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SEX-BIASED PARASITISM AND THE REPRODUCTIVE COSTS OF PARASITES IN A SOCIAL AFRICAN GROUND SQUIRREL

by

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ABSTRACT

Vertebrate males frequently carry higher numbers of parasites than females. This bias in parasite loads could be a consequence of sexual selection. Grouping species are also assumed to be afflicted with larger numbers of parasites than solitary animals and associated costs of this parasitism could vary with group size or structure. I examined sex-biased parasitism and the influence of group size on parasite loads in Cape ground squirrels (*Xerus inauris*), a highly social species that occurs in the arid regions of southern Africa. Males carried three times as many ectoparasites as females, but females harbored nearly three times more endoparasites than males. Amount of time spent (per hour) autogrooming was similar between males and females, but amount time spent allogrooming by adult female was over eleven times that of adult males. Longer allogrooming of group members could be decreasing the numbers of ectoparasites of group members and ultimately the group. Males infrequently give or receive allogrooming and travel in very large home ranges, potentially increasing their exposure to ectoparasites. However, movement throughout a large home range may result in males foraging in areas with lower densities of fecal pellets, which could explain the lower endoparasite loads observed in males. When I considered the age class of group members, female age classes were similarly parasitized but male age classes were not. Sub-adult males carried similar ectoparasite loads to adult males and similar endoparasite loads to adult females. This result is of particular interest because sub-adult males are becoming scrotal but typically remain in the group until adulthood. Sexual selection does appear to influence parasite loads in this species, and parasite removal or avoidance potentially mitigates individual parasite loads and their associated costs.

Parasites can be detrimental to the health, longevity, and reproduction of their hosts, but these costs are rarely quantified. I removed ectoparasites and endoparasites from Cape ground squirrels for three months and evaluated changes in female body mass, reproduction, burrow use, and grooming in response to parasite removal. Female body mass did not increase with parasite removal, but reproductive success (per capita offspring raised to emergence) increased nearly four-fold, while allogrooming by treated females decreased. Since breeding is highest in the late winter dry season when fewer resources are available, the impact of parasites may be highest during this season. Lactation and gestation are the most physiological stressful processes that females undergo, and the dramatic increase in reproductive success in treated females suggests that these females are able to allocate more resources to reproduction than females afflicted with parasites. These results suggest that studies investigating reproduction and fecundity must consider the vulnerability of the host to parasite infection and the potential impact on reproductive success.

To my wonderful and adoring family, for your support and help.

Without all of you I would never have completed this project!

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GENERAL INTRODUCTION

Parasites can have a myriad of physiological and behavioral effects on their hosts (Hoogland and Sherman 1976, Altizer et al. 2003, Hart, George-Nascimento et al. 2004, Poulin and George-Nascimento 2007). Parasites can cause blood loss, increased chance of infection, and increased time spent on grooming, which decreases time vigilant and foraging (Kollars et al. 1997, Neuhaus 2003, Johnson et al. 2004). These and other effects of parasitism can be detrimental to survival and reproduction. For example, daily survival may decrease as parasitism increases (Brown and Brown 2004), and female reproduction can be negatively impacted by parasites (Haim et al. 1987, Van Vuren 1996, Decker et al. 2001, Neuhaus 2003, Nilsson 2003, Brown and Brown 2004). Such effects can vary with degree of sociality, grouping, host size, sex, and age (Folstad and Karter 1992, Mooring et al. 1996, Rolff 2002, Altizer et al. 2003, Ferrari et al. 2004, Mooring et al. 2004, Perez-Orella and Schulte-Hostedde 2005, Isomursu et al. 2006, Fauchald et al. 2007).

Sex and age, in particular, are very important influences on parasite infestation in vertebrates (Sheldon and Verhulst 1996, Zuk and Johnsen 1998, Verhulst et al. 1999, Bilbo and Nelson 2001, Rolff 2002, Brei and Fish 2003, Hoby et al. 2006, Isomursu et al. 2006). Males are typically parasitized at a higher rate than females, and differences among sex and age classes have been ascribed to hormonal or behavioral influences based on sexual selection (Schalk and Forbes 1997, Deviche et al. 2001, Isomursu et al. 2006, Fauchald et al. 2007). Androgens, specifically testosterone (a male sex hormone), generally inhibit immune function and influence ornamentation and behavior (Folstad and Karter 1992, Verhulst et al. 1999, Bilbo and Nelson 2001, Hughes and Randolph 2001a, Kakuma et al. 2003, Deviche and Parris 2006, Hoby et al.

2006). Because of the links between hormones and behavior, interpreting patterns of parasite infestation may not be difficult.

In this thesis I investigated patterns of parasite infestation related to sexual selection and group size in a social African ground squirrel (Chapter 1). I also examined the impact of parasites on reproduction, body mass, and behavior by removing ectoparasites and endoparasties from adult females (Chapter 2). The results from this study highlight the strong influence that parasites can have on reproductive success and social interactions in free-ranging mammals.

CHAPTER 1: PARASITE LOAD, SEX BIAS, SOCIALITY AND ANTI-PARASITE BEHAVIOR

Introduction

Different reproductive strategies of males and females have led to the evolution of many differences in their physiology, morphology, and behavior (Mooring et al. 1996, Rolff 2002, Tella 2002, Mooring et al. 2006a, Stoehr and Kokko 2006). In many species, sexual selection has produced males with larger body size (to compete for females), larger home ranges (to find females), or large ornaments (to attract females; Dobson 1992, Deviche and Cortez, 2005, Perez-Orella and Schulte-Hostedde, 2005, Deviche and Parris, 2006, Hoby et al. 2006, Nunn and Dokey 2006, Poulin and Lefebvre 2006). However, this heavy investment by males to compete for females may carry a cost of increased vulnerability to predators or parasites (Folstad and Karter 1992, Moller et al. 1999, Moore and Wilson 2002, Rolff 2002, Ottova et al. 2005, Kilpimaa et al. 2007).

In vertebrates, males frequently carry higher parasite loads than females (Schalk and Forbes 1997, Deviche et al. 2001, Freeman-Gallant et al. 2001, Moore and Wilson 2002, Ferrari et al. 2004, Perez-Orella and Schulte-Hostedde 2005, Deviche and Parris 2006, Isomursu et al. 2006). Ecological and morphological mechanisms for this sex difference in parasite load include differences in movement patterns, habitat choice, diet, body size, and ornamentation (Verhulst et al. 1999, Sheridan et al. 2000, Rolff 2001, Ferrari et al. 2004, Hoby et al. 2006, Stoehr and Kokko 2006). Differences in male home range or territory size can affect parasite load and transmission. Males with larger home ranges carry more parasites than female conspecifics because they encounter more parasite-dense areas (Greenwood 1980, Ims 1987, Nunn and Dokey

2006). However, sex-biased parasite loads could be an artifact of sexual size dimorphism because body size is often associated with degree of parasitism. Larger males may be able to tolerate higher parasites loads (Schalk and Forbes 1997, Moore and Wilson 2002), as the energetic pressure (measured by basal metabolic rate) exerted by parasites on smaller hosts appears greater, per gram of body mass (George-Nascimento et al. 2004). Yet even when accounting for differences in body size and home range, sex-biased parasite loads are often higher in species with strong sexual selection (Moore and Wilson 2002).

Sex-biased parasitism may be due to a trade-off between investment in sexually selected traits and immune function (Folstad and Karter 1992, Sheldon and Verhulst 1996, Hosken and O'Shea 2001). The immunocompetence handicap hypothesis suggests that male sexual traits may lower the ability to resist pathogens and parasites through steroid suppression of the immune system (Folstad and Karter 1992). Testosterone directly suppresses immune function and indirectly influences many physical and behavioral attributes, resulting in higher male parasite loads (Sheldon and Verhulst 1996, Schalk and Forbes 1997, Deviche et al. 2001, Moore and Wilson 2002, Deviche and Parris 2006, Hoby et al. 2006, Isomursu et al. 2006). However, testosterone and parasite loads are not correlated in all species (Bilbo and Nelson 2001, Hughes and Randolph 2001). An alternative explanation for this trade-off is that the energetic costs of maintaining many sexually selected traits conflict directly with the cost of fighting off infection (Sheldon and Verhulst 1996, Hosken and O'Shea 2001) or that, males just invest less in immunity than females (Rolff 2002).

Parasites also could be a major cost of sociality (Hoogland and Sherman 1976, VanVuren 1996, Loehle 1997, Tella 2002, Altizer et al. 2003, Brown and Brown 2004 Johnson et al. 2004, Hoby et al. 2006). As group size increases, there are more individuals carrying parasites into the group in close quarters, augmenting parasite transmission (Hoogland and Sherman 1976, Hoogland 1995). However, no relationship between grouping and parasites is expected if social mammals mitigate the increased costs of parasitism with grouping through direct behavioral strategies such as autogrooming (self grooming) and allogrooming (grooming another individual; Mooring and Hart, 1992, Hart 1994, Kollars et al. 1997, Johnson et al. 2004, Hawlena et al. 2006).

Intense sexual selection in Cape ground squirrels (*Xerus inauris*) is evident from several aspects of their mating system and morphology, including 1) a short and intense period of female receptivity (Waterman 1996), 2) a high operational sex ratio on day of mating (Waterman 1998), and 3) extremely large testes, suggesting sperm competition is an important determinant of male reproductive success (Waterman 1998, 2007). Cape ground squirrels are also highly social. Females allogroom more than males and therefore may influence group ectoparasite loads (Waterman 1995). In this study I determined if degree of parasitism is related to sex, dispersal, group size, and/or behavior. I hypothesized that variation in parasitism of Cape ground squirrel populations is influenced by: 1) group size; because increase in parasite transmission is expected in larger groups, 2) male dispersal; because larger home range size can expose males to larger numbers of ectoparasites and decrease time foraging in fecal contaminated areas 3) group composition (i.e. number of males, females, adults, sub-adults, and juveniles); because of sex and age differences in home range size, behavior, and sex hormones can influence parasites, and 4) time spent autogrooming or allogrooming. I predicted that 1) ecto- and endoparasite loads would increase with group size; 2) dispersed males would have greater numbers of ectoparasites than non-dispersed males, but would have similar endoparasitism 3) groups with more females will have fewer ectoparasites; adult males would carry more ectoparasites than females but fewer endoparasites; 4) an increase in ectoparasitism will increase autogrooming and allogrooming.

Methods

Biology of the study animal

Cape ground squirrels live in the arid regions of southern Africa (Waterman 1995) and have high potential for parasite transmission due to their sociality and communal living. Females live in matrilineal groups with other related adult females and their sub-adult young. These groups usually contain one to three adult females and up to nine sub-adults of either sex (Waterman 1995). Within a female group, animals share a communal sleeping burrow (part of one burrow system), which may allow external parasites to transfer to another individual through bedding and direct contact (Hoogland 1995, Altizer et al. 2003). Adult females allogroom more than adult males (Waterman 1995).

Adult males are slightly larger than females (1.08:1.0; Waterman 1996) and usually disperse by 16 months of age to join all-male bands that travel and sleep together independent of female groups (Waterman 1997). Home ranges of these males are 3 times the size of female home ranges (Waterman 1995). However, some males delay dispersal and remain with their natal group for 2-4 years (resident males; Waterman 1995) even though they are reproductively active. Breeding occurs year-round and adult males spend much of their time searching for receptive females (Waterman 1997, 1998); thus adult males are fully scrotal year-round.

Documented parasites of Cape ground squirrels include *Ctenocephallaes connatus*, *Echidniphaga bradyta*, *Echidniphaga gallinacea*, *Neohaematopinus faurei*, and *Synosternus* *caffer* (Straschil 1975), *Rhipicephalus theileri* (Waterman 2002), and *Xeroxyuris parallela*, which is exclusive to this species of ground squirrel (Hugot 1995).

Trapping and handling

The study was conducted at the S.A. Lombard Nature Reserve near Bloemhof, South Africa (27°35’S, 25°23’E) from May - September 2004. This period coincides with the dry season, peak breeding, and time of lowest available food resources (Herzig-Straschil 1978, Waterman 2002). Social groups were located on a natural floodplain, where the habitat is uniform short grass (Van Zyl 1965). I trapped all squirrels in eighteen social groups with Tomahawk live traps (15x15x50cm) using trapping and handling techniques described in Waterman (1996, 2002). I recorded body mass, reproductive condition, and sex. For identification from a distance, animals were dye-marked (Rodol D, New York) and freeze-marked (Quik-freeze®, Miller-Stephenson Product, Morton Grove, Illinois, Rood and Nellis 1980). Animals were also tagged with small transponders under the skin for permanent identification (AVID Inc., Folsom, Louisiana). Squirrels were classified as juveniles up to 6 months after first emergence from the natal burrow. If first emergence was not observed, age was estimated from a regression of age against body mass (Waterman 1996). Squirrels were classified as sub-adults from 6 months of age until reaching sexual maturity (around 8 months for males and 9 months for females; Waterman 1996, Pettitt 2006). At maturity (first estrus) female nipples swell and remain permanently elongated (Waterman 1996). Male maturity is evident from descent of the testes; adult males are scrotal year-round, while sub-adult males are partially or non-scrotal (Waterman 1996, 2002). Scrotal development most likely is facilitated by large increases in androgens (Deviche et al. 2001, Deviche and Cortez 2005, Hoby et al. 2006).

Ectoparasites were collected from each captured squirrel by combing all individuals with a metal flea comb using three strokes on each plane of the back (left, middle, and right), from the shoulders to the base of the tail. Ectoparasites (fleas, ticks, and lice) were collected in 95% ethanol in a petri dish and counted immediately. Endoparasite loads were estimated from fecal samples. Feces were collected using plastic tarp sections placed under live traps (Pettitt et al. 2007). Feces were collected with forceps dipped in 95% ethanol and sealed in labeled plastic bags. Subsequently, 0.5g of fecal matter was weighed out and frozen. These frozen samples were later thawed and prepared by fecal floatation in magnesium sulfate solution (McCurin and Bassert 2002), which caused eggs released by adult endoparasites to float. Prepared samples were then observed under a compound microscope for endoparasite egg identification and count. Some squirrels did not defecate in the traps, decreasing the sample size for endoparasite data, relative to ectoparasite data.

Behavioral observations

Cape ground squirrels are diurnal and live in open habitats (Smithers 1971, Herzig-Straschil 1978). The low vegetative cover on the floodplain allowed for relatively easy observation from hides on the roof of vehicles or observation towers. Observations focused on morning and evening hours (700 - 1000hrs and 1500 – 1800hrs) when the squirrels are nearest the burrows (Waterman 1995). I arrived before squirrels emerged from burrows for morning observations, and evening observations continued until all squirrels immerged for the night. Behavioral data were collected using all-occurrences methods (Altmann 1974) to record autogrooming and allogrooming (Waterman 1995), including the occurrence and duration (seconds) of the behavior and the identity of any squirrel being allogroomed (Waterman 1995).

The amount of time (sec) spent allogrooming (or autogrooming) was divided by the total amount of time that animal was observed (hrs). This produced the proportion of time (sec/hr) that an individual spent allogrooming (or autogrooming). To examine differences among group members whom received allogrooming, for each squirrel I calculated the allogrooming proportion for each age class receiving allogrooming and divided by the number of squirrels of that age class within that social group; i.e., # of allogrooms of squirrels in age class *a* / total observation time (hrs) / # of squirrels in age class a in the group (where *a* = adult male, adult female, sub-adult male, or sub-adult female).

Analysis

I used trapping data from June to analyze body mass, parasite loads and reproductive condition. Behavioral data were collected from June to September. All data were checked for homogeneity and normality, and transformed if necessary. Data that could not be normalized or homogenized were analyzed with non-parametric statistics (Fry 1993). I used social group identity as a main factor in my analyses (e.g., 2-way ANOVA) to account for potential differences among groups and influence of males on ectoparasite loads. Total group size was considered in data analysis as well as the number of adult females in the group. Due to high adult female allogrooming rates that could influence the results (e.g., number of ectoparasites and group size, allogrooming rate and group size correlations), I compared proportion of time spent autogrooming and allogrooming for all individuals with a minimum total observation time of 60 minutes. One group that disbanded in June was excluded from behavioral analyses. Friedman's χ^2 test requires balanced data; thus, only squirrels that both allogroomed and had at least 1 group member in every sex/age class were included in the comparison of allogrooming by sex and age.

To test my predictions 1) I tested correlations between group size and ecto- and endoparasites; 2) dispersal and ecto- and endoparasitism was tested using a *T'*-test and Mann-Whitney *U*; 3) the relationship of ectoparasitism and endoparasitism with sex and age was analyzed using body mass a covariate and colony location as a main factor in an ANCOVA; 4) allogrooming and autogrooming were analyzed using a 2-way ANOVA, Mann-Whitney U-test, and Friedman's χ^2. A 0.05 probability of a Type I error was considered significant (SPSS 11.0, The Software MacKiev Company).

Results

Body mass of adult males (mean ± SE; 703 ± 8 g) and females (638 ± 7 g) differed (ANOVA $F_{1,96} = 35.79$, $P < 0.001$), although the male-female body mass ratio was low (1.1:1). Groups consisted of at least one adult female (range 1 – 6) and their sub-adult and juvenile offspring. Many groups had 1-2 adult males (resident males) sleeping in the burrow cluster with the group but these males rarely remained at the cluster during morning observations. Adult males, resident and dispersed, carried endoparasites including roundworms (15.0%), hookworms (25.0%), coccidian (20.0%), and other types (40.0%).

Parasite loads

Group size did not affect numbers of ectoparasites (Spearman's correlation $R = 0.14$, $P = 0.35$, $N = 49$) or endoparasites ($R = 0.18$, $P = 0.28$, $N = 37$; Fig. I). Number of adult females or resident males in the group showed no effect on parasite loads (ectoparasites, females: $R = -0.09$, $P = 0.53$, $N = 49$, resident males: $R = 0.19$, $P = 0.19$, $N = 49$; endoparasites, females: $R = 0.14$, $P = 0.40$, $N = 37$, resident males: $R = -0.01$, $P = 0.96$, $N = 37$).

Resident (N= 23) and dispersed (N= 20) adult males did not differ in total ectoparasite loads (T-test t'= 1.38, df = 32.48, P = 0.18) or specific ectoparasites (fleas U = 191.0, P = 0.33; ticks U = 204.5, P = 0.46; lice U = 213.5, P = 0.68). Resident and dispersed males also had similar endoparasite loads (mean ± SE; resident 1.3 ± 0.5 eggs, dispersed 1.2 ± .4 eggs; Mann-Whitney U = 72.00, P = 0.36, N = 28). Thus, data from all adult males were pooled for subsequent analyses.

Body mass had no effect on ectoparasite loads in either adult males or adult females (males; R^2 = 0.002, $F_{1,43}$ = 0.086, P = 0.77; females; R^2 = 0.010, $F_{1,51}$ = 0.473, P = 0.50; Fig. I A&B). Also, ectoparasite numbers (square root transformed) were not influenced by body mass (as a covariate) when controlling for social group and sex (N = 128; body mass ANCOVA $F_{1,67}$ = 0.01, P = 0.96). Adult males were more parasitized by fleas, ticks and lice than adult females (fleas Mann-Whitney U = 600.0, P < 0.001; ticks, U = 941.0, P = 0.039 lice, U = 724.5, P = 0.001; Table I). Overall, total numbers of ectoparasites (square root transformed) were also significantly higher on males than females (Fig. IIA) for adults (2-way ANOVA $F_{1,62}$ = 23.22, P < 0.001, N = 96) and sub-adults ($F_{1,8}$ = 5.79, P = 0.043, N = 26), but not in juveniles (2-way ANOVA juveniles $F_{1,1}$ = 2.05, P = 0.39, N = 11).

Adult females (N= 41) had greater total endoparasite loads than adult males (N = 30) (Mann-Whitney U = 406.50, P = 0.012; Fig. IIB). Although, specific endoparasites including roundworms, hookworms, coccidia, and other endoparasites were not different between adult males and adult females (roundworms U = 2.00, P = 0.35, N = 18; hookworms U = 2.00, P = 0.35; coccidia U = 2.50, P = 0.43; other U = 4.50, P = 1.00; Table I). No sex difference was found in sub-adult or juvenile endoparasite loads (sub-adults, U = 26.50, P = 0.74, N = 19; juveniles, U = 3.00, P = 1.00, N = 5).

Age class did not affect number of specific ectoparasites (i.e., fleas, ticks, or lice) on males ($N = 57$; df = 2) or females (N =76; df = 2 Table I). Likewise, total ectoparasite loads did not differ among age class for females ($F_{2,73} = 0.41$, $P = 0.66$) but total male ectoparasite loads tended to differ among age classes ($F_{2,54} = 2.90$, $P = 0.064$), with adult males carrying more ectoparasites than juvenile males (Tukey's HSD = 1.37, $P = 0.050$). Total endoparasite loads did not differ among age classes for either males ($\chi^2 = 0.97$, df = 2, $P = 0.62$, N =36) or females ($\chi^2 = 0.79$, df = 2, $P = 0.67$, $N = 59$; Fig. IIB).

Behavioral observations

Autogrooming (sec/hr; square root transformed) did not differ among age class ($F_{2,58} = 2.12$, $P = 0.14$, $N = 64$) or sex ($F_{1,58} = 0.39$, $P = 0.54$, Fig. IV). Dispersal did not affect autogrooming ($F_{1,20} = 0.946$, $P = 0.34$).

Resident and dispersed males did not differ in time spent allogrooming (Mann-Whitney $U = 33.0$, $P = 0.14$, $N = 23$). However, adult females allogroomed significantly more than adult males ($U = 163.0$, $P = 0.008$, $N = 51$, Fig. IV) and these adult allogrooming data were positively correlated to female group size (Spearman's rho, $R = 0.41$, $P = 0.014$, $N = 35$) but showed no relationship to overall group size ($R = -0.10$, $P = 0.55$). Sub-adult males were preferentially allogroomed, by females ($U = 62.00$, $P = 0.039$, $N = 33$), at a higher rate (frequency per hour) than any other sex/age class (Friedman's $\chi^2 = 8.36$, df = 3, $P = 0.039$, $N = 14$).

Discussion

Ectoparasite loads were highest in males (adults and sub-adults), but endoparasite loads were greatest in adult females. These differing patterns of sex-biased parasitism suggest that different mechanisms may be operating, depending on the life-history characteristics of the parasites. For ectoparasites, the extensive daily movements of males through grass and brush and interactions with multiple female groups may expose them to greater numbers of ectoparasites. However, home range differences cannot explain the high ectoparasite loads of sub-adult males, whose home range size is the same as their female group members (Waterman, 1995). The sex-biased ectoparasite load in the sub-adult age class persists even though sub-adult males are preferentially allogroomed by the adult females in the group. Thus, there appears to be a physiological basis to sex-biased parasitism in this species.

Male and female differences in androgens (typically testosterone) can indirectly affect behavior or directly inhibit immune function, thereby influencing parasite loads (Moller et al. 1999, Bilbo and Nelson 2001, Rolff 2002, Khokhlova et al. 2004, Hawlena et al. 2006, Hoby et al. 2006). Males generally have higher concentrations of testosterone and under the immunocompetence handicap hypothesis should then be more susceptible to parasitic infections than females (Folstad and Karter 1992, Bilbo and Nelson 2001, Deviche et al. 2001, Hughes and Randolph 2001, Rolff 2002). Age-related and seasonal changes in testosterone have been related to parasitic infections in a variety of taxa (Schalk and Forbes 1997, Deviche et al. 2001, Isomursu et al. 2006). For example, experimentally increasing testosterone levels increased parasite prevalence in dark-eyed Juncos (*Juncos hyemalis*; Deviche et al. 2001). In a free-ranging ungulate, androgen and cortisol output levels were correlated to high lungworm larvae estimates (*Rupicapra rupicapra rupicapra*; Hoby et al. 2006). Folstad and Karter (1992) empirically determined that testosterone can decrease immunocompetence but an increase in immune function can also inhibit expression of secondary sexual characteristics (male ornamentation). This androgen/immune function feedback loop was also observed in meta-analysis by

Muehlenbein and Bribiescas (2005). In Cape ground squirrels, reproduction is not seasonal, and males' continued investment in reproduction could come with a cost of higher parasite loads year-round. This investment begins when males mature during the sub-adult age class (the transition age from non-scrotal to fully scrotal) and testosterone increases (Bilbo and Nelson 2001, Hughes and Randolph 2001, Hoby et al. 2006, Isomursu et al. 2006).

Endoparasite loads were also sex-biased, but in the opposite direction predicted by the immunocompetence handicap hypothesis. Females had more endoparasites than males, but this difference was significant only in adults (Fig. 1B). This sex bias may be due to the life cycles of intestinal parasites, where inoculation occurs generally through ingestion of contaminated food or debris (oral-fecal contracted; Gemmell 1990, Ferrari et al. 2004). Cape ground squirrel females have smaller home ranges than males (Waterman 1995) and are therefore more frequently exposed to conspecific fecal pellets found in foraging areas around their burrow clusters. Adult males, however, move over large areas and sleep in vacant burrow clusters (Waterman 1995), avoiding lengthy exposure to areas with high concentrations of endoparasites. In this species male avoidance of endoparasites and thus lower endoparasite loads, may be a positive consequence of sexual selection.

I expected male dispersal to affect parasite load because dispersed males with their larger home ranges (Manjerovic unpubl. data) would be exposed more frequently to ectoparasites (Nunn and Dokey 2006). However, neither ecto- nor endoparasite loads were affected by male dispersal. Since dispersed and resident males have similar circulating testosterone concentration (Scantlebury et al. *submitted*), but different ranging patterns, these data also support a hormonal basis for sex biases in parasite loads in Cape ground squirrels.

In mammals, promiscuous mating systems, social contact, and coloniality increase exposure to parasites, with transmission of ectoparasites through social contact and endoparasites primarily through feces (Hoogland and Sherman 1976, Gemmell 1990, Arnold and Lichtenstein 1993, Loehle 1995, Tella 2002, Altizer et al. 2003, Ferrari et al. 2004, Johnson et al. 2004). However, group size and parasite (both ecto- and endoparasites) were not correlated (Fig. III). While exposure to ectoparasites may increase in larger groups, social groups may reduce ectoparasite load by auto- and allogrooming to combat higher transmission rates (Mooring and Hart 1997, Mooring et al. 2006a, Mooring et al. 2006b). Although autogrooming was not related to group size in Cape ground squirrels, females allogroomed longer than males (Fig. III). Adult allogrooming rates also increased with the number of females in the group, suggesting that female allogrooming is a means to reduce group ectoparasite loads (Hoogland and Sherman 1976, Rolff 2002, Neuhaus 2003, Brown and Brown 2004).

My results indicate that the life history of parasites strongly affect the likelihood of infection. Investigating either ectoparasite or endoparasite infections alone would have led to very different conclusions about sex-biased parasitism in this species, as only patterns of ectoparasite infection were consistent with the immunocompetence handicap hypothesis. In male Cape ground squirrels, parasite resistance may be suppressed directly by androgens affecting leucocyte production or merely may be a trade-off between investments in reproduction versus immune function. In females, parasitism may suppress metabolism (Scantlebury et al. 2007). To determine the evolutionary costs of parasitism in this species I need to determine both if physiological effects exist and the potential impact on reproductive success.

Tables and Figures

Table I: Parasite loads (mean ± SE) of Cape ground squirrels by sex and age (sample size in parentheses, italicized letters were compared as follows for ectoparasites and endoparasites: Males (*a*) Kruskal-Wallis χ^2 =3.83, *P* = 0.15, (*b*) χ^2 =4.59, *P* = 0.101, (*c*) χ^2 = 1.62, *P* = 0.45, Females (*A*) χ^2 = 0.05, *P*= 0.98, (*B*) χ^2 = 5.42, *P* = 0.067, (*C*) χ^2 = 0.06, *P* = 0.97; Endoparasites (*d*) Mann-Whitney *U* = 2.00, *P* = 0.35, (*e*) *U* = 2.00, *P* = 0.35, (*f*) *U* = 2.50, *P* = 0.43, (*g*) *U* = 4.50, *P* = 1.00).

Age class		Males				Statistics	Females				Statistics
Adult	Fleas	3.0	±	0.6	(44)	*a*	0.9	±	0.2	(52)	*A*
	Lice	2.5	±	0.5		*b*	1.0	±	0.3		*B*
	Ticks	1.5	±	0.5		*c*	0.2	±	0.1		*C*
	Roundworm	0.7	±	0.6	(9)	*d*	1.4	±	0.6	(9)	*d*
	Hookworm	1.1	±	0.4		*e*	2.0	±	1.3		*e*
	Coccidia	0.8	±	0.3		*f*	0.7	±	0.3		*f*
	other	1.6	±	1.4		*g*	1.3	±	0.6		*g*
Sub adult	Fleas	4.4	±	1.3	(9)	*a*	1.0	±	0.3	(17)	*A*
	Lice	0.9	±	0.3		*b*	0.8	±	0.3		*B*
	Ticks	0.4	±	0.2		*c*	0.2	±	0.1		*C*
Juvenile	Fleas	1.0	±	0.4	(4)	*a*	1.4	±	0.9	(7)	*A*
	Lice	0.5	±	0.5		*b*	0.0	±	0.0		*B*
	Ticks	0.0	±	0.0		*c*	0.1	±	0.1		*C*

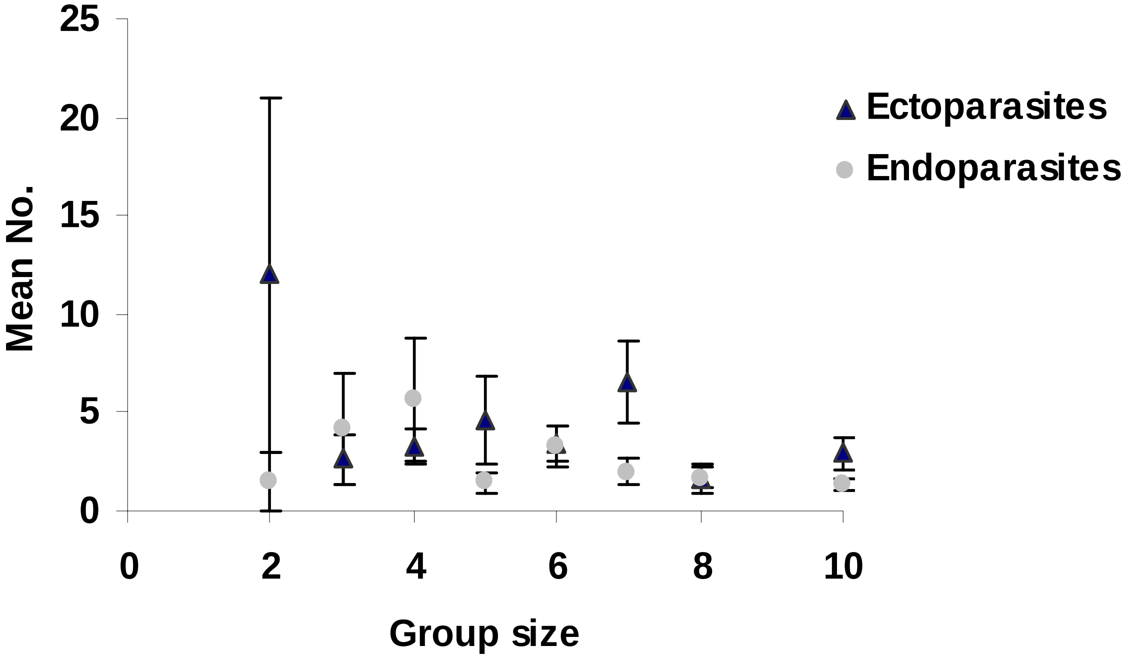

Figure I: Relationship between mean number of parasites (± SE) and group size. Each point represents a different social group (Ectoparasites, Spearman's correlation *R* =0.14, *P* = 0.35; endoparasites *R* = 0.18, *P* = 0.28).

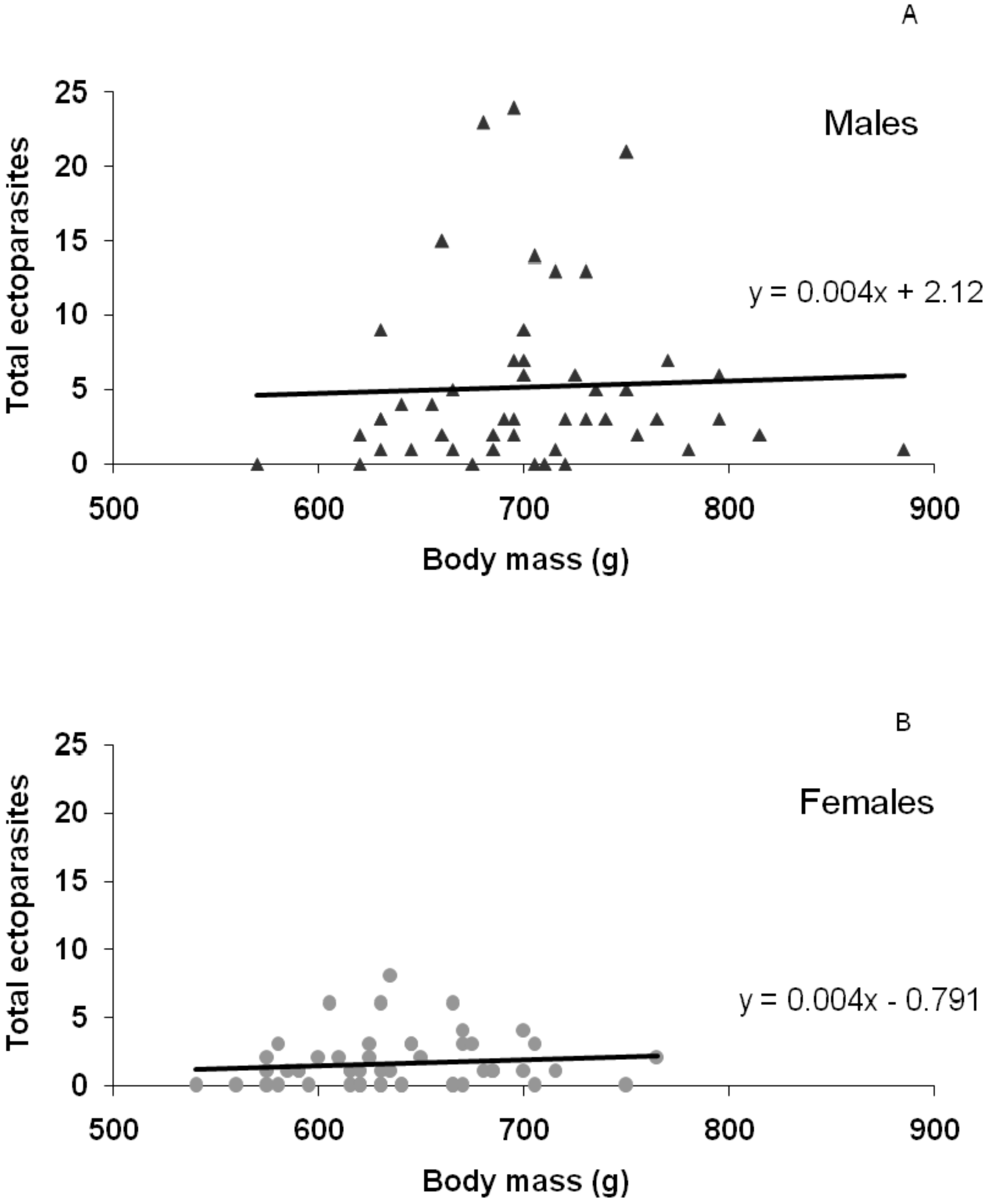

Figure II: Body mass and ectoparasite numbers on A) Males. B) Females. Slopes of regression lines were non-significant for both males and females (A) $R^2 = 0.002$, $P = 0.77$; (B) $R^2 = 0.01$, $P = 0.50$.

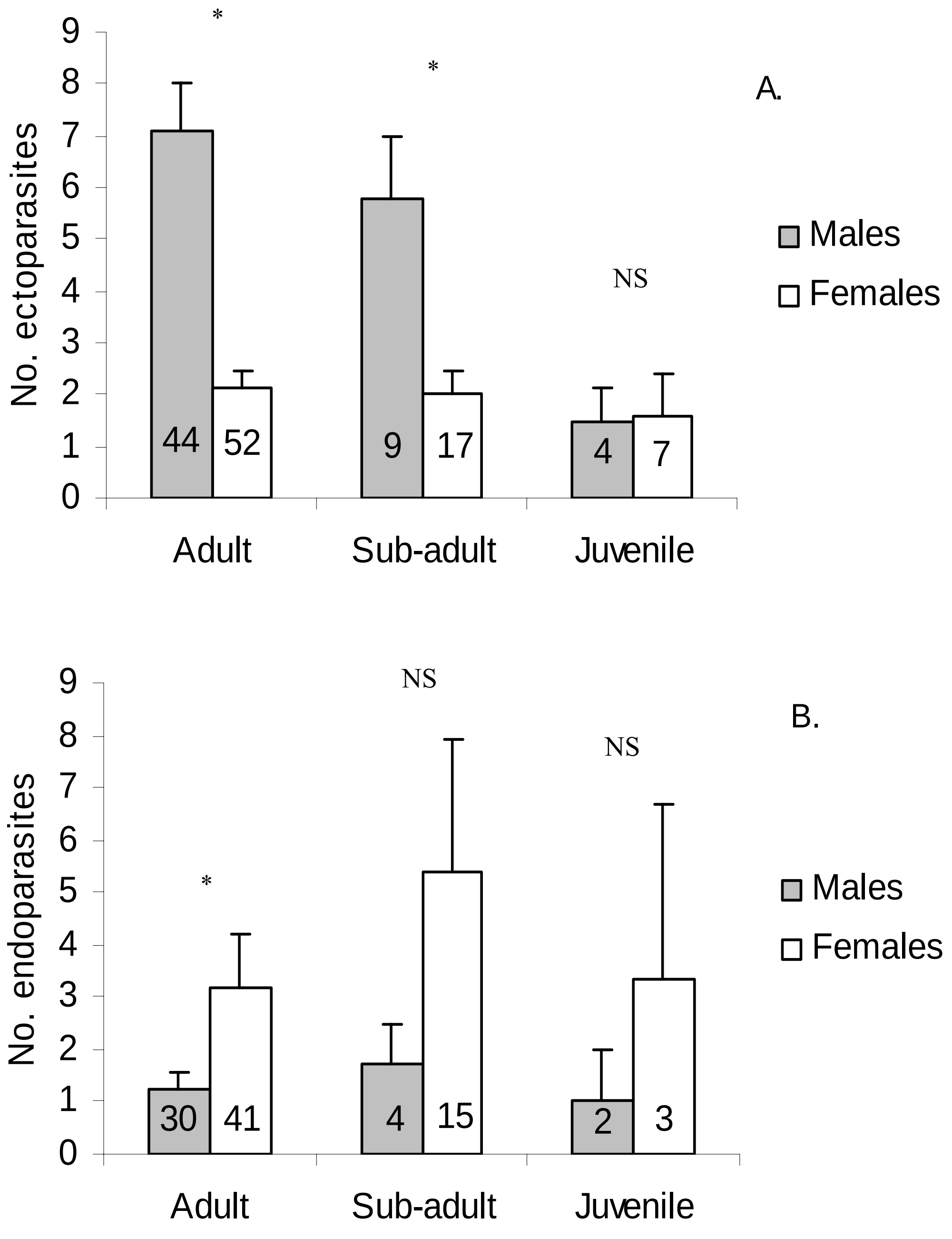

Figure III: Mean (± SE) number of parasites collected from male and female Cape ground squirrels by age class. A) Ectoparasites. B) Endoparasites. (* *P* <0.05, NS = non-significant, error bars = SE, numbers on bars are sample sizes).

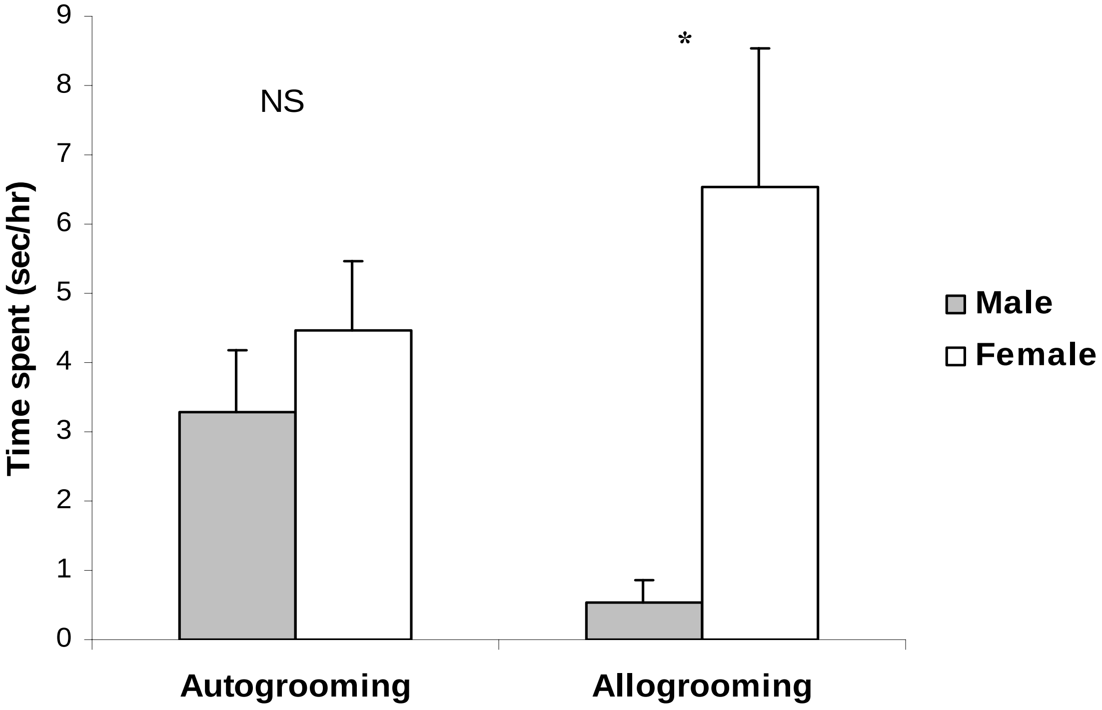

Figure IV: Time spent grooming by males (*N* = 23) and females (*N* = 24) autogrooming and allogrooming. (* *P* <0.05, NS = non-significant; error bars = SE)

CHAPTER 2: PARASITE IMPACTS ON REPRODUCTION

Introduction

Costs associated with parasitism vary highly depending on social structure, age, and sex of the host, as well as the type of parasite (VanVuren 1996, Deviche et al. 2001, Rolff 2002, Skorping and Jensen 2004, Deviche and Parris 2006, Fauchald et al. 2007). Even though males typically carry greater numbers of parasites, the impact of parasites is often greatest on female reproduction (Arnold and Lichtenstein 1993, Hoogland 1995, VanVuren 1996, Neuhaus 2003, Skorping and Jensen 2004). Potential costs of parasitism to a host include delayed reproduction as in marmots (*Marmota spp*) (Arnold and Lichtenstein 1993, VanVuren 1996) and decreased reproductive success as in prairie dogs (*Cynomys ludivcianus*; (Hoogland 1995), as well as blood loss, increased chance of secondary infection, and increased time spent autogrooming (decreasing time vigilant or foraging), which can translate into loss of lifetime reproductive success (Kollars et al. 1997, Rolff 2002, Neuhaus 2003, Johnson et al. 2004).

Parasite loads are expected to increase with increasing numbers of individuals in a group (Brown and Brown 2004), but individuals may mitigate increasing costs of parasites by grooming themselves (autogrooming; Hart 1992, 1994, Kollars et al. 1997) and other conspecifics (allogrooming; Hart 1992, 1994, Johnson et al. 2004), or by moving away from infested areas (Hausfater and Meade 1982, Mooring and Hart 1992, Johnson et al. 2004).

Previous research on patterns of parasitism in the Cape ground squirrel (*Xerus inauris*) found no effect of group size on parasite loads (Chapter 1) and concluded that increased allogrooming in larger groups reduces the costs in larger groups. This conclusion assumes that parasites are costly; however, whether these parasite loads actually impact behavior and reproduction in this species has not been investigated. In this study I measured the costs of parasitism by determining the impact of parasite removal on body mass, reproductive success, grooming, and burrow use of adult female Cape ground squirrels. I predicted squirrels treated for parasites would increase in body mass and reproductive success because parasites are energetically taxing to the host, decreasing the resources available to the host for growth and reproduction. Anti-parasite treated squirrels should decrease time spent grooming because they will harbor fewer ectoparasites to stimulate grooming. Finally, shifting between sleeping burrows will decrease for treated than untreated squirrels if parasite accumulation in burrows and nesting material is causing these shifts.

Biology of the species

Cape ground squirrels are a highly social semi-fossorial species inhabiting the arid areas of southern Africa. Females live in matrilineal groups with other related adult females and their sub-adult and juvenile young, sharing a communal sleeping burrow (part of one burrow system; Waterman 1995). High social activity and communal burrows can enhance external parasite transfer between animals. Cape ground squirrels move frequently from one burrow system to another within their home range (Waterman unpubl.data). Burrow movement may serve to decrease high ectoparasite loads accruing in bedding and sleeping burrows. Female groups forage near their burrows during the day where fecal matter is found frequently (Hillegass unpubl. data). Mode of endoparasite transmission (fecal matter at or near food sources; Gemmell 1990, Ferrari et al. 2004) indicates a potential for large numbers of endoparasites in female Cape ground squirrels Adult females can have up to four estrus cycles annually with a maximum of two for those who successfully gestate and lactate (only about 30% are successful; Waterman 1996, 1998). Gestating females isolate from their group prior to parturition and return after offspring are weaned (typically 7 days after emergence; Waterman 1996). Gestation and lactation are approximately 50 and 52 days, respectively (Zumpt 1970, Waterman 1996) producing 1or 2 offspring per litter (Herzig-Straschil 1978, Waterman 1996).

Methods

This study was performed on S. A. Lombard Nature Reserve near Bloemhof, South Africa (27°35'S, 25°23'E) from May to September 2004. Cape ground squirrel social groups were located in burrow clusters on a floodplain, where the habitat is uniform short grass (Van Zyl 1965). Austral winter is May through September, coinciding with the dry season, peak breeding, and time of lowest available food resources (Herzig-Straschil 1978, Waterman 2002). This reduction in resources at a time when reproduction is high suggests that physiological stress on squirrels may be highest, and the impact of parasites on the animals should be the most apparent (Soler et al. 1999, Villanua et al. 2007).

Using trapping and handling techniques described in Waterman (1995, 2002) all squirrels in eighteen social groups were trapped using Tomahawk live traps (15x15x50cm) and marked in May 2004. Squirrels were re-trapped each month from June to September, and at each capture I recorded body mass and reproductive condition. Adult females were identified by their long, swollen nipples (swelling occurs after first estrus and remains over lifetime; Waterman 1996). Animals were tagged with small transponders (AVID Inc., Folsom, Louisiana) under the skin for permanent identification. Identification at a distance was achieved through dye marking (Rodol D, New York) and freeze marking animals (Quik-freeze®, Miller-Stephenson Product, Morton

Grove, Illinois, Rood and Nellis 1980). Ectoparasites were quantified for every squirrel monthly using techniques described in Scantlebury et al. (2007). Each squirrel's dorsal surface was divided into three planes (left, middle, and right) and combed with three strokes on each plane, from the shoulders to the tail base using a metal flea comb. Ectoparasites were collected in 95% ethanol and then counted for each captured squirrel once a month. All squirrels were handled in accordance with the animal care guidelines of the American Society of Mammalogists (Gannon and Sikes 2007) and the Animal Care and Use Committee of the University of Central Florida.

Endoparasite egg counts from feces were used to estimate endoparasite loads (Villanua et al. 2007). Two fecal samples were collected, one in June and one in July, using plastic tarp sections placed under live traps (Pettitt et al. 2007). Feces from captured squirrels were collected with forceps and placed in labeled plastic sealable bags. Forceps were then placed in 95% ethanol for cleaning and 0.5 g of feces were weighed out and frozen for later use in endoparasite quantification. Fecal samples were thawed, ground, and combined with a solution of magnesium sulfate and allowed to sit for 5 minutes in a cuvette, which caused eggs shed by adult endoparasites to float (McMurin and Bassert 2002). Prepared samples were then observed under a compound microscope (100x) for endoparasite egg count.

Nine social groups were assigned as treatment groups (ecto- and endoparasites were removed) and nine were assigned as control groups. Treatment and control colonies were selected across the floodplain with two large groupings of controls alternating with three large areas containing treated groups. This allowed the control animals to be fairly isolated from treated groups and experience no affect of anti-parasite treatments. Squirrels in treatment groups received a monthly systemic anti-parasite treatment (0.1mL, 0.1% solution ivermectin) to remove endoparasites (Campbell et al. 1983). This drug is absorbed into the blood stream and removes both adult and larval endoparasites from major phyla of nematodes found in the gut, as well as some arthropods, lasting approximately four weeks (Campbell et al. 1983, Heukelbach et al. 2004). To remove ectoparasites I used the topical anti-parasitic agent FRONTLINE® (fipronil 0.29%, Merial, Duluth, Georgia) which kills fleas, ticks, and lice. Ectoparasites are concentrated behind the head, down the back, and around the hind regions (Nilsson 1981)1.5mL FRONTLINE® was sprayed topically over the back of each squirrel, protecting their entire bodies from parasites. FRONTLINE® (fipronil) was tested for safety and effectiveness on rats with a 9.7% solution oral LD50-97mg/kg and dermal LD50-2000mg/kg (Merial Material Safety Data Sheet-FRONTLINE® TOP SPOT**™** 2001). The amount applied to Cape ground squirrels was thus 145 times lower than the oral LD50 and 1400 times lower than the dermal LD50. This drug an external treatment only as it does not move past the dermis of the animal and is effective for over thirty days (Metzger and Rust 2002). Due to the attachment of fipronil to the hair follicles in the dermal skin layer and evaporation of remaining ingredients from the epidermis within 24 hours (Kahn 2005), a minimal impact on grooming and allogrooming behaviors is expected. These anti-parasite treatments are effective against multiple ecto- and endoparasites in this Cape ground squirrel population (Scantlebury et al. 2007). No anti-parasite treatments were given to juveniles (< 6 months of age).

Cape ground squirrels are diurnal and live in open habitats, which allowed for detailed behavioral data collection (Smithers 1971, Herzig-Straschil 1978). Observations from towers focused on morning and evening hours (700 - 1000 hrs and 1500 - 1800 hrs), when the squirrels were most active (Waterman 1996). I recorded identity and sleeping burrow location for all squirrels in a burrow cluster. Linear distance was calculated from each emergence or immergence site to the next consecutive location. Burrow clusters of the Cape ground squirrel can range in size from 120-1500 m^2 containing close to 60 burrow openings that house distinct burrow systems with multiple sleeping areas (Waterman 1995, Waterman and Fenton 2000). I considered a movement of 10 meters or greater from one emergence location to the next immergence location as a shift to a new sleeping burrow. I compared the minimum numbers of sleeping burrow shifts between treated and control groups. Behavioral data were collected using all-occurrences methods (Altmann 1974) focusing on any occurrence of autogrooming, allogrooming, and movement into and out of a burrow (Waterman 1995). Duration of autogrooming or allogrooming behavior was recorded in seconds. Autogrooming and allogrooming data were calculated from behavioral observations July through September and squirrels used in analysis had a minimum observation time of 60 minutes.

All colonies were closely watched for emergence of young. Offspring born during the study (July to August) were used to calculate the per capita number of offspring for treated and control groups. Data were analyzed using SPSS 11.0, $\alpha=0.05$ (The Software MacKiev Company). Parametric tests were used when assumptions of normality and homogeneity were met or data could be normalized and homogenized through transformations; otherwise non-parametric analyses were used (Fry 1993). One treatment colony disbanded in late June, decreasing our sample size for behavioral and reproductive comparisons from 18 groups to 17 groups. Occasionally not all individuals in a social group were captured at exactly the same time for treatment, but parasites were still substantially reduced even in these groups (Scantlebury et al. 2007). Four individuals that never allogroomed were not included in the allogrooming analysis.

Results

Body mass of adult, non-pregnant females did not change from June to August in either control (Paired T-test, t_{16} = -1.18, P =0.26; mean ± SE, June: 593.8 ± 15.8g, August: 610.0 ± 17.4g) or treated (t_{17} = -0.64, P = 0.53; June: 618.9 ± 13.4g, August: 625.3 ± 13.7g) individuals. However, per capita reproductive success was much higher in treated groups (U = 13.5, P = 0.02; Fig. IV). Time spent autogrooming (sec/hr) by squirrels in control and treated groups differed (U = 118.0, P = 0.050, N = 38; Fig. V). Time spent allogrooming by adult females were also significantly lower in treated than control groups (Mann-Whitney U = 87.0, P = 0.001, N = 38; Fig. V). The minimum number of burrow shifts made by control and treated groups did not differ (Mann-Whitney U = 24.0, P = 0.23, N=17; Fig. VI).

Discussion

The four-fold increase in the per capita reproductive success of treated females in our manipulation suggests that the reproductive costs of parasites on this species are substantial. Reproductive failure is common in this species, with 37.5% of females either failing to get pregnant or spontaneously aborting during gestation, and 27.5% of females losing litters during lactation (Waterman 1996). Costs of gestation and lactation can be very high (Millesi et al. 1999), especially the demands of lactation during dry seasons in the arid areas of southern Africa. Litter size in this species is so constrained (only 1 or2 offspring) that differences in reproductive success between control and treated females was most likely due to increase in juvenile survival for treated females and not an increase in litter size.

Although removing parasites did not affect overall body mass in this study, parasite removal did increase percent body fat (Scantlebury et al. 2007). Animals must make trade-offs in the amount of time invested in feeding, avoiding predators, and reproduction. Parasites not only cause infection and loss of blood or mass, but also direct time away from feeding (Hart 1990). Removing parasites from Cape ground squirrels increased the percent of time spent feeding (Scantlebury et al. 2007), which could have led to the improved body condition. Furthermore, body condition is an important influence on the reproductive success of female mammals (Holmes 1988, Risch et al. 2007, Millesi et al. 1999, Temple et al. 2003). For example, condition affects litter size in Richardson's ground squirrels (Risch et al. 2007) and timing of estrus and ovulation in European ground squirrels (Millesi et al. 1999). Costs of gestation and lactation can be very high, especially lactation (Millesi et al. 1999), and this cost would be even higher during dry seasons in the arid areas of southern Africa. The investment in feeding instead of parasite removal appears to have allowed female Cape ground squirrels to increase body condition and investment in reproduction.

Transmission of ectoparasites through social contact and endoparasites primarily through feces is very high in social mammals (Hoogland and Sherman 1976, Hoogland 1995, Altizer et al. 2003). Baboons will switch their sleeping nest sites in response to parasite infestations (Hausfater and Meade 1978, 1982), and likewise pallid bats switch sleeping roost sites in relation to increasing ecotoparasite loads (Lewis 1996). The sleeping burrows of semi-fossorial species may also be the site of much of the transmission of ectoparasites among individuals. When parasites were experimentally removed in Brant's whistling rats (*Parotomys brantsii*), animals reduced their rate of nest chamber switching (Roper et al. 2002). Likewise in European badgers (*Meles meles*), removal of parasites decreased the shifting of badgers from one set to another

(Butler and Roper 1996). Intense sociality and communal living of the Cape ground squirrels create an environment ideal for parasite transmission, both in and out of the burrow system. Bedding materials can accumulate ectoparasites (Hoogland 1995. However, in Cape ground squirrel the number of burrow shifts did not decrease with parasite removal (Fig. VI). Since Cape ground squirrels (particularly young animals) are frequently preyed upon by snakes (Waterman 1997), switching sleeping burrows may be a means of avoiding predators as well as parasites.

Autogrooming, as an asocial activity, was thought to function primarily as parasite removal and predicted to be significantly lower in treated squirrels than controls. Instead of feeding, parasitized animals may have to spend more time actively removing parasites through grooming (Hart 1990, 2000). The major role of grooming in the rodent *Meriones crassus* was to remove fleas, and time spent grooming increased with increasing flea infestation at the expense of time spent resting. Removal of parasites did decrease autogrooming in Cape ground squirrels. Autogrooming as a stimulus driven response to biting parasites is supported in this species (Hart 2000, Mooring et al. 2004). Autogrooming was reduced in treated animals but persisted as compared to the dramatic reduction in allogrooming after treatment. Therefore, autogrooming may not merely be a mechanism of ectoparasite removal, but also function in this semi-fossorial animal for dermal hygiene (e.g., removal of dirt and other debris along hair shafts).

I predicted allogrooming would decrease with anti-parasite treatments if parasite removal was the primary motivation for allogrooming behavior. However, in many species allogrooming is an important component in dominance and other social interactions independent of infestation (Spruijt et al. 1992, Stopka and Graciasova 2001, Kutsukake and Clutton-Brock 2006). In Cape ground squirrels there is no evidence that females form dominance hierarchies (Waterman 1996) and treated females almost stopped allogrooming, suggesting the primary function of allogrooming in this species is to reduce ectoparasite loads.

In conclusion, the impact of parasites on the reproductive success of female Cape ground squirrels is considerable. Females in this arid living species are frequently unsuccessful in raising offspring especially during periods of low rainfall and this failure appears to be magnified by the physiological costs of bearing parasites. Thus, the anti-parasite treatments of females resulted in a dramatic increase in per capita offspring survival. The costs of parasitism in this species appear to be mitigated by removal through auto- and allogrooming but not by movements away from high parasite sleeping sites. With these data I was unable to assess quality of offspring which may be a determining factor in offspring survival. This should be investigated in future research as well as the metabolic cost of producing offspring to directly quantify the parasite cost in reproducing females.

Tables and Figures

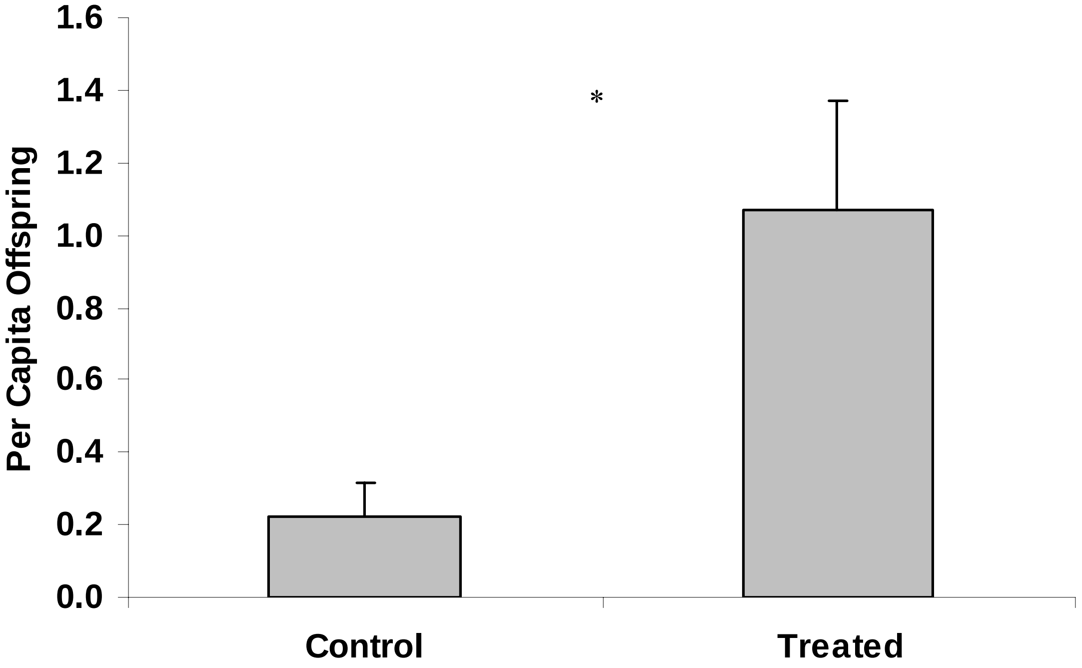

Figure V: Per capita number of Cape ground squirrel offspring surviving to emergence in treated and control groups; control *N* =9, treated *N* =8. (* *P* < 0.05; error bars = SE)

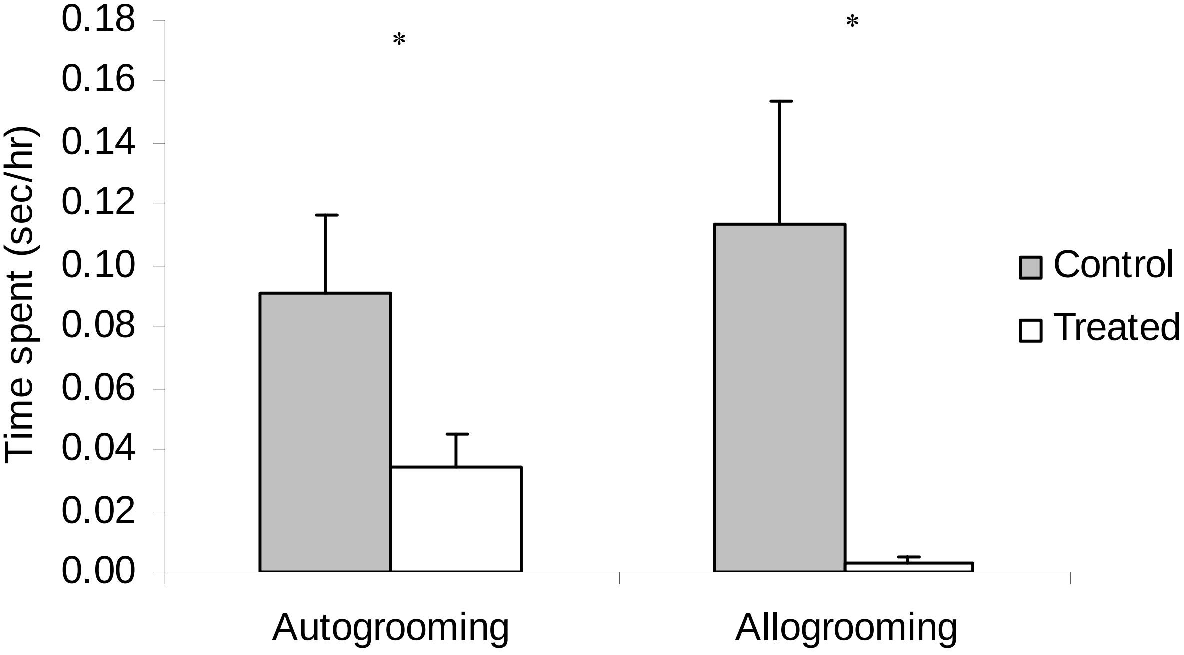

Figure VI: Time spent autogrooming and allogrooming by female Cape ground squirrels: control *N* =21, treated *N* =17. (* *P* < 0.05; error bars = SE).

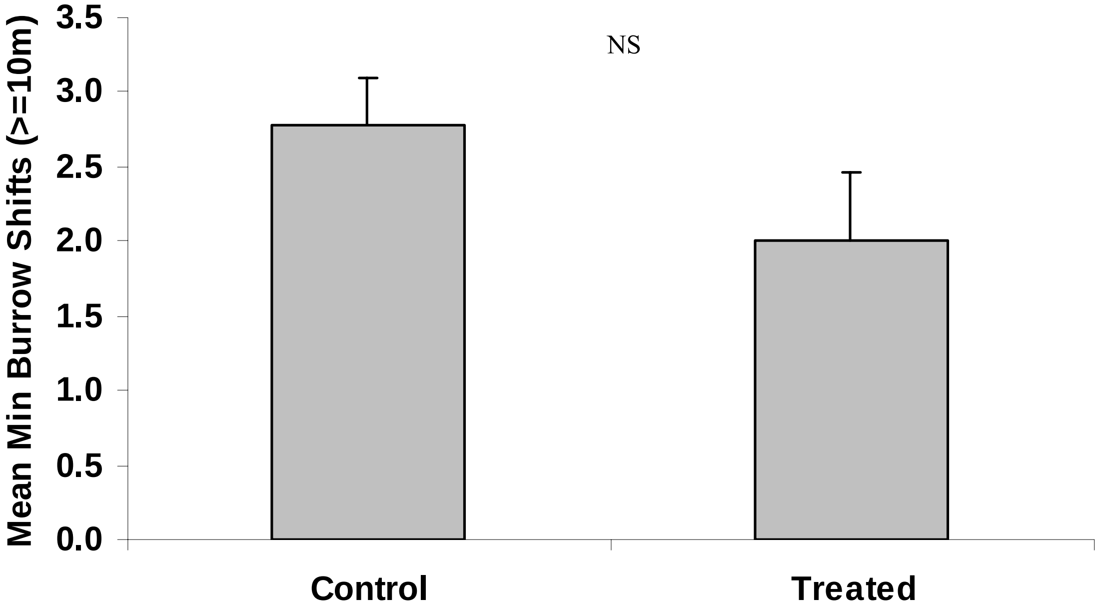

Figure VII: Mean minimum number of burrow shifts (≥10 m) in control and treated colonies from July-September; control *N* = 9, treated *N* = 8. (NS = non-significant; error bars = SE)

GENERAL DISCUSSION

I found sex-biased parasitism in both male and female Cape ground squirrels, by looking at both ecto- and endoparasites. Most studies in the literature have supported the hypothesis that males will have higher parasite loads because of the consequences of sexual selection (Schalk and Forbes 1997, Skorping and Jensen 2004, Hoby et al. 2006, Isomursu et al. 2006). However, although I found a male bias in ectoparasites, I found a female bias in endoparasite numbers. Home range size was not supported as the reason why ecotoparasites were higher on males, as sub-adult males (who are becoming reproductive but have small home ranges) also had higher ectoparasite loads. These data support the sex bias in ectoparasites as a consequence of hormonal or an increased investment in reproduction by males. A hormonal basis for sex biased parasitism has also been documented in avian, ungulate, and rodent species (Sheridan et al. 2000, Deviche et al. 2001, Hughes and Randolph 2001b, Hoby et al. 2006). The higher endoparasite loads of females are probably a function of ecological differences between males and females. Females have much smaller home ranges and forage near burrow clusters resulting in increased exposure to fecal material (transmitting endoparasites; Gemmell 1990, Waterman 1995). While adult males suffer from greater numbers of ectoparasites, their large home ranges may be a benefit to avoid endoparasites.

When treated with anti-parasitic agents, female reproduction increased. The per capita number of offspring raised to emergence was greater in groups where parasites were reduced significantly. Clearly females experience large costs of parasites during peak reproduction (gestation and lactation are costly; VanVuren 1996, Millesi et al. 1999). This indicates that modes of parasite reduction are especially important to females during peak breeding.

Employing allogrooming and autogrooming females may decrease the detrimental effects of ectoparasitism.

While ecto- and endoparasitism were unrelated to group size or number of females in a group, adult females allogroomed more than males and preferentially allogroomed sub-adult males. Some female social groups did include adult resident males. Adult males were the most highly parasitized and would be expected to receive the most allogrooming and autogroom more. My data fails to confirm either of these predictions. A possible cause of this may be that the costs of ectoparasitism on adult males are less than the cost of high autogrooming. Also, lack of allogrooming received by these males may be the result of few social interactions with females that decreases transmission of ectoparasites. Female groups sleep communally and bedding materials are then thought to accumulate ectoparasites over time (Hoogland and Sherman 1976). While females may be allowing the adult males to sleep in the burrow cluster it can not be confirmed that these groups are allowing the adult male members to sleep communally. Burrow mapping or tracking individuals may clarify these data. Females may focus their ectoparasite removal on group members with the highest parasites loads that are still sharing a sleeping burrow with them (e.g., sub-adult males). Quantification of androgens and quality of offspring may allow for more specific interpretations of adult male parasitism and female reproductive costs.

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