Available online at www.sciencedirect.com
SCIENCE DIRECT®
ACADEMIC PRESS
Hormones and Behavior
Hormones and Behavior 43 (2003) 474–479
www.elsevier.com/locate/yhbeh

Social status does not predict corticosteroid levels in postdispersal male spotted hyenas

Wolfgang Goymann,[a,b,*] Marion L. East,[a,c] Bettina Wachter,[a,c,d] Oliver P. Höner,[a,c,d] Erich Möstl,[e] and Heribert Hofer[a,c]

[a] *Max-Planck-Institute for Behavioural Physiology, D-82319 Seewiesen/Post Starnberg, Germany*
[b] *Max-Planck-Research-Centre for Ornithology, Von-der-Tann-Strasse 7, D-82346 Andechs, Germany*
[c] *Institute for Zoo and Wildlife Research, P.O. Box 60 11 03, D-10252 Berlin, Germany*
[d] *Ethologische Station Hasli, University of Bern, CH-3032 Hinterkappelen, Switzerland*
[e] *Institute of Biochemistry, Veterinarian University, Veterinärplatz 1, A-1210 Vienna, Austria*

Received 5 September 2002; revised 2 December 2002; accepted 3 December 2002

Abstract

In social species with low rates of direct male competition levels of corticosteroids should not correlate with social status. Male spotted hyenas acquire social status by observing strict queuing conventions over many years, and thus levels of male–male aggression are low, and male social status and tenure are closely correlated. In this study, we investigated whether the low rate of direct male competition in spotted hyenas was reflected in fecal corticosteroid levels of adult males in the Serengeti National Park. Also, interactions with dominant females may influence corticosteroid levels of males, and it has been suggested recently that males with a long tenure (high rank) are more stressed by females than males with a short tenure (low rank). We tested whether there is a difference in the likelihood of being aggressively challenged by dominant females between long-tenured and short-tenured males. Short-tenured males were more likely to elicit an aggressive response by females than long-tenured males, but previous work suggests that they also interacted less frequently with females, thus avoiding putting themselves in a potentially stressful situation. Thus, as expected, the comparison of males in three different clans revealed no correlation between social status or tenure and fecal corticosteroid levels. However, males of the largest clan had the highest levels of fecal corticosteroids, possibly reflecting higher rates of social interactions in larger clans.

Keywords: Spotted hyena; Corticosteroids; Cortisol; Social status; Stress; Tenure; Noninvasive monitoring; Mate choice

Introduction

In vertebrates, adverse stimuli (stressors) are known to activate the hypothalamic–pituitary–adrenocortical axis, which results in the release of corticosteroids. As a consequence, plasma corticosteroid levels are considered good indices of stress (reviewed, e.g., in Bonga, 1997; Wingfield and Ramenofsky, 1999; Sapolsky, 2002). Social conflict within group living species may result in social stress. For example, low-ranking male baboons (*Papio anubis*) are subject to the highest rates of physical and "psychological" aggression from higher ranking males (Sapolsky, 1993) and this may be why low-ranking males have higher plasma cortisol levels, the primary corticosteroid in most mammals, than high-ranking males (Sapolsky, 1982). In contrast, when the rate of social interactions among group members declines (as in the case of a severe drought, when all animals devote virtually all their time to foraging) plasma cortisol concentrations in subordinate baboons also significantly decline (Sapolsky, 1986). Acute social stress caused by fighting for social dominance among female spotted hyenas (*Crocuta crocuta*) also results in elevated levels of fecal corticosteroids (Goymann, East, Wachter, Höner, Möstl, Van't Hof, and Hofer, 2001).

* Corresponding author. Max-Planck-Research Centre for Ornithology, Von-der-Tann-Strasse 7, D-82346 Andechs, Germany. Fax: +49-8152-373-133.
E-mail address: goymann@erl.ornithol.mpg.de (W. Goymann).

0018-506X/03/$ – see front matter
doi:10.1016/S0018-506X(03)00032-1

In polygynous mammalian species there is typically strong competition among males for access to females, resulting in high rates and intense levels of conflict among competing males. The mating system of spotted hyenas has been described as polygynous (Frank, 1986a, 1986b). As immigrant males obey strict queuing conventions (sensu Kokko Lindström, Alatalo, and Rintamäki, 1998) to acquire social status within a stable, linear dominance hierarchy the frequency and intensity of interactions among males is low, and male social status is determined by the duration of tenure in the clan into which they disperse (East and Hofer, 2001). Thus, levels of social stress due to physical and psychological aggression among males in the male social queue might be minimal and as a consequence we predict that there is no association between low social status and elevated corticosteroid concentrations (see also Sapolsky, 2002).

On the other hand, high-ranking males consort with (shadow) reproductively valuable females more often than low-ranking males and exclude subordinate males from approaching their female consorts (East and Hofer, 2001). These male–female association patterns suggest that social stress due to competition for access to reproductively valuable females among high-ranking males may be high and that, as a result, high-ranking males may have higher levels of corticosteroids than low-ranking males. In the Masai Mara, Kenya, where spotted hyena clans are more territorial (Frank, 1986a) than in the Serengeti (Hofer and East, 1993a, and see below), plasma cortisol levels among immigrant male members of a clan were correlated with tenure (which was used as a measure of social status). Holekamp and Smale (1998) suggested that cortisol levels might have been higher in long-tenured males because they were more likely to be aggressively challenged by females, the dominant sex in spotted hyenas.

Corticosteroid levels may be influenced not only by social status, but also by access to food resources on the clan territory. In the Serengeti National Park, Tanzania, communal territories of spotted hyena clans experience large fluctuations in the abundance of migratory herbivores. When large migratory herds are present, all clan members forage inside the clan territory. However, when these herds migrate elsewhere (which is usually the case for three-quarters of the year), there is insufficient prey within the clan territory to feed all clan members. At such times, clan members travel to the nearest large concentration of migratory herbivores to feed (Hofer and East, 1993a, 1993b, 1993c). Goymann et al. (2001) have shown that female spotted hyenas in the Serengeti National Park that forage as socially subordinate intruders in other hyena territories have higher fecal corticosteroid concentrations than females in a more strictly territorial population in the adjacent Ngorongoro Crater. If foraging as an intruder in another clan territory, away from the predictable social environment of the clan, is stressful to males, then males in the Serengeti should have higher levels of fecal corticosteroids than males in the Ngorongoro Crater which mainly feed on resident prey within the borders of the clan territory.

In this contribution we examine (1) whether rank related levels of intraspecific conflict with social group members affected fecal corticosteroid levels of free-ranging postdispersal male spotted hyenas in the Serengeti, (2) whether males with a long tenure are more likely to be aggressively challenged by females than short-tenured males, and (3) whether there are population differences between males of the Serengeti and the Ngorongoro Crater.

Methods

Animals and study area

Spotted hyenas live in large, stable multifemale and multimale groups termed clans that are fission–fusion societies in which members are often solitary but also join to form small groups (Kruuk, 1972; Frank, 1986a; Hofer and East, 1993a). Each clan defends an exclusive group territory with a communal denning site, where females rear their offspring (Kruuk, 1972; East, Hofer, and Tuerk, 1989). Adult females are dominant over adult males and intra sexual hierarchies are maintained in both sexes (Kruuk, 1972; Frank, 1986b; East and Hofer, 1991; Hofer and East, 1993a). Females stay in their natal clan for life, whereas males usually disperse and join a new clan. Some males, however, gain breeding status within their natal clan and are termed "nondispersers" (East and Hofer, 2001). In the following, we refer to both immigrant males and nondispersers as "postdispersal males" or "males." Data from "predispersal males" that operate within the social system of their natal clan as offspring of their mother were not included. We studied three clans that held territories in the center of the Serengeti National Park in Tanzania, East Africa (Hofer and East, 1993a). The mean number of males for each of these clans was calculated as the mean number of postdispersal males during the period in which fecal samples were obtained. For a comparison of populations we also included fecal samples from five clans in the Ngorongoro Crater.

Hyenas were individually recognized by spot patterns (Hofer and East, 1993a). Social status of males was determined chiefly from submissive acts (retreat, avoidance of an approach, cower, tail between legs, ears back, head bobbing, head upside down) and occasionally from aggressive acts (direct approach, push, stand over, lung, chase, bite) in dyadic interactions recorded ad libitum (Altmann, 1974). The death or "disappearance" of males and rank reversals altered the dominance hierarchy. When such changes occurred a new rank for all male clan members was determined from dyadic interactions. The rank of an individual was thus known on the day it was sampled. Males were assigned a standardized rank for comparison of ranks across clans. Standardized ranks were calculated for all males after assigning the male with the highest social status the standardized rank 1 and the male with the lowest social status the standardized rank −1.

Tenure of Serengeti males was calculated as described by East and Hofer (2001). Briefly, tenure was the period between the date on which the male was first observed in the new clan and the date of the behavioral event. Following East and Hofer (2001) we then classified males with no more than 3 years of tenure as short-tenured males and males with more than 3 years of tenure as long-tenured males. A minimum (censored) period of tenure was calculated for immigrant males that were already established in a clan when the study commenced. Male–female interaction data were obtained from focal samples of males observed chiefly at the communal den or recorded ad libitum during encounters between males and females. To avoid pseudoreplication we included only one interaction by a specific male with a specific female in analyses of behavioral data. If more than one interaction between a particular male–female combination occurred, a single interaction was selected randomly. The response of a female toward a male was classified as aggressive, when the female either chased or bit the male, or when she threatened him without making direct contact (glaring, approach him with her tail raised, push, or lunge). The response of the female was classified as neutral when she either did not react to the male or responded affiliatively.

Collection of feces and measurement of fecal corticosteroids

Seventy-one fecal samples from the Serengeti were obtained and included in the analysis from 42 postdispersal males from the Isiaka ($N = 11$), the Mamba (20), and the Pool clans (11), collected during periods of social stability. To avoid pseudoreplication (Hurlbert, 1984) we calculated the mean fecal corticosteroid level and the mean social status of males that were sampled more than once and included the means in the analysis. For the comparison between populations we used a further 18 fecal samples from 13 males in the Ngorongoro Crater. Fecal corticosteroids reflect the cumulative secretion and elimination of biologically active corticosteroids over a number of hours or days (Whitten, Brockman and Stavisky, 1998). We measured fecal metabolites of cortisol with the "ICN-corticosterone" EIA described and validated for spotted hyenas previously (Goymann, Möstl, Van't Hof, East, and Hofer, 1999) and followed the fecal sampling, storage, and assay protocol described by Goymann et al. (2001).

Standard curves (range of standards: 2.9 to 1500 pg) and sample concentrations were calculated with Immunofit 3.0 (Beckman, Inc., Fullerton, CA), using a four-parameter logistic curve fit ($y = [a - d]/[1 + \{x/c\}^b] + d$). The lower detection limit of the standard curve was determined as the first point outside the 95% confidence intervals for the zero standard and was 120 pg/ml. Assay accuracy was 97.6 ± 4.5% (mean ± SEM, $N = 32$) and intraassay coefficients of variation were 7.7 ± 0.8% for a high concentration pool ($N = 24$) and 7.5 ± 1.0% for a low concentration pool ($N = 24$). Interassay coefficients of variation were 5.0% for the high pool and 8.1% for the low pool. All samples were assayed in duplicate and concentrations are expressed as nanograms per gram of fecal dry matter.

Statistical analysis

Statistical analyses were performed with SYSTAT 9.01 (SPSS Science, Inc., Chicago, IL), following Sokal and Rohlf (1995). The significance level was set to $\alpha = 0.05$ and P values are reported for two-tailed tests. Fecal corticosteroid data were log-transformed to meet normality criteria. After checking for homogeneity of slopes and homogeneity of variance we used an ANCOVA to analyze fecal samples from males of three different clans (Isiaka, Mamba, and Pool) in the Serengeti. We included clan as factor and social status as a covariate. Post hoc comparisons of clans were conducted with Fisher's LSD test. Social status is the most appropriate measure of male status in a clan and in contrast to tenure social status does not contain censored data. However, to compare our results with those of Holekamp and Smale (1998) we conducted the same kind of analysis replacing the covariate social status with tenure. Tenure and social status cannot be included in the same model as they are highly correlated with each other (East and Hofer, 2001). Since clan membership turned out to be an essential part of the model (see results), the samples from the 13 males in the Ngorongoro Crater could not be included due to low per-clan sample size in this population. We thus compared fecal corticosteroid levels of the populations in the Serengeti and the Ngorongoro Crater in a separate analysis using a Mann–Whitney U test. Behavioral interaction data of males and females in the Serengeti were analyzed with a G test.

Results

In the Serengeti, social status and clan explained 16.5% of the variance in fecal corticosteroid data of postdispersal males. Clan had a significant effect ($F_{2,38} = 3.728$, $P = 0.033$): Males of the large Mamba clan (23.1 ± 1.7 males, 27.4 ± 1.8 females) had significantly higher levels of fecal corticosteroids ($P = 0.014$; Fig. 1) than males of the smaller Pool clan (14.6 ± 2.5 males, 23.7 ± 3.3 females) and tended to have higher levels of fecal corticosteroids ($P = 0.078$; Fig. 1) than males of the smaller Isiaka clan (10.2 ± 2.5 males, 18.2 ± 2.7 females). Social status, however, did not have a significant effect on fecal corticosteroid levels ($P > 0.75$; Fig. 2A).

To further compare our data with those of Holekamp and Smale (1998) we repeated the same analysis, but replaced social status with tenure as a covariate. Again, clan membership had a significant effect ($F_{2,38} = 4.153$, $P = 0.023$)

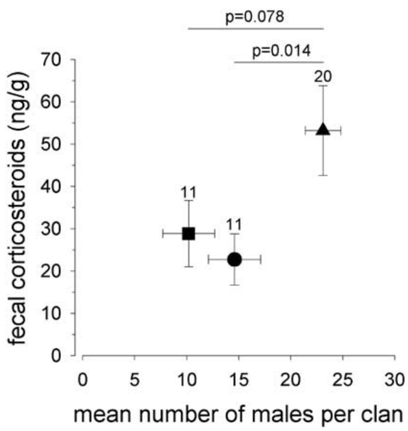

Fig. 1. Mean number of males per clan during the fecal sampling interval and backtransformed mean (±SEM) fecal corticosteroid levels of Isiaka (square), Mamba (triangle), and Pool (circle) clans in the Serengeti (numbers above symbols refer to number of males from which fecal samples were collected).

in that Mamba clan males had significantly higher levels than males of the Pool clan ($P = 0.009$) and tended to have higher levels than Isiaka males ($P = 0.080$). In contrast, tenure did not have a significant effect ($P > 0.25$; Fig. 2B).

Females responded to short-tenured males aggressively in 55% of all interactions (56 of 102), whereas they responded to long-tenured males aggressively only in 40% of all cases (78 of 194). Thus, females were significantly more likely to respond aggressively to short-tenured males than to long-tenured males ($G = 5.787$, $P < 0.017$).

Mean (±SEM) levels of fecal corticosteroids were 49.6 ± 6.5 ng/g in the Serengeti and 35.5 ± 8.1 ng/g in the Ngorongoro Crater. The difference was not significant ($P > 0.25$).

Discussion

In male spotted hyenas of the Serengeti, social status (or tenure) did not correlate with fecal corticosteroid levels. In contrast, clan membership explained a significant proportion of the variance: males residing in the Mamba clan had higher levels of fecal corticosteroids than males in the other two clans, regardless of social status or tenure. The Mamba clan contained roughly twice as many postdispersal males than the two smaller clans. Perhaps such a difference in clan size influences corticosteroid levels. With a larger number of individuals, social interactions may become more complicated and less transparent for the individual, a factor that may have been important in the evolution of neocortex size in primates and spotted hyenas (Dunbar, 1992; Dunbar and Bever, 1998). Also, social interaction rate at kills or around females might be higher in large compared to small clans. If so, the effect is likely to be male-specific, since clan membership or clan size did not have an effect on fecal corticosteroid levels in female spotted hyenas (see Goymann et al., 2001, and unpublished data).

Unlike free-ranging baboons (Sapolsky, 1982) low-ranking postdispersal male spotted hyenas from the Serengeti did not have higher fecal corticosteroid concentrations than high-ranking males. This is likely to be a result of the low frequency and intensity of agonistic interactions among male spotted hyenas (Frank, 1986b; East and Hofer, 1991, 2001; East, Hofer, and Wickler, 1993). In hyenas, females exert a high degree of mate choice; thus, males need to develop relationships with females through shadowing and affiliative behavior (East and Hofer, 2001; East et al., 1993). Thus, mating success may depend on affiliative relationships with females rather than direct competition between males, and males would not increase their mating success by fighting other males. Our results thus support the hypothesis that corticosteroid levels are not affected by social status in species with low frequencies and intensities of agonistic interactions between males (Sapolsky, 2002).

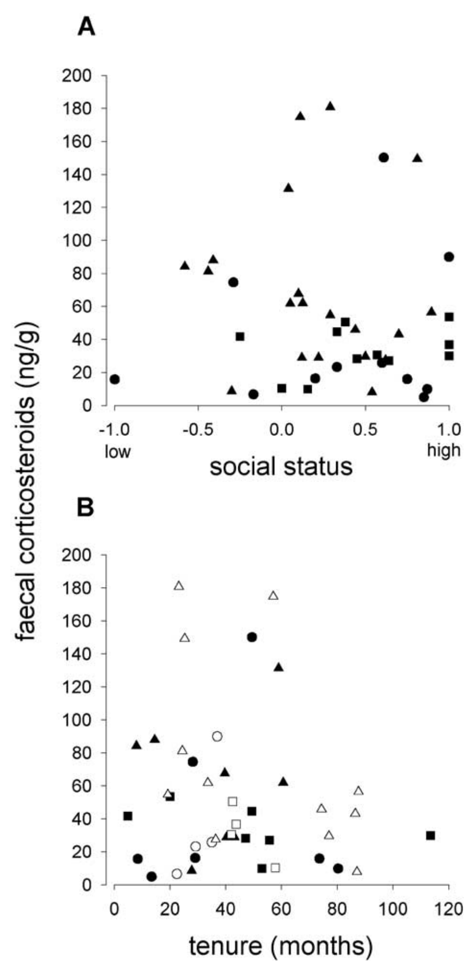

Fig. 2. (A) Fecal corticosteroid levels as a function of social status (rank 1 is the top rank) in Isiaka (squares), Mamba (triangles), and Pool clan (circles) males. (B) Fecal corticosteroid levels as a function of tenure. Open symbols represent censored data, i.e., the males were already established in the clan when the study commenced and tenure was calculated as the time period between the onset of the study and the collection of the sample. Closed symbols represent uncensored data, i.e., represent the exact tenure of the respective males.

Furthermore, the behavioral data from the Serengeti provide only limited support for the hypothesis that long-tenured males should be more stressed by interactions with females than short-tenured males (Holekamp and Smale, 1998). While previous work suggests that long-tenured males interact more frequently with females (East and Hofer, 1991), they were much less likely to provoke aggressive responses from females than short-tenured males. Why then, was there a significant effect of tenure (=social status) in Holekamp and Smale's (1998) study, in that long-tenured males had higher plasma cortisol levels than short-tenured males? In our view, the effect of tenure Holekamp and Smale found is mainly driven by low levels of plasma cortisol in males with a tenure of less than 1 year (Holekamp and Smale, 1998, their Fig. 4). In Holekamp and Smale's (1998) study, 52% of all males (14 of 27) were sampled during the first year of tenure, whereas in our study corticosteroid data were more evenly distributed over the range of all tenures and only 7% of all males (3 of 42) were sampled during their first year of tenure. Thus, Holekamp and Smale's (1998) and our results highlight different periods of male tenure and are thus not contradictory. In the Serengeti, males with a tenure of less than 1 year rarely interacted with females or other males at all (East and Hofer, 1991, 2001), probably because they have a low chance of being accepted by females and therefore they infrequently compete for females. If the same is true in the Masai Mara, males with a tenure of less than 1 year may have lower levels of plasma cortisol, because they rarely participate in the social life of the clan. In order to compare our results with the appropriate sample from Holekamp and Smale (1998), we selected from their published Fig. 4a all males with a tenure of more than 1 year and repeated their analysis. The resulting r_s was 0.284 ($N = 13$), which is not significant. Thus, both Holekamp and Smale's (1998) and our data suggest that there is no effect of tenure or social status, once males have been in a clan for more than 1 year. Hence, low or high plasma or fecal corticosteroid levels may be described by a threshold function that is determined by the onset of regular participation in social life of the clan rather than by a linear function of social status or tenure.

In contrast to our results in females (Goymann et al., 2001) there was no significant difference in fecal corticosteroid levels between males in the Serengeti and those in the Ngorongoro Crater. Fecal corticosteroid levels of males of both populations were similar to the levels of females in the Ngorongoro Crater or nonlactating females in the Serengeti (Goymann et al., 2001). Lactating females in the Serengeti had significantly higher levels than nonlactating females in the Serengeti or females in the Ngorongoro Crater (Goymann et al. 2001). In contrast to lactating females which frequently return to the communal den to nurse their cubs, males in the Serengeti commute less often and stay with the herds for much longer periods of time (Hofer and East, 1993c). As a consequence commuting may be less energetically demanding and less physiologically stressful for males than for lactating females, explaining the lack of a reflection in fecal corticosteroid levels of males.

In conclusion, despite a polygynous mating system male spotted hyenas do not fiercely compete for access to females and male mating success is likely to be greatly influenced by female mate choice (East et al., 1993, East and Hofer, 2001). These behavioral traits probably best explain why there is no relationship between social status and fecal corticosteroid levels in males of this species. Differences in the manner of how dominance status is acquired and maintained may be the key to understanding social status related differences in levels of corticosteroids (W. Goymann and J.C. Wingfield, submitted). Taking these factors into account will help to improve predictions about how social status should affect the production of corticosteroid hormones and resolve some of the confusing issues in this area of research.

Acknowledgments

We are grateful to the Tanzania Commission of Science and Technology for permission to conduct the study, the Director Generals of the Tanzanian Wildlife Research Institute and Tanzania National Parks for co-operation and support, the Fritz-Thyssen Stiftung, the Stifterverband der deutschen Wissenschaft, the Institute of Zoo and Wildlife Research Berlin, Wolfgang Wickler from the Max-Planck-Institut für Verhaltensphysiologie and Eberhard Gwinner from the Max-Planck Research Centre for Ornithology for funding, and R. Albert, A. Francis, W. Golla, R. Klein, B. Knauer, G. Orio, V. Runyoro, D. Thierer, L. Trout, A. Türk, and K. Wilhelm for their assistance.

References

Altmann, J., 1974. Observational study of behavior: sampling methods. Behavior 49, 227–267.

Bonga, S.E.W., 1997. The stress response in fish. Physiol. Rev. 77, 591–625.

Dunbar, R.I.M., 1992. Neocortex size as a constraint on group size in primates. J. Hum. Evol. 20, 469–493.

Dunbar, R.I.M., Bever, J., 1998. Neocortex size predicts group size in carnivores and some insectivores. Ethology 104, 695–708.

East, M.L., Hofer, H., 1991. Loud calling in a female-dominated mammalian society: II. Behavioral contexts and functions of whooping of spotted hyenas. Crocuta crocuta. Anim. Behav. 42, 651–669.

East, M.L., Hofer, H., 2001. Male spotted hyenas (*Crocuta crocuta*) queue for status in social groups dominated by females. Behav. Ecol. 12, 558–568.

East, M.L., Hofer, H., Tuerk, A., 1989. Functions of birth dens in spotted hyaenas (*Crocuta crocuta*). J. Zool. 219, 690–697.

East, M.L., Hofer, H., Wickler, W., 1993. The erect "penis" is a flag of submission in a female-dominated society: greetings in Serengeti spotted hyenas. Behav. Ecol. Sociobiol. 33, 355–370.

Frank, L.G., 1986a. Social organization of the spotted hyaena (*Crocuta crocuta*). I. Demography. Anim. Behav. 34, 1500–1509.

Frank, L.G., 1986b. Social organization of the spotted hyaena (*Crocuta crocuta*). II. Dominance and reproduction. Anim. Behav. 34, 1510–1527.

Goymann, W., East, M.L., Wachter, B., Höner, O.P., Möstl, E., Van't Hof, T.J., Hofer, H., 2001. Social, state-dependent and environmental modulation of faecal corticosteroid levels in free-ranging female spotted hyenas. Proc. R. Soc. B 268, 2453–2459.

Goymann, W., Möstl, E., Van't Hof, T., East, M.L., Hofer, H., 1999. Noninvasive fecal monitoring of glucocorticoids in spotted hyenas. Crocuta crocuta. Gen. Comp. Endocrinol. 114, 340–348.

Hofer, H., East, M.L., 1993a. The commuting system of Serengeti spotted hyaenas: how a predator copes with migratory prey. I. Social organization. Anim. Behav. 46, 547–557.

Hofer, H., East, M.L., 1993b. The commuting system of Serengeti spotted hyaenas: how a predator copes with migratory prey. II. Intrusion pressure and commuter's space use. Anim. Behav. 46, 559–574.

Hofer, H., East, M.L., 1993c. The commuting system of Serengeti spotted hyaenas: how a predator copes with migratory prey. III. Attendance and maternal care. Anim. Behav. 46, 575–589.

Holekamp, K.E., Smale, L., 1998. Dispersal status influences hormones and behavior in the male spotted hyena. Horm. Behav. 33, 205–216.

Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54, 187–211.

Kokko, H., Lindström, J., Alatalo, R.V., Rintamäki, P.T., 1998. Queuing for territory position in the lekking black grouse (*Tetrao tetrix*). Behav. Ecol. 9, 376–383.

Kruuk, H., 1972. The Spotted Hyena. A Study of Predation and Social Behavior. Univ. of Chicago Press, Chicago.

Sapolsky, R.M., 1982. The endocrine stress-response and social status in the wild baboon. Horm. Behav. 16, 279–292.

Sapolsky, R.M., 1986. Endocrine and behavioral correlates of drought in the wild baboon. Am. J. Primatol. 11, 217–228.

Sapolsky, R.M., 1993. Endocrinology alfresco: psychoendocrine studies of wild baboons. Rec. Progr. Horm. Res. 48, 437–468.

Sapolsky, R.M., 2002. Endocrinology of the stress response, in: Becker, J.B., Breedlove, S.M., Crews, D., McCarthy, M.M. (Eds.), Behavioral Endocrinology, 2nd ed., MIT Press, Cambridge, MA, pp. 409–450.

Sokal, R.R., Rohlf, F.J., 1995. Biometry. Freeman, New York.

Whitten, P.L., Brockman, D.K., Stavisky, R.C., 1998. Recent advances in noninvasive techniques to monitor hormone-behavior interactions. Yearbook Phys. Anthropol. 41, 1–23.

Wingfield, J.C., Ramenofsky, M., 1999. Hormones and the behavioral ecology of stress, in: Balm, P.H.M. (Ed.), Stress Physiology in Animals, Sheffield Academic, Sheffield, pp. 1–51.