the health of individuals of different status is compared in other mammals.

ACKNOWLEDGMENTS

We thank the Government of Tanzania, Serengeti Wildlife Research Institute and Tanzania National Parks for permission to conduct the research; the Royal Society, National Geographic Society, Nuffield Foundation, Frankfurt Zoological Society and Science and Engineering Research Council, U.K. for funding; and David Wildt and the National Zoological Park, Washington D.C. for the cortisol data. Biological material was collected and transported in full compliance with federal fish and wildlife permits (CITES: endangered and threatened species) issued to the National Cancer Institute by the U.S. Fish and Wildlife Service of the Department of the Interior. We also thank Monique Borgerhoff Mulder, Marcus Borner, Mitch Bush, John Fanshawe, Nick Georgiadis, Mark Jago, Karen Laurenson, Steve O'Brien, Craig Packer, Karoline Schneider and David Wildt for help in the field; Centronic Sales Ltd and Christine Hawkey for loan of equipment; and Margaret Harding for laboratory assistance. Monique Borgerhoff Mulder, Nick Davies, David Wildt and two anonymous referees made helpful comments on the manuscript.

REFERENCES

Anderson, S. S. & Fedak, M. A. 1985. Grey seal males: energetic and behavioural links between size and sexual success. *Anim. Behav.*, 33, 829–838.

.rcese, P. & Smith, J. N. M. 1985. Phenotypic correlates and ecological consequences of dominance in song sparrows. *J. Anim. Ecol.*, **54**, 817–830.
ertram, B. 1978. *Pride of Lions.* London: J. M. Dent & Sons.
aro, T. M. 1987. Cheetah mothers' vigilance: looking out for prey or for predators? *Behav. Ecol. Sociobiol.*, **20**, 351–361.
aro, T. M. In press. Determinants of asociality in felids. In: *Comparative Socioecology of Mammals and Man* (Ed. by V. Standen & R. Foley), Oxford: Blackwell Scientific Publications.
aro, T. M. & Bateson, P. 1986. Organization and ontogeny of alternative tactics. *Anim. Behav.*, **34**, 1483–1499.
aro, T. M. & Collins, D. A. 1986. Male cheetahs of the Serengeti. *Nat. Geog. Res.*, **2**, 75–86.
aro, T. M. & Collins, D. A. 1987a. Male cheetah social organisation and territoriality. *Ethology*, **74**, 52–64.
aro, T. M. & Collins, D. A. 1987b. Ecological characteristics of territories of male cheetahs (*Acinonyx jubatus*). *J. Zool.*, **211**, 89–105.
aro, T. M., Holt, M. E., FitzGibbon, C. D., Bush, M., Hawkey, C. M. & Kock, R. A. 1987. Health of adult free-living cheetahs. *J. Zool.*, **212**, 573–584.
utton-Brock, T. H., Guinness, F. E. & Albon, S. D. 1982. *Red Deer, the Behavior and Ecology of Two Sexes.* Chicago: University of Chicago Press.
avies, N. B. 1982. Behaviour and competition for scarce resources. In: *Current Problems in Sociobiology* (Ed. by King's College Sociobiology Group, Cambridge), pp. 363–380. Cambridge: Cambridge University Press.
unbar, R. I. M. 1984. *Reproductive Decisions. An Economic Analysis of Gelada Baboon Social Strategies.* Princeton: Princeton University Press.
uncan, J. R. & Praise, K. W. 1986. *Veterinary Laboratory Medicine. Clinical Pathology.* 2nd edn. Ames: Iowa State University Press.
rant, S. M., Caro, T. M., Collins, D. A., Alawi, R.M. & FitzGibbon, C. D. 1988. Migration patterns of Thomson's gazelles and cheetahs on the Serengeti Plains. *Afr. J. Ecol.*, **26**, 257–268.
ame, G. W. 1984. Cheetah. In: *The Encyclopedia of Mammals. Vol. I* (Ed. by D. MacDonald), pp. 40–43. London: Allen & Unwin.
ame, G. & Frame, L. 1981. *Swift and Enduring: Cheetahs and Wild Dogs of the Serengeti.* New York: E. P. Dutton.
ttleman, J. L. & Harvey, P. H. 1982. Carnivore home-range size, metabolic needs and ecology. *Behav. Ecol. Sociobiol.*, **10**, 57–63.
rcourt, A. H. & Stewart, K. J. 1981. Gorilla male relationships: can differences during immaturity lead to contrasting reproductive tactics in adulthood? *Anim. Behav.*, **29**, 206–210.
low, H. J., Thorne, E. T., Williams, E. S., Belden, E. L., & Gern, W. A. 1987a. Adrenal responsiveness in domestic sheep (*Ovis aries*) to acute and chronic stressors as predicted by remote monitoring of cardiac frequency. *Can. J. Zool.*, **65**, 2021–2027.
low, H. J., Thorne, E. T., Williams, E. J., Belden, E. L. & Gern, W. A. 1987b. Cardiac frequency: a potential predictor of blood cortisol levels during acute and chronic stress exposure in Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*). *Can. J. Zool.*, **65**, 2028–2034.
Hausfater, G. & Watson, D. F. 1976. Social and reproductive correlates of parasite ova emissions by baboons. *Nature, Lond.*, **262**, 688–689.
Hogg, J. T. 1984. Mating in bighorn sheep: multiple creative male strategies. *Science N.Y.*, **225**, 526–529.
Hudson, R. J. 1973. Stress and in vitro lymphocyte stimulation by phytohemagglutinin in Rocky Mountain bighorn sheep. *Can. J. Zool.*, **51**, 479–482.
Hudson, P. J. 1986. The effect of a parasite nematode on the breeding production of red grouse. *J. Anim. Ecol.*, **55**, 85–92.
Jensen, M. M. & Rasmussen, A. F. 1970. Audiogenic stress and susceptibility to infection. In: *Physiological Effects of Noise* (Ed. by B. L. Welch & A. S. Welch), pp. 7–19, New York: Plenum Press.
Kenagy, G. J. 1987. Energy allocation for reproduction in the golden-manteled ground squirrel. In: *Reproductive Energetics in Mammals* (Ed. by A. Loudon & P. A. Racey), pp. 259–273, Oxford: Oxford University Press.
Kuenkel, R. 1978. Cheetahs—swift cats of the Serengeti. *Geo Magazine*, **1**, 94–110.
LeBoeuf, B. J. 1974. Male-male competition and reproductive success in elephant seals. *Am. Zool.*, **14**, 163–176.
Lee, A. K. & Cockburn, A. 1985. *Evolutionary Ecology of Marsupials.* Cambridge: Cambridge University Press.
McNatty, K. P. & Thurley, D. C. 1973. The episodic nature of changes in ovine plasma cortisol levels and their response to adrenaline during adaptation to a new environment. *J. Endocrinol.*, **59**, 171–180.
McVittie, R. 1979. Changes in the social behaviour of south west African cheetah. *Madoqua*, **11**, 171–184.
Martin, P. 1987. Psychology and the immune system. *New Scient.* **114 (1555)**, 46–50.
Mason, J. W., Harwood, C. T. & Rosenthal, N. R. 1957. Influence of some environmental factors on plasma and urinary 17-hydroxycorticosteroid levels in the rhesus monkey. *Am. J. Phys. Anth.*, **190**, 429–433.
Maynard Smith, J. 1982. *Evolution and the Theory of Games.* Cambridge: Cambridge University Press.
Moss, R. & Watson, A. 1985. Adaptive value of spacing behaviour in population cycles of red grouse and other animals. In: *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour* (Ed. by R. M. Sibly & R. H. Smith), pp. 275–294. Oxford: Blackwell Scientific Publications.
O'Brien, S. J., Wildt, D. E., Bush, M., Caro, T. M., FitzGibbon, C.D., Aggundey, I. & Leakey, R. 1987. East African cheetahs: evidence for two population bottlenecks? *Proc. natn. Acad. Sci.*, **84**, 508–511.
O'Brien, S. J., Wildt, D. E., Goldman, D., Merril, C. R. & Bush, M. 1983. The cheetah is depauperate in genetic variation. *Science N.Y.*, **221**, 459–462.
Packer, C. 1986. The ecology of sociality in felids. In: *Ecological Aspects of Social Evolution* (Ed. by D. I. Rubenstein & R. W. Wrangham), pp. 429–451. Princeton: Princeton University Press.
Sakellaris, P. C. & Vernikos-Danellis, J. 1975. Increased rate of response of the pituitary-adrenal system in rats adapted to chronic stress. *Endocrinology*, **97**, 597–602.

Sandell, M. 1986. Movement patterns of male stoats *Mustela erminea* during the mating season: differences in relation to social status. *Oikos*, **47**, 63–70.
Schaller, G. B. 1972. *The Serengeti Lion.* Chicago: University of Chicago Press.
Schalm, O. W., Jain, N. C. & Carroll, E. J. 1985. *Veterinary Hematology.* 4th edn. Philadelphia: Lea & Febiger.
Schinkel, P. G. & Short, B. F. 1961. The influence of nutritional level during pre-natal and early post-natal life on adult fleece and body characteristics. *Austral. J. agric. Res.*, **12**, 176–202.
Suttie, J. M. 1980. Influence of nutrition on growth and sexual maturation of captive red deer stags. In: *Proceedings of the Second International Reindeer/Caribou Symposium (Roros, Norway)* (Ed. by E. Reimers, E. Garre & S. Skjenneberg), pp. 341–349. Trondheim: Direktoratet for vilt og ferskvannsfisk.
Watson, A. 1985. Social class, socially-induced loss, recruitment and breeding of red grouse. *Oecologia (Berl.)*, **67**, 493–498.
Wildt, D. E., Meltzer, D., Chakraborty, P. K. & Bush, M. 1984. Adrenal–testicular–pituitary relationships in the cheetah subjected to anaesthesia/electroejaculation. *Biol. Reprod.*, **30**, 665–672.
Wildt, D. E., O'Brien, S. J., Howard, J. G., Caro, T. M., Roelke, M. E., Brown, J. L. & Bush, M. 1987. Similarity in ejaculate-endocrine characteristics in captive versus free-ranging cheetahs of two subspecies. *Biol. Reprod.*, **36**, 351–360.
Wirtz, P. 1982. Territory holders, satellite males, and bachelor males in a high density population of waterbuck (*Kobus ellipsiprymnus*) and their associations with conspecifics. *Z. Tierpsychol.*, **58**, 277–300.

(Received 18 August 1988; revised 3 October 1988; MS. number: A5372)