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Running title: Rainfall and reproductive tactics

Alternative tactics in male African ground squirrels: the impact of variable rainfall on condition and physiology

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Alternative reproductive tactics occur when conspecifics of the same sex use different behavioral processes to maximize reproductive success. Resource availability can have significant impacts on the proximate factors impacting the success and persistence of alternative tactics, such as an individual's physiology, immunity, and body condition. Male Cape ground squirrels (*Xerus inauris*) display two alternative tactics, with some mature males dispersing from their natal groups and joining bands of non-related males (band males), whereas others do not disperse and remain philopatric in their natal groups past sexual maturation (natal males). Despite differences in metabolism, home ranges and behavior, there is no difference in reproductive success between the two tactics, allowing us to test if rainfall (as a measure of primary productivity) influences body condition and physiological indices in tactics when fitness is equal. Over a period of six years, rainfall was positively related to body condition (mass-spine length residuals) in band males (N = 76), but not in natal males (N = 75). When we followed 18 males prior to and after dispersal, we also found a positive relationship between body condition and age following dispersal, but not prior to dispersal, and natal males maintained a better body condition in low rainfall years. During two years of low rainfall, band males (N = 39) had higher total ectoparasite abundance, and white blood cell differentials, implying they are less able to tolerate parasitic infection than natal males (N = 31). We found no difference in bacterial growth inhibition between tactics, suggesting that both band and natal males are equally resistant to parasites. The poorer body condition of band males during lower rainfall suggests they are less tolerant to parasites in these years. Dispersal during years of low rainfall may thus increase the costs to body condition and parasite infection, but the reproductive benefit of overlapping with more females may contribute to maintaining equal fitness between tactics.

Keywords: dispersal status, body condition, parasites, testosterone, resources, sociality

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Alternative reproductive tactics occur when conspecifics of the same sex use different behavioral processes to maximize reproductive success (Taborsky et al. 2008; Schradin and Yuen 2011). Studies addressing alternative reproductive tactics often focus on variation in the ultimate benefits (fitness) among tactics (Gross 1996). Alternative reproductive tactics have been characterized into three separate strategies: 1) Alternative strategies where tactics are genetically distinct from each other and have equal fitness, 2) Mixed strategies where tactics are genetically monomorphic and have equal average fitness, and 3) Conditional strategies where tactics are genetically monomorphic and one tactic has increased fitness when compared to the other (Gross 1996). Individuals following different alternative reproductive tactics can also vary in physiology (proximate causes, Scantlebury et al. 2008a; Taborsky et al. 2008; Taborsky and Brockmann 2010; Corlatti et al. 2012). Previous studies which have examined differences in physiology and immunocompetence between alternative reproductive tactics have often focused on conditional strategies featuring dominant versus subordinate tactics, or territorial versus satellite tactics (reviewed in Taborsky and Brockman 2010; Demas and Nelson 2012). It is thought that dominant tactics offset the increased energetic and immunological costs associated with their tactic, either ultimately through the increased fitness benefits associated with dominance, or proximately through access to high-quality resources (Demas and Nelson 2012). Mixed strategies are thought to be rare in wild populations (Gross 1996), yet offer a unique opportunity to address how access to resources, body condition, physiology, and immunological differences between tactics contribute to the proximate factors that maintain alternative tactics when the tactic is not genetically determined and when fitness is equal.

Environmental conditions, such as rainfall, can have significant impacts on resource availability, territory quality and female distribution and have been shown to play an important role in non-genetically established alternative reproductive tactics (Schradin and Lindholm 2011). Conditional strategies typically rely on the dominant, or bourgeois, tactics monopolizing access to females and resources, while subordinate individuals are unable to directly compete and develop an alternative tactic to gain reproductive opportunities (Taborsky and Brockman 2010). Schradin and Lindholm (2011) looked at alternative reproductive tactics in male African striped mice (*Rhabdomys pumilio*) and found that environmental conditions affecting population density had significant effects on the prevalence and fitness of the alternative reproductive tactics. In years when there was a high density of mice, the alternative reproductive tactics follow a conditional strategy, where the large territorial males had significantly higher fitness than either the roamer males, or philopatric males that remained in their natal social groups. Interestingly, in years of intermediate population density, they follow a mixed strategy where only two alternative tactics were present, territorial males and roamer males, and their fitness was equal, and finally in a year with low density, due to drought, only the roamer tactic was present (Schradin and Lindholm 2011). This study highlights the importance of variable environmental conditions on alternative reproductive tactics.

The Cape ground squirrel (*Xerus inauris*) offers a unique system for addressing questions about the proximate factors (body condition, physiology, immunity) underlying alternative reproductive tactics, as sexually mature males either disperse from their natal family groups and join roving bands of non-related males (hereafter: band males); or they may delay dispersal and remain in their natal family groups past sexual maturation (hereafter: natal males; Waterman 1995, 1997; Scantlebury et al. 2008a). Natal males rarely mate with females in their own group, but do mate with females in neighboring groups (Manjerovic and Waterman 2015). In a population of Cape ground squirrels in South Africa, males regardless of tactic, do not display dominance hierarchies (Manjerovic 2010), are not territorial, and do not engage in male-male fighting for access to females (Waterman 1997), which differs from conditional strategies. In addition, there is no difference in their average reproductive success, supporting the notion that male Cape ground squirrels follow a mixed strategy (Manjerovic and Waterman 2015). Unlike many other male mammals with alternative tactics (e.g, African striped mice, Schradin and Yuen 2011), in this species there is no difference in circulating plasma testosterone and testes size between natal and band males, which suggests both tactics have similar reproductive investment and further suggests they follow a mixed strategy (Scantlebury et al. 2008a). Band males have higher resting metabolic rates, are more mobile, spend less time feeding, and have larger home ranges than natal males (Scantlebury et al. 2008a; Manjerovic and Waterman 2015). Despite these higher costs, band males were in better body condition (mass-size residuals) than natal males in a previous study (Manjerovic and Waterman 2015). This better body condition may indicate that band males (who are older and more experienced than natal males) may forage more efficiently, or allocate their energy budgets differently compared to natal males (Scantlebury et al. 2008a). However, Manjerovic and Waterman (2015) examined the body condition of tactics during two years (2005-2006) of higher than average rainfall, and presumably higher resource availability. In arid and semi-arid environments rainfall is the primary driver of plant productivity and resource variability (Happold and Happold 1992; Shenbrot 2014.). How tactics differ under low resources may not be the same as under high resources, posing the question; how do natal and band males differ in their body condition, physiology and immunologically during years of low rainfall and lower resource availability?

The objective of this study is to examine the relationship between variable rainfall, indices of body condition, physiology, immunity, and infection in relation to alternative male tactics in Cape ground squirrels, particularly during below-average rainfall. If dispersal increases energetic costs and decreases the energy available to allocate to immunity and maintenance, then when resource availability is low, during low-rainfall years, we predict that band males will present with poorer body condition, possess higher parasite levels, and lower measures of immunocompetence than males that choose the non-dispersing tactic. If band males are more efficient foragers than natal males (Scantlebury et al. 2008a), we predict they will remain in better body condition than natal males despite changes in rainfall because they have, overall, more energy available and that older males have better body condition relative to younger males (Scantlebury et al. 2008a). As testosterone often differs between tactics in other species and can be negatively related to the immunity of an organism (Demas and Nelson 2012; O'Brien et al. 2018), we included measurement of plasma testosterone in our study in an attempt to understand the relationship between alternative tactics and immunity.

MATERIALS AND METHODS

Cape ground squirrels occur throughout the arid regions of southern Africa (Waterman 1995). This species is in the African tribe Xerini, which diverged from the basal lineage in the Sciuridae much earlier than the North American ground squirrels in the tribe Marmotini (Herron et al. 2004). Cape ground squirrel family groups are composed of 1-6 related adult females and up to 9 sub-adults of either sex (Hillegass et al. 2008; Waterman 1995). Breeding occurs year-round, and female reproductive success is affected primarily by predation and parasitism (Waterman 1996; Pettitt et al. 2008; Hillegass et al. 2010). Males reach sexual maturity at 8-10 months of age and either disperse to join non-kin "roving" bands of males or remain nondispersed in their natal group for up to five years, although all males eventually disperse (Waterman 1995; Manjerovic and Waterman 2015). The home range of a male band overlaps with an average of 30 family groups (Manjerovic and Waterman 2015). Overall, 62.5% of males delay dispersal and consequently natal males are, on average, younger than band males (Scantlebury et al. 2008a). The primary benefit of grouping in this species, for both family groups and all-male bands, is enhanced predator detection and deterrence (Waterman 1995, 1997; Unck et al. 2009; Edwards and Waterman 2011).

Study site and rainfall. – We studied male Cape ground squirrels on the S.A. Lombard Nature Reserve, a population that has been studied since 2002 (3660 ha, 18 km north-west of Bloemhof, South Africa, 27°35′S, 25°23′E), except for 2008-2010, when we were not able to access the site. Rainfall in this region occurs during the summer months, between November and April (Herzig-Straschil 1978). During 2002-2017, rainfall at this site averaged 531 mm per annum (range 336-700). We calculated annual rainfall by environmental year (July to June), to fully capture the growing season (Pettitt et al. 2008). During the study of Manjerovic and Waterman (2015), the annual rainfall was 669.1 mm (July 2004 to June 2005) and 661.6 mm (July 2005 to June 2006). For the current study, we also calculated annual rainfall from July 2011 to June 2017 (see Fig. 1 for a summary of rainfall in different years).

Trapping and marking. – We trapped squirrels using Tomahawk traps (Tomahawk Live Trap Inc., WI, USA; 15 X 15 X 50 cm) checked every 30 - 45 min and handled them in cone-shaped bags (Koprowski 2002). From 2011 to 2017, we trapped 694 individuals (354 adult and subadult males, and 340 adult and subadult females). Upon the very first trapping of a new individual, we would permanently mark them using PIT tags (AVID Inc., LA, USA; Hillegass et al. 2008) implanted subcutaneously in the dorsal region, and temporarily marked them dorsally for observations using black hair dye (Rodol D; Lowenstein and Sons Inc., NY, USA). We determined the reproductive tactic of males based on observations made using 10X50 binoculars and 15-45X60 spotting scopes from hides on top of vehicles or observation towers as described by Scantlebury et al. (2008a). We used radio collar transmitters (model #PD-2C, Holihil Systems Ltd., ON, Canada) and behavioral observations to determine where and with whom males were sleeping. We classified males as natal if they continued to sleep and associate with their natal family group, and as band males if they were known to sleep alone, or only with other adult band males. Band males do not sleep with family groups (Waterman 1995). If we were unable to determine male status with confidence, we excluded them from the analysis.

To examine the body condition of males we took the residuals of the ordinary least squares regression between spine length, measured from the base of the skull to the base of the caudal vertebrae, and mass ± 5.0 g using a spring scale (Pesola AG, Switzerland) (Schulte-Hostedde et al. 2005; Manjerovic and Waterman 2012). We first compared the body condition of all males in each tactic where we had data for six different years (2012-2017). As we could not examine the age of band males who had dispersed onto our site as adults and because some natal males may not successfully disperse, we also wanted to compare the body condition of successful dispersers of known age prior to and after dispersal. When males switch tactics (disperse), the majority move beyond our study site and we are not able to recapture them. However, from 2012 to 2017, eighteen males switched tactics and moved to another area of our study site, allowing us to calculate their body condition and age in the year before and the year after switching tactics. All measurements to calculate the body condition of the squirrels were made at the beginning of the dry season (late May or early June) from 2012 to 2017.

Physiological and immunological measures. – Between May-August 2012 and May-October 2013, we collected detailed physiological indices of body condition, immunity and infection of both natal and band males. Ectoparasites were quantified by combing along the three planes of the back (left, center and right) from head to tail with a metal flea comb (as described in Hillegass et al. 2008) and by careful examination of the inner thighs and groin region (O'Brien et al. 2018; Beaumont et al. 2019). We stored ectoparasites in 70% ethanol for quantification. We focused on ectoparasites (fleas and lice) as male Cape ground squirrels are predominately affected by ectoparasites and have low endoparasite loads (Hillegass et al. 2008). The latter study examined parasite infections during a rainfall year (2004: 510 mm) that was just below the 17-year average. We examined the mean abundance of parasites (which represents the mean number of ectoparasites of all squirrels) and the prevalence, which represents the proportion of hosts with an infection (Rózsa et al. 2000).

We collected a blood sample (0.5-1ml) from the femoral vein using a sterile 26-gauge needle and a 1ml syringe within the first 15 minutes of handling. Blood samples were immediately placed in a cooler box with ice packs and returned to the lab to process. We used blood hematocrit as an estimate of the percent red blood cells in circulation as an additional measure of body condition (Boonstra et al. 1998; Beldomenico et al. 2010; Gilot-Fromont et al. 2012; Breuner et al. 2013). Plasma, used in both hormone and immunocompetence assays, was separated from whole blood by centrifugation at 6000 rpm for 5 minutes (Spectrafuge mini, Labnet International, NJ, USA) and frozen at -20^{o}C until processed at the University of Pretoria, South Africa.

White blood cell differentials (WBC) of each individual for both years were completed by the clinical pathology laboratory at the University of Pretoria by counting 100 WBC on a single layer of whole blood smear stained with Diff-Quick (recording the number of lymphocytes, neutrophils, basophils, eosinophils and monocytes (Bachman 2003)). Basophils occurred in very small proportions (mean 0.88 ± 0.16%, respectively), and as no significant changes were observed between tactics, we excluded them from the analysis. Neutrophils are part of the innate immune system that respond quickly to pathogens and increases in response to infection and inflammation (Beardsell and Howell 1984). Lymphocytes are important components of the adaptive immune system and increase in response to ectoparasites (Christe et al. 2002) and monocytes primarily respond to inflammation and infection (Falcone et al. 2001; Davis et al. 2008). High numbers of eosinophils provide an indication of macroparasitic infections such as nematodes (Harvey 2012). Interpretation of WBC differentials has varied widely in the past (Davis et al. 2008), and while they cannot inform on the ability of the individual to mount an immune response, they are a good relative measure to compare the immune status of individuals (Boonstra 1998; Davis et al. 2008). Higher neutrophil:lymphocyte (N:L) ratios are also considered an indicator of a greater stress response, increased immobilization of the immune system, and are related to lower body condition (Johnstone et al. 2012; Boonstra et al. 2017).

As an additional measure of innate immune ability, we used bacterial killing assays in 2013 (Matson et al. 2005; Tieleman et al. 2005; Liebl and Martin 2009; Merrill et al. 2014), as they measure complement and lysozyme activity by evaluating the plasma's ability to kill a known dilution of a novel bacteria (Millet et al. 2007). We followed the procedure outlined by Liebl and Martin (2009), preparing a working solution of 10^5 bacteria/ml of *Escherichia coli* (Lyophilized *E. coli* ATCC #8739, Microbiologics, MN, USA), and using 24.5 µl of plasma to make a 1:4 dilution to test the plasma's ability to inhibit bacterial growth overnight. Each sample was tested in quadruplet, incubated in 96-well plates and absorbance was measured at 595 nm using a spectrophotometer (Multiskan Ascent, Thermo Labsystems, PA, USA). There were two negative controls in quadruplet (growth medium only) and two positive controls in quadruplet (bacteria and growth medium only) on each plate. We calculated the percent of bacterial growth inhibited by comparing the absorbance of the samples and the absorbance of the positive controls.

To measure circulating testosterone we used a commercially available coated tube assay kit (Coat-a-Count TKTT1, Diagnostic Products Corporation, CA, USA) as previously described (Scantlebury et al. 2008a; O'Brien et al. 2018). The assay detectable range was 10-1600 nmol/L testosterone and cross-reactivity of the Coat-a-Count testosterone antibody was 16% with 11-ketotestosterone, < 5% with dihydrotestosterone and 19-hydroxyandrostenedione, and less than 1% with other steroids tested according to the manufacturer. Serial dilution of Cape ground squirrel plasma demonstrated good parallelism with the testosterone standard curve (data not shown). The intra-assay coefficient of variation was 8.4% and the inter-assay coefficient was 12%.

All procedures were approved by the University of Manitoba's Animal Care and Use Committee (Protocol #F10-030 to JMW) and followed the guidelines of the American Society of Mammalogists (Sikes et al. 2011). Permission for the project was provided by Northwest Province Parks and Tourism Board, South Africa.

Data analysis. – To examine the body condition of natal and band males, we used linear mixed models (LMM) using Gaussian distributions. We calculated the residuals (mass on spine length) of all the males across 2012-2017 and included individual tag number as a random factor and rainfall as a fixed factor. We could not examine age in this large dataset because we did not know the age of most band males. However, 18 of the males from this larger dataset switched tactics (dispersed to become band males) during our study. For these males we knew their exact age and we had residuals prior to and after switching tactics. In addition, the larger analysis could not rule out that differences in body condition between tactics could be because of innate differences in the "quality" of males, so we examined the body condition of individual before and after successful dispersal in this smaller subset of animals. We used these data, included individual tag number as a random factor, and rainfall and age as fixed factors and reported the F statistic.

To assess the effect of reproductive tactic and sampling year (2012-2013) on ectoparasite abundance, we used a generalized linear mixed model (GLMM) with a Poisson distribution and reported the Wald's Chi-square statistic. To assess body condition, immunocompetence measurements, and testosterone, we used linear mixed models (LMM) using Gaussian distributions and reported the F statistics. To determine if status in 2012-2013 affected each response variable, we performed a type 3 ANOVA (R-Package ***lme4*** version 1.1-7). We were unable to get spine length from one individual in 2013. We included individual tag number as a random factor in these analyses to account for repeated measures across the two years, and we also controlled for year in the models and found no significant interactions between year (2012-2013) and male status. Testosterone levels were log-transformed, while hematocrit and all WBC proportions except eosinophils were arcsine transformed to satisfy normality. We could not normalize the eosinophil proportions, thus we used a Mann-Whitney U test to compare eosinophils between tactics and analyzed 2012 and 2013 separately because of repeated individuals in each year. Because bacterial growth inhibition was only measured in 2013, a Mann-Whitney U test was used to compare the differences between tactics, as the data were nonnormal. We used R (version 3.1.1) or JMP 14.0 (SAS Institute Inc., Cary, NC, U.S.A.) for our statistical analysis. We compared the prevalence of parasites between tactics with an exact unconditional test using Quantitative Parasitology version 3.0 (Rózsa et al. 2000). Data are reported with mean ± standard error, and statistical significance was set at $\alpha \leq 0.05$.

RESULTS

Yearly rainfall from July 2011 to June 2017 averaged 460.9 mm (range 336 – 551 mm; Fig. 1). Mean number of band males from 2012 to 2017 was 23.3 ± 2.2 (range 16 to 31), while mean number of natal males was 17.7 ± 2.0 (range 13 to 27). From 2012 to 2017, the body condition (mass-size residuals) of band males was positively related to rainfall ($F_{1,122} = 13.63$, $P = 0.0003$, $R^2 = 0.67$; 76 individuals), while that of natal males was not related to rainfall ($F_{1,73} = 1.47$, $P = 0.233$, $R^2 = 0.84$; 75 individuals; Fig. 2). From 2012 to 2017, 18 males switched tactics (dispersed to become band males). Mean age of switching tactics was 3.33 ± 0.29 (N = 18 males; range 2 - 6 years). The mean body mass of these 18 males before and after dispersal did not differ (paired t-test, $t_{17} = 0.17$, $P = 0.87$; before 717.2 ± 14.6 g and after 719.2 ± 12.2 g). However, similar to the last analysis, body mass was influenced by rainfall only after dispersal ($F_{1,16} = 5.9$, $P = 0.027$, $R^2 = 0.27$) and not before dispersal ($F_{1,16} = 0.21$, $P = 0.65$, $R^2 = 0.013$). Likewise, the body condition of males before dispersal was not related to rainfall ($F_{2,15} = 0.26$, $P = 0.62$, $R^2 = 0.12$), but the body condition of these same males was related to rainfall in the year after dispersal, with lower residuals in low rainfall years and higher residuals in higher rainfall years ($F_{2,15} = 10.37$, $P = 0.024$, $R^2 = 0.28$, Fig. 3). Age was also not significantly related to body condition in males before dispersal ($F_{2,15} = 2.01$, $P = 0.18$, $R^2 = 0.12$), but band males that were older after they switched tactics had better body condition than younger band males ($F_{2,15} = 28.55$, $P < 0.0001$, $R^2 = 0.75$, Fig. 4).

We examined detailed differences in indices of body condition, immunity and infection of males during 2012 and 2013, when rainfall was below the 16-year average of our site (2012 = 336 mm; 2013 = 508 mm). We measured 34 adult males (15 natal and 19 band males) in 2012 and 36 adult males (16 natal and 20 band males) in 2013. As Cape ground squirrels are a long-lived species, we sampled some of the individuals in both 2012 and 2013. Over the two years of the study, we handled 57 unique individuals, with only two individuals changing tactics, becoming band males in the second year.

In 2012-2013, there was no difference in body mass or spine length between natal and band males (Table 1). Band males had lower body condition indices than natal males (Table 1). Likewise, band males had a lower hematocrit compared to natal males (Table 1). Band males had a higher prevalence of fleas (97.4%) than natal males (74.2%; unconditional test, $P = 0.004$). Similarly, band males had higher prevalence of lice (79.5%) than natal males (45.2%; $P = 0.003$). The mean abundance of ectoparasites (total ectoparasites: fleas and lice) was higher in band males, as were the abundances of fleas and lice examined separately (Table 1). There were no differences in the plasma testosterone concentration between alternative male tactics (Table 1).

In 2012-2013, WBC differentials (except for eosinophils) differed between male tactics, and the N:L ratio of band males was higher compared to natal males (Table 1). Eosinophils did not differ between tactics in either 2012 (band males, 1.84 ± 0.49 ($N = 19$); natal males, 1.47 ± 0.45 ($N = 15$); $U = 249.5$, $P = 0.663$) or 2013 (band males, 1.80 ± 0.41 ($N = 20$); natal males, 1.37 ± 0.47 % ($N = 16$); $U = 296.0$, $P = 0.36$). There was no significant difference between tactics for bacteria killing ability (band males, 38.5 ± 6.6 % ($N = 20$); natal males, 41.9 ± 3.3% ($N = 16$); $U = 318.0$, $P = 0.10$).

DISCUSSION

The annual rainfall during this study was below average for this site (2011-2017 average: 460.9 mm versus 2002-2017 average: 531 mm; Fig. 1) and included the lowest rainfall year during our time at this site (2012: 336 mm), providing an opportunity to examine the relationships among body condition, immunity and infection between natal and band males when resources were less abundant.

The lower body condition (mass-size residuals), physiological indices (hematocrit, higher N:L ratios, WBC differences) and higher ectoparasite infections were indicative of band males having poorer body condition, immunity and other physiological measures than natal males during low rainfall years (2012-2013), supporting the hypothesis that dispersal affects the physiological status of male Cape ground squirrels. These results stand in contrast to high rainfall years (2005 and 2006, 660 mm; Manjerovic and Waterman 2015), where band males were in better body condition at the same study site. The differences between that study and the current one may be a reflection that body condition and physiological measures, along with other factors that influence alternative reproductive tactics, may not be fixed, but instead change from year to year (Schradin and Lindholm 2011), and are dependent on environmental factors such as rainfall, which ultimately influences resource availability.

Whether a natal male had higher or lower body condition indices (mass-size residuals) compared to a band male was affected by rainfall and age. Overall, the body condition of band males was positively related to rainfall levels, whereas those of natal males were not affected. Males who switched tactics (dispersed) before, or during a below-average rainfall year (below 531 mm) were in poorer condition than males that switched before or during an above-average rainfall year. Older natal males in the band tactic were in better body condition as well, suggesting that males that delay dispersal may have an advantage over younger dispersers. However, rainfall and age did not influence the body condition of these same males before dispersal, when they were still living with their natal families. The poorer body condition of band males during low rainfall was consistent with findings during rainfall years that were just below average (2004: 510mm) that band males have higher resting metabolic rates than natal males (Scantlebury et al. 2008a), which suggests they are metabolizing energy at a higher rate, and do not have additional energy to store (Demas and Nelson 2012). As breeding occurs year-round and estruses are unpredictable, males must be prepared to mate at any time of the year (Waterman 1998). Band males may also have less energy available because they spend less time feeding than natal males and they engage in more energetically expensive behaviors such as having larger home ranges and spending more time searching for females (Scantlebury et al. 2008a). The lack of change in the body condition of natal males during low rainfall years suggests they may be benefiting from staying in their natal group.

In species displaying alternative reproductive tactics, better body condition is most commonly attributed to the tactic with the best fitness payoff, while individuals in poorer condition are forced to make the "best of a bad job" and are less reproductively successful, consistent with conditional strategies (Taborsky and Brockmann 2010). In anurans (*Bufo woodhousii* and *Bufo cognatus*) the males that followed the "calling" tactic resulted in the highest fitness and were in better body condition than the satellite males who were in poorer body condition and not able to meet the energetic costs of calling (Leary et al. 2005). Likewise, in Eurasian red squirrels (*Sciurus vulgaris*), the males that followed the leader tactic had the highest fitness, highest body mass and were also the oldest, compared to males that followed subdominant or sneaker tactics, and thus had more energy to invest in defending estrous females (Wauters et al. 1990). Yet the “best of a bad job” is not always supported, as male hyenas (*Crocuta crocuta*) that disperse were not better phenotypically than philopatric males, and both tactics had similar fitness (Davidian et al. 2016). Similarly, in high rainfall years, band males have better body condition than natal male Cape ground squirrels, but they did not differ in their reproductive success (Manjerovic and Waterman 2015). It is unknown how the poorer body condition observed in band males in this study during low rainfall may have impacted their relative fitness, but it is possible that alternative male tactics in Cape ground squirrels may not always follow a mixed strategy as has been found in African striped mice, where the prevalence and fitness success of differing alternative male tactics fluctuates with environmental conditions (Schradin and Lindholm 2011).

In low rainfall, band Cape ground squirrel males had higher ectoparasite abundances than natal males, possibly as a result of their poorer body condition leaving them unable to mount a strong immune response to resist infection (Sheldon and Verhulst 1996). Alternatively, the higher parasite abundances may be contributing to the poorer body condition, similar to the situation reported in female Columbian ground squirrels (*Urocitellus columbianus*; Neuhaus 2003). Band males may also have higher ectoparasite abundances as a consequence of their larger home ranges overlapping with more conspecifics and increasing the exposure to ectoparasites compared to natal males, that have overall smaller home ranges (Moore and Wilson 2002; Manjerovic and Waterman 2015). However, Hillegass et al. (2008) did not find that larger home ranges were a factor in parasite infection in males. Natal males may also have lower parasite abundances due to their better body condition and more energy available to fight off infestation (Sheldon and Verhulst 1996; Hawlena et al. 2008), but they may also be benefitting from staying in their natal group. Hillegass et al. (2008) found that adult females spent significantly more time allogrooming than any other sex or age class, particularly compared to band males in their all-male bands. Autogrooming has been suggested to be more important than the immune response for controlling ectoparasites in Sundevall's jird (*Meriones crassus*, Hawlena et al. 2007) and in Columbian ground squirrels (Roth et al. 2019). As Cape ground squirrel tactics do not differ in the amount of time spent autogrooming (Hillegass et al. 2008), the lower ectoparasite abundances on natal males may reflect the increased allogrooming received from the females in their family groups.

Increased parasite loads can significantly affect the survival, growth and fitness of a host (Agnew et al. 2000; Hawlena et al. 2006; Watson 2013). Parasites impose some cost on their host by consuming the host’s resources (Combes 2001) and parasites have significant negative effects on the reproductive success of female Cape ground squirrels (Hillegass et al. 2008). A meta-analysis by Moore and Wilson (2002) found a positive correlation between parasites on male mammals and male mortality, suggesting that the increased parasite infections of Cape ground squirrel band males could negatively impact on their survivorship, a cost of dispersing during a low rainfall year. Parasites do not always have the expected negative effects on host survival and fitness and an additional stressor, such as a food shortage or contaminants, can be required for parasites to affect the hosts negatively (Marcogliese and Pietrock 2011). Individuals in poor condition may exhibit higher parasite loads, but the parasites may have a minimal effect on the condition (Roth et al. 2019). Negative effects arising from parasitism only occur in Sundevall’s jird when in poor body condition and these negative effects were lost if they had a surplus of energy or access to unlimited resources (Hawlena et al. 2008). Similarly, the poorer body condition of Cape ground squirrel band males during low rainfall could be acting as an additional stressor that may amplify the negative effects of parasites.

Band and natal male Cape ground squirrels displayed distinctly different WBC profiles. The N:L ratio can be an additional indicator of immunity and chronic stress (Davis et al. 2008; Breuner et al. 2013; Boonstra et al. 2017). In red squirrels (*Tamiasciurus hudsonicus*), breeding males had higher N:L ratios compared to non-breeding males, evidence of poor body condition in breeders (Boonstra et al. 2017). In Cape ground squirrels, band males had higher N:L ratios relative to natal males during low rainfall, and were also in poorer body condition, suggesting they were suffering from higher levels of chronic stress. These results are inconsistent with Scantlebury et al. (2008a,b) who found that natal males had significantly higher plasma cortisol concentrations than band males during rainfall years that were just below the 17 year average of the site. Scantlebury et al. (2008b) attributed the increased cortisol in natal males to higher levels of aggressive behaviors from females. Variation in resource availability year to year, and variation in natal group composition could explain the difference seen in stress estimates between this study and Scantlebury et al. (2008a,b). The higher proportion of monocytes displayed by Cape ground squirrel band males during low rainfall is also indicative of a response to infection (Falcone et. al. 2001; Davis et al. 2008). Drought acted as a stressor in olive baboons (*Papio anubis*), where testosterone was suppressed, aggression decreased, and males increased their time spent foraging to maintain their body mass (Sapolsky 1986). However, the dominance relationships amongst the male baboons remained unchanged during this time.

Despite the differences in body condition, parasite abundance, and WBC differential between the tactics, the results from our bacteria growth inhibition assays indicated that the innate immune systems of both natal and band males were equally capable of fighting off novel pathogens. Host defense against parasites/pathogens has been conceptualized into two different strategies; resistance and tolerance (Råberg et al. 2009). Resistance occurs when the host's immune system directly targets parasites and pathogens to limit their population growth and/or to eliminate them (Råberg et al. 2009; Bordes et al. 2012). However, a tolerance strategy does not reduce parasite and pathogen infections, but instead attempts to limit the damage incurred to the host (Råberg et al. 2009; Bordes et al. 2012). As immunity measures, such as bacteria growth inhibition, are often used as measurements of resistance, our results indicate that both male tactics are equally resistant to parasites (Bordes et al. 2012). Tolerance is commonly measured as body condition, where better body condition is associated with better tolerance (Bordes et al. 2012). Due to the increased energetic demands of dispersal, males of the dispersed tactic (band males) may be less able to, or less willing to tolerate ectoparasites during low rainfall, leaving them more vulnerable to environmental stressors than natal males (Marcogliese and Pietrock 2011).

Testosterone is considered a proximate mechanism affecting immunity through a trade-off between the positive effects of increased testosterone on a male’s reproductive potential, via increased sperm production as well as secondary sexual characteristics such as sexual displays, and the negative effects of a suppressed immune system (Folstad and Karter 1992). Folstad and Karter (1992) initially proposed this trade-off as the mechanism behind “honest” signaling of male quality to females. Despite differences in their parasite infections and body condition, males of different tactics in Cape ground squirrels showed no difference in their circulating testosterone concentrations (this study, Scantlebury et al. 2008a).

The trade-off between immunity and testosterone may be mediated through the differential allocation of resources (Rolff 2002; O'Brien et al. 2018). A review by Agnew et al.

(2000) found that across several species, when faced with a chronic infection like parasites, hosts preferentially allocate resources toward reproduction. Male Cape ground squirrels may preferentially allocate resources to reproduction despite the costs to their body condition and increased infection. Traditionally pre-copulatory male-male competition for females such as dominance hierarchies, territoriality, and male-male aggression (Wong and Candolin 2005) give advantages to males in good body condition (Schradin and Lindholm 2011). Male Cape ground squirrels present an interesting variation of this norm as they do not display dominance hierarchies in this population (Manjerovic 2010), are not territorial or aggressive and do not engage in fighting for access to females (Waterman 1998). However, they presumably invest heavily in post-copulatory competition via sperm competition, as indicated by their large testes (Manjerovic et al. 2008; Manjerovic and Waterman 2015). It may be that band males continue to allocate resources toward reproduction and sperm production as well as immunity, at a cost to their body condition, to minimize the ultimate fitness costs of reduced reproductive investment during low rainfall or that the reproductive success of either tactic is variable under different environmental conditions.

Our results suggest that whether it is better to remain as a natal male, or switch to the band male tactic may depend on rainfall. Even when reproductive investment and reproductive success are equal, alternative male tactics under different environmental conditions can result in differences in physiological status and body condition. These differences may reflect variations in the energetic demands of dispersal and social benefits of remaining in their natal group (Davidian et al. 2016). These differences may also explain why the two tactics persist. Band males can encounter a larger number of potential mates as they have larger home ranges than natal males (Scantlebury et al. 2008a, Manjerovic and Waterman 2015), which may offset the cost of dispersal and maintain equal fitness between tactics. During high rainfall, band males also have a better body condition than natal males (Manjerovic and Waterman 2015), but they may take on more costs during low rainfall years. Delaying dispersal by natal males may increase their survival through low rainfall years and during these times the fitness of the tactics may differ. As natal males receive increased aggression from females (Scantlebury et al. 2008b) and the presence of natal males contributes to the reproductive suppression of immature females (Pettitt and Waterman 2011), males may eventually be forced out of family groups by the breeding females of the group. Future studies looking at the variability of social group composition, resource availability, and relative fitness (reproduction and survival) when males switch tactics could help clarify when and why natal males ever leave.

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Figures legends

Fig. 1. Annual (July to June) rainfall (mm) at the study site in central South Africa from 2001 to 2018 and the comparative years of the study from Manjerovic and Waterman (2015) and the current study on this site.

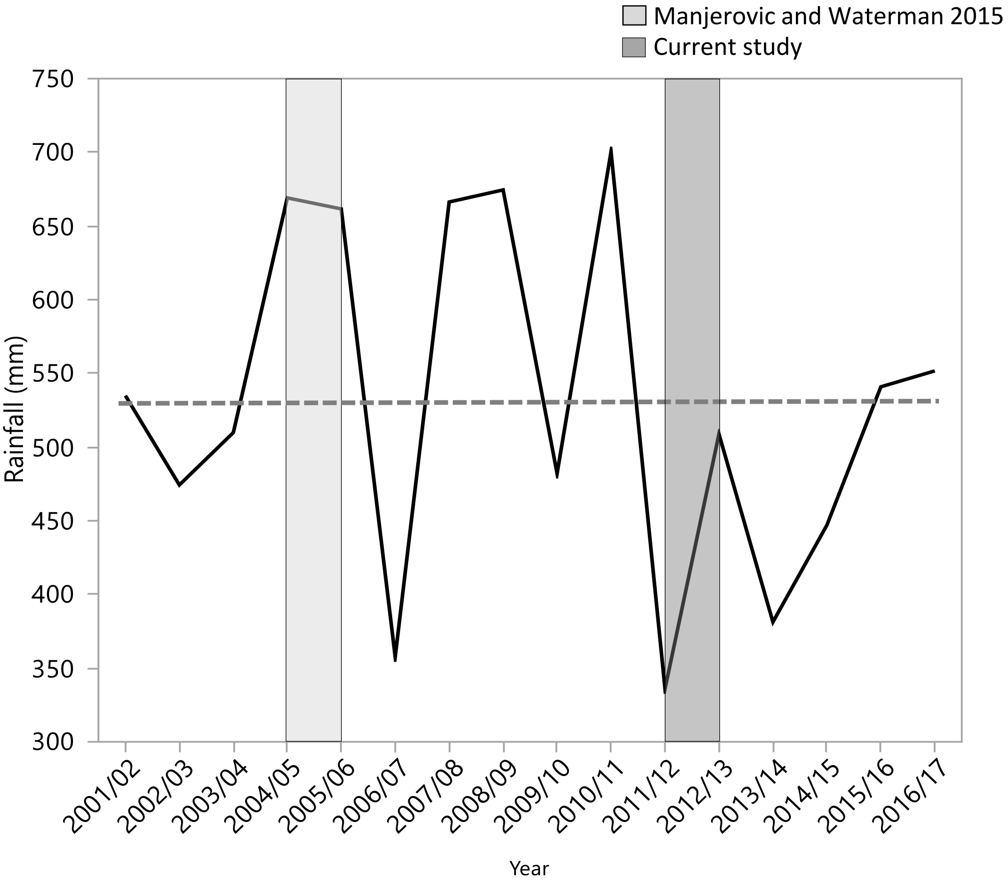
Fig. 2. Body condition estimates, calculated as the residuals of body mass (g) versus spine length (cm) of (A) 76 band (dispersed) and (B) 75 natal (philopatric) Cape ground squirrel males versus rainfall (mm) from 2012 to 2017.

Fig. 3. Body condition estimates, calculated as the residuals of body mass (g) versus spine length (cm), of 18 male Cape ground squirrels in the year after dispersal (A) and the year prior to dispersal (B) versus rainfall (mm) from 2012 to 2017.

Fig. 4. Body condition estimates, calculated as the residuals of body mass (g) versus spine length (cm), of 18 male Cape ground squirrels in the year after dispersal (A) and the year prior to dispersal (B) versus age (years) from 2012 to 2017.

Table 1. Mean (± SE) mass, spine length, body condition, hematocrits, parasites abundance, testosterone and white blood cells of band (n = 34 individuals, 5 seen in both years) and natal (n = 25, 6 seen in both years) male Cape ground squirrel (*Xerus inauris*) in 2012 and 2013. Values with * indicate Wald Chi-square statistics.

	Natal	Band	*F*	df	*P*
Body mass (g)	713.5 ± 7.9	693.18 ± 7.6	1.85	1, 65	0.18
Spine length (cm)	18.43 ± 0.12	18.42 ± 0.11	0.003	1, 64	0.96
Body condition (residuals)	10.13 ± 7.14	-8.27 ± 6.90	3.85	1, 64	0.049
Hematocrit (%)	52.6 ± 1.02	49.9 ± 0.85	4.56	1, 65	0.04
Testosterone (ng/ml)	1.43 ± 0.30	1.32 ± 0.22	0.057	1, 65	0.81
% Lymphocytes	54.6 ± 3.1	38.3 ± 2.7	16.7	1, 65	<0.0001
% Neutrophils	32.9 ± 3.2	51.1 ± 3.0	16.5	1, 65	<0.0001
% Monocytes	10.4 ± 1.1	7.8 ± 0.9	4.67	1, 65	0.03
N:L ratios	0.88 ± 0.2	2.24 ± 0.5	6.74	1, 65	0.0094
Total ectoparasite abundance	4.65 ± 0.58	10.5 ± 1.06	17.6*	1, 66	<0.0001
Flea abundance	2.9 ± 0.9	6.3 ± 0.5	7.07*	1, 66	0.007
Lice abundance	1.4 ± 0.5	3.6 ± 0.4	4.26*	1, 66	0.04


Manjerovic and Waterman 2015
Current study
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650
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550
500
450
400
350
300
Rainfall (mm)
2001/02
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2004/05
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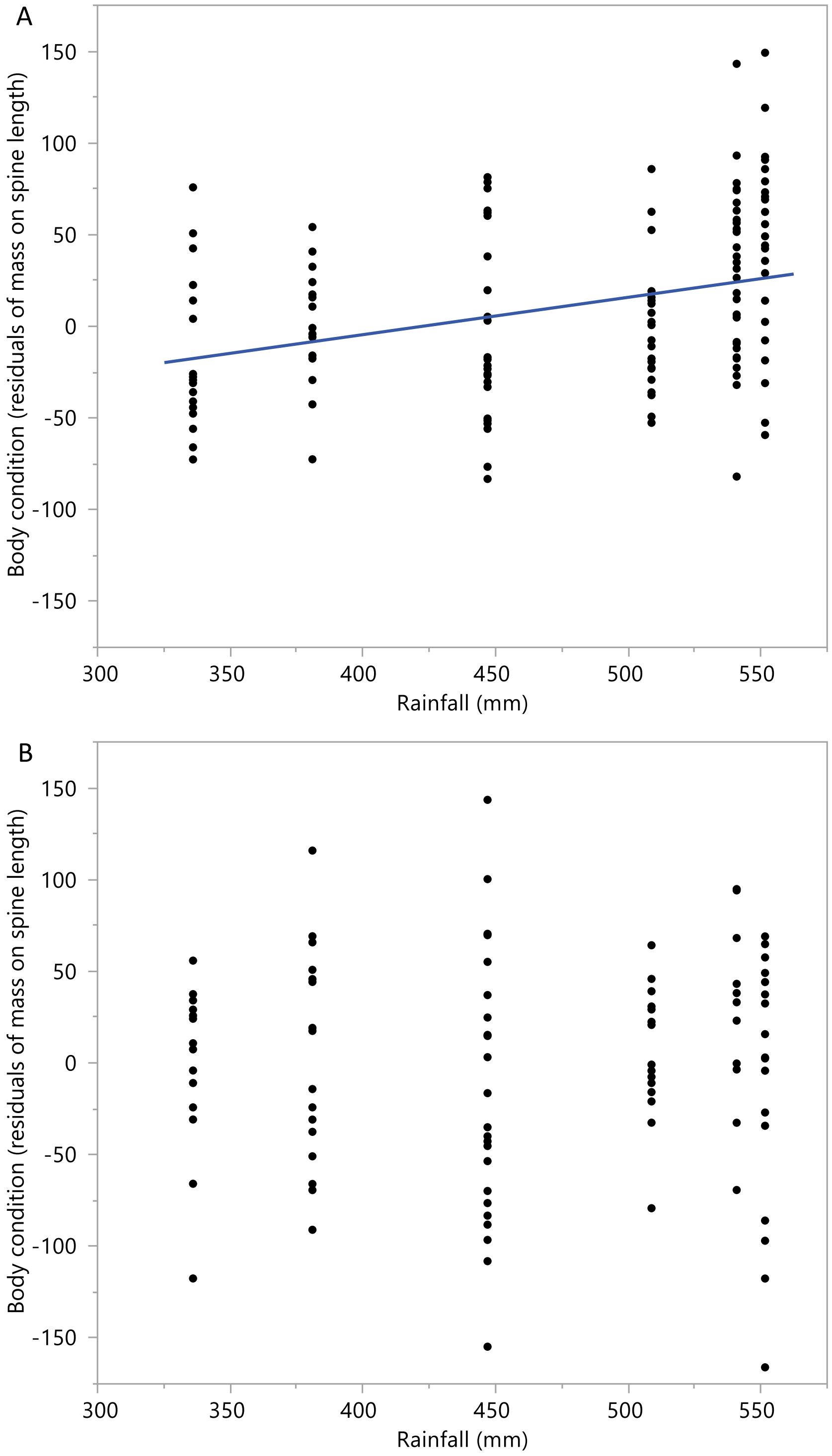
2014/15
2015/16
2016/17
Year


A
Body condition (residuals of mass on spine length)
150
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-50
-100
-150
300
350
400
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500
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Rainfall (mm)
B
Body condition (residuals of mass on spine length)
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-50
-100
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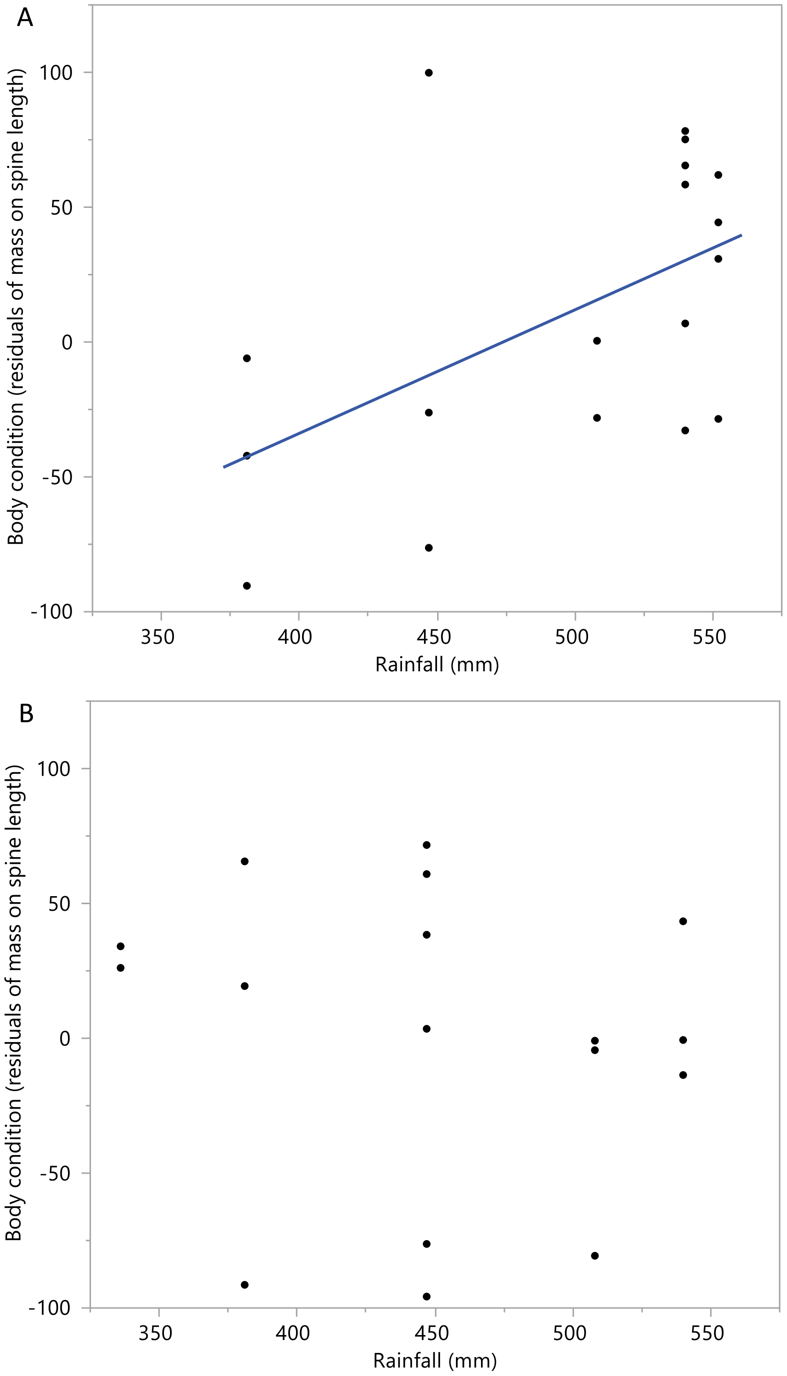
Rainfall (mm)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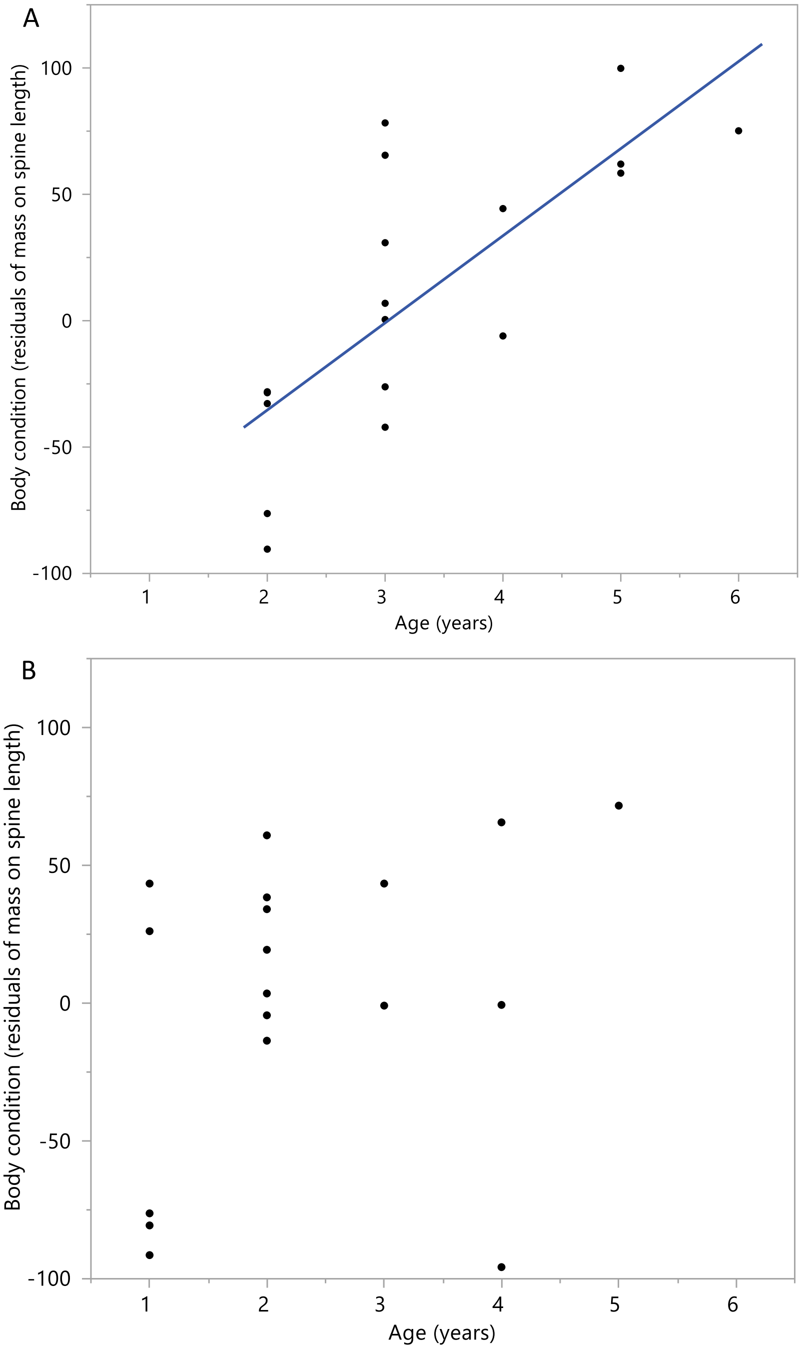
A
Body condition (residuals of mass on spine length)
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-100
1
2
3
4
5
6
Age (years)
B
Body condition (residuals of mass on spine length)
100
50
0
-50
-100
1
2
3
4
5
6
Age (years)