Size matters:

Host body mass overshadows climate change in parasite prevalence among semi-arid ground squirrels (*Xerus inauris*)

by

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Abstract

Climate change is a phenomenon in which global temperatures are rising, and animals respond by undergoing thermal stress, which may be linked to increased susceptibility to ectoparasites. Environmental temperature greatly influences ectoparasites as they rely on external heat sources to regulate their body temperature. This study investigated the effects of increasing maximum and minimum temperatures on ectoparasites abundance (number of parasites on an individual) and prevalence (number of infected individuals) of adult female African Cape ground squirrels (*Xerus inauris*). This study also investigated the effects of host body mass and host body condition on ectoparasite abundance and prevalence. We did not find a relationship between rising temperatures and ectoparasite loads (abundance and prevalence), nor did we find a relationship between body condition and ectoparasite loads. We speculate that the thermoregulatory behaviours of Cape ground squirrels mitigate ectoparasite loads. We did not find evidence for a relationship between host body mass and abundance; however, we found a significant negative relationship between host body mass and parasite prevalence. Our results show that a higher proportion of individuals are infected with fleas compared to lice. It remains uncertain whether the inverse relationship between host body mass and prevalence is due to increased skin strength or other traits in larger individuals. The different life history traits of the parasites could explain why fleas are more prevalent than lice. Fleas, being facultative parasites, can avoid the grooming behaviour of hosts. In contrast, lice, being obligate parasites, are bound to remain on their host, thus, are more vulnerable to being removed. As climate change persists, the host-parasite relationship between Cape ground squirrels and ectoparasites may be worth revisiting.

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Introduction

Climate change is estimated to have caused the extinction of 15-37% of Earth's free-living species and has negatively affected the survival and reproduction of many animal populations (Thomas et al. 2004). The effects on the demographics of animals are associated with the physiological stress of temperature extremes as a result of decreased resource availability (Sinervo et al. 2010). It is estimated that for free-living species, shifts in climate suitability will decrease the size of occupied ranges and may lead to extinction (Parmesan and Yohe 2003). Furthermore, increases in thermal stress among animals have been linked to increased susceptibility to fatal infections, and the spread of micro- and macro-parasites among interacting species may rise due to severe droughts or other changes (Munson et al. 2008; Randall & Van Woesik 2015). Parasites, however, are also likely to shift with climate suitability among species, but they may not necessarily increase or decrease (Lafferty 2009).

Ectoparasites are external macroparasites that exert multiple effects on their host such as raising an immune response to infection and causing direct tissue damage by feeding on the external surface of their hosts (Delahay et al. 1995). Additionally, infections due to climate change may be more prevalent among animals living in social groups (Paniw et al. 2022). Animals that live in social groups can improve the survival and reproductive success of group members and divert the negative outcomes of climate change on resource availability through resource sharing and efficient foraging (Groenewoud & Clutton-Brock 2020). However, sociality may accelerate the rate of infection by ectoparasites as with an increase in group size, more individuals may carry parasites into the group augmenting overall parasite transmission (Hoogland and Sherman

1976; Hoogland 1995). Ectoparasite transmission may be mitigated, however, if the social animals partake in behavioural strategies such as autogrooming (self-grooming) and allogrooming (grooming another individual; Hawlena et al. 2006). Allogrooming can serve many functions in addition to being antiparasitic, such as parental and nepotistic functions, and influence bonding within social groups (Schino 2001). Grooming, however, may deplete energy reserves and diminish time for other behaviours; therefore, hosts must mitigate the costs and benefits of grooming with the costs of ectoparasites (Mooring et al. 2004).

Ectoparasites are influenced by many intrinsic and extrinsic factors, such as changes in environmental conditions (Studer et al. 2010). Changing environmental conditions such as global warming and its effects on insect-borne infections are likely to be greatest in areas affected by increases in average temperatures (Massad et al. 2011). Increasing temperatures can influence the rate of emergence of cercariae (larval endoparasites) in amphipods and increase the production of new cercariae (Studer et al. 2010). Similarly, parasite prevalence (number of infected individuals) was positively associated with temperature in avian hosts (Holand et al. 2019). Host attributes such as body mass are another factor that influences parasite and host interactions. In Yarrow Spiny Lizards (*Sceloporus jarrovii*) a strong positive relationship between body size and parasites has been found, and body size was the primary cause for increased ectoparasite and endoparasite loads in both males and females (Halliday et al. 2014). Furthermore, as body mass is a good indicator of body condition, a decrease in body mass may be indicative of increased parasite loads among animals living in social groups (Wauters & Dhondt 1989; Hillegass et al. 2010). In kangaroo rats (*Dipodomys merriami*), animals infected with endoparasites had lower body condition (Hurtado et al. 2021). The infection of kangaroo rats may have been caused by chronic immune stress, which in turn reduces body condition (Hurtado et al. 2021).

Cape ground squirrels (*Xerus inauris*) are a highly social species of squirrel residing in the arid regions of southern Africa, areas that have variable levels of precipitation (Herzig-Straschil 1979; Skurski & Waterman 2005). Evidence suggests that these ground squirrels are responding to climate change (increasing temperatures) by decreases in body size (spine length) and increases in foot size, responses attributed to Bergmann's and Allen's rules (Warrington and Waterman, 2022). The shape-shifting phenomenon of these animals broadens the scope of inquiry towards other factors that may be influenced by climate change, such as ectoparasites. Cape ground squirrels are an excellent species to examine changes in ectoparasite infections regarding climate change as subsampling techniques can be applied to standardize the estimation process by decreasing the surface area that is examined (Beaumont et al. 2019). Parasitized female Cape ground squirrels have reduced body fat, lower resting metabolic rates, and fewer offspring than parasite-free females (Hillegass et al. 2008; Scantlebury et al. 2007). Additionally, as female Cape ground squirrels do not form dominance hierarchies, allogrooming functions solely to control ectoparasites and it is not related to social cues or dominance (Waterman 1996; Hillegass et al. 2008, 2010). This latter finding may explain why social group size and ectoparasite abundance (number of parasites on an individual) are not related in this species (Hillegass et al. 2008).

The abundance of parasites may not only be affected by ambient temperature but also by the temperature of the burrows that Cape ground squirrels reside in (Herziig-

Straschil 1979). As Cape ground squirrels are strictly diurnal, nights are spent within burrows, and these burrows usually consist of networks of tunnels and chambers approximately 60-70 cm below the ground level (Herziig-Straschil 1979). These burrows experience small temperature fluctuations when compared to ambient temperatures at the surface at different times of the year, providing a homeostatic environment within the burrows (Herziig-Straschil 1979). For instance, throughout July/August, the ambient temperature fluctuates from minus 7.5 °C to more than 26 °C, meanwhile, temperatures inside the burrow vary from 12.5 °C to 15 °C (Herzig-Straschil 1979). Additionally, the temperature may be higher inside the burrow when more than one individual stay together as the overall surface area of the animal exposed is reduced (Herziig-Straschil 1979; Scantlebury et al. 2012). As the burrows that the squirrels reside in act as a buffer towards colder temperatures, the change in parasite abundance and prevalence (number of infected individuals in the population) related to ambient temperature change may not be as significant (Medvedev and Krasnov 2006). However, as the life history traits of fleas and lice differ, the buffering effect of the burrows may impact various parasite types differently (Medvedev and Krasnov 2006).

The objective of my study is to examine if climate change has influenced parasite infections in Cape ground squirrels over the past nine years. I first hypothesize if temperatures influence ectoparasite loads, then over the last nine years, we predict an increase in ectoparasite loads in adult female Cape ground squirrels (Table 1; Paniw et al. 2022). However, if a rise in temperature leads to smaller body sizes over time, and the surface area of an animal is the most important factor determining parasite loads, then the reduction in body size in female Cape ground squirrels will result in reduced ectoparasite loads (Table 1; Halliday et al. 2014). Finally, I hypothesize that if increased temperatures are negatively affecting resources, which would lead to a lower-body condition in hosts, we predict that ectoparasite loads among female Cape ground squirrels would increase with lower body condition, which is related to reduced investment in immunity (Table 1; Sun et al. 2015; O’Brien et al. 2021).

Table 1. Hypotheses and predictions following the changes of ectoparasite loads on female Cape Ground Squirrels (*Xerus inauris*) dependent on temperature, body size and body condition.

Hypothesis	**Predictions**	**Predictions over time due to climate change**
Increasing temperatures (max/min) over time impacts parasites	Positive relationship between temperature and parasites	Increase in ectoparasites over time
Body size of host affects parasite infections	Positive relationship between body size and parasites	Decline in ectoparasites over time
Body condition of host affects parasite abundance	Negative relationship between body condition and parasites	Increase in ectoparasites over time

Methods

Study Site

Fieldwork has been conducted at a study site located in the semi-arid environment of the S. A. Lombard Nature Reserve, 18 km Northwest of Bloemhof, South Africa (27°35'S, 25°35'E) from the years 2002 to 2022, excluding the years 2008 to 2010 and 2020 (Waterman 1995; Scantelbury et al. 2007). The reserve is 3,660 ha in size and consists of Kalahari grassland and *Cymbopogon-Themeda* veld on a floodplain (Van Zyl 1965; Pettitt & Waterman 2011). The study site receives an average annual rainfall of 500 mm which is primarily confined to the period of November to April (Pettitt et al. 2008).

Biology of the study animal

Cape ground squirrels are diurnal non-hibernating rodents that live in the arid regions of southern Africa and display high levels of sociality resulting in a high potential for parasite transmission (Waterman 1995; Hillegass et al. 2008; Pettitt & Waterman 2011). Females live in family groups of 1-5 related adult females and up to nine subadults of either sex and share a communal sleeping burrow (Waterman 1995; Hillegass et al. 2008). The communal sleeping burrows may allow external parasites to transfer from one individual to another through direct contact (Waterman 1995; Altizer et al. 2003).

Cape ground squirrels tolerate chronic levels of external ectoparasites (Straschil 1975; Waterman 2002). The documented ectoparasites of Cape ground squirrels include fleas such as *Ctenocephallas onatus, Echidniphaga bradyta, Echidniphaga gallinacean* and *Synosternus caffer*; lice such as *Neohaematopinus faure* (Straschil 1975) and ticks such as *Rhipicephalus theileri* (Waterman 2002). Lice are true parasites and are obligate, permanent parasites of specific mammalian hosts, inhabiting their hosts' fur (Kim 2006).

Lice are characterized as wingless insects that have complex piercing-sucking mouthparts (Kim 2006). Additionally, the lives of lice depend completely on the circumstance of their mammalian hosts (Kim 2006). Once lice are established on the host animal, they will carry out their lives from one generation to the next until the host animal's life has ended (Kim 2006).

Fleas represent a small order of wingless holometabolous insects (Medvedev and Krasnov 2006), and 70 % of flea-mammal associations involve rodents (Medvedev and Krasnov 2006). Fleas are adapted not only to a host's body but the microclimatic conditions of its burrow (Medvedev and Krasnov 2006). Unlike lice, fleas are not obligate parasites (facultative) on mammalian hosts and usually reside in a host's burrow (Medvedev and Krasnov 2006). Female fleas (of some species) oviposit on the host, and the eggs subsequently fall off into the burrow (Medvedev and Krasnov 2006). Flea eggs residing in the burrow are vital as it has been documented that larvae and pupae cannot withstand air temperatures exceeding 35°C (Silverman et al. 1981; Silverman and Rust 1983). As heat loads imposed on Cape ground squirrels can exceed 40°C, flea eggs, larvae and pupae would not survive outside the burrow (Bennett et al. 1984; Silverman et al. 1981; Silverman and Rust 1983). Additionally, fleas' survival and reproduction depend on many factors, including desired climatic conditions for development and the seasonal changes in their life history parameters (abundance and reproduction rate; Medvedev and Krasnov 2006).

Trapping and handling

Cape ground squirrels were trapped using live traps (Tomahawk Live Trap Inc., WI, USA; 15X15X50 cm) following the long-term protocols described in Hillegass et al.

(2008). We baited the Tomahawk live traps with a combination of bird seed and peanut butter, and we placed them out from 6:30 to 17:30 daily. We repositioned the traps approximately every 1.5 hours to ensure that the plastic covers of the Tomahawk live traps provided perpetual shade to the squirrels (Waterman 1995). Once the squirrels were captured, they were transferred from the trap to a cone-shaped handling bag that kept them immobile and permitted access to different parts of the body (Koprowski 2002). We measured body mass (±5.0 g) using Pesola spring scales (Pesola AG, Baar, Switzerland; O'Brien et al. 2018) and measured spine length from the occipital condyles to the base of the caudal vertebrae using a tape measure (Manjerovic & Waterman 2012). We also measured the length of the right hindfoot from the base of the foot to the tip of the middle toe using digital calipers (Mitutoyo Inc., Tokyo, Japan; Warrington & Waterman, 2022). We marked the squirrels with passive integrated transponder (PIT) tags (AVID USA and Shenzhen XCC RFID Technology Co., Ltd. China) for permanent identification (Warrington & Waterman, 2022). We freeze marked (Freeze Spray, CRC Industries Inc., USA; Rood and Nellis 1980) male Cape ground squirrels, and both sexes were temporarily marked with black hair dye on the dorsal region for identification from a distance (Rodol D, Lowenstein & Sons Inc., New York, NY, USA; Scantlebury et al. 2007; Hillegass et al. 2008). All animals were released at their site of capture. Squirrels were re-measured periodically upon re-capture (Phillips and Waterman 2014). I trapped, handled, and measured squirrels in 2022 to increase our long-term dataset.

The age of sexual maturity in female Cape Ground squirrels was defined as the first estrus determined through a series of behavioural, hormonal, and morphological data (Pettitt and Waterman 2011). After first estrus (sexual maturity) female nipples swell and remain permanently elongated (Waterman 1996). Behaviours regarding the day of estrus including increased male activity such as sniffing, chasing, and copulating with estrous females were indicative of sexual maturity (Pettitt and Waterman 2011). If estrous behaviours were not observed, maternal isolation (parturition) and juvenile emergence were backdated using a growth curve (Pettitt and Waterman 2011). Body mass, nipple length, and vulva characteristics can be used in the absence of hormonal and behavioural data to determine if females are adults (i.e., reproductive; Waterman 1996; Pettitt and Waterman 2011). In this study, we only included adult females to control for size differences between subadults and full-grown adults (Waterman 1996). Male Cape ground squirrels have been removed from the analysis for simplification as males differentiate into two groups (natal and band males; Waterman 1995) and would require proper placement into either category, whereas females remain in one group. Previous studies have found that the body condition of dispersed males is affected by rainfall, but the body condition of non-dispersed males is not (O'Brien et al. 2021), thereby complicating the analysis as rainfall would have to be considered. Pregnant female Cape ground squirrels were also removed to reduce outliers when running a linear regression of body mass on spine length. As pregnant females are more likely to have increased mass, and different hormone levels from non-pregnant females, they may skew the data if included in the analysis (Shofstall, unpublished data).

Ectoparasite abundance of squirrels was estimated by combing three regions of the dorsal area (two lateral and a medial plane) with a metal flea comb from shoulders to tail base; and combing each plane three times (Scantelbury et al. 2007; Hillegass et al. 2008). Additionally, the groin and inner thigh area of the squirrels were also examined for ectoparasites (Beaumont et al. 2019). Ectoparasites combed off the squirrels were placed directly into a dish containing 95% ethanol, counted, and recorded for further analysis (Scantlebury et al. 2007). All trapping and handling were in accordance with the University of Manitoba Animal Care Committee (Protocol #F18-039).

Statistical Analysis

All statistical analyses were performed using R Studio Desktop (Version 4.2.1), and an alpha value of 0.05 was used to indicate significance. Models that had an R^2 value less than 0.30 and a p-value < 0.05 were considered significantly weak and classified as not affecting the tested variables (Moore and Kirkland 2007). The estimated value was used to determine the direction of the model. All N/A's were removed from the dataset to avoid analyzing squirrels that were not counted for parasites. N/A's refer to individuals that were not checked for ectoparasites, and represented as blanks in the dataset. Removing N/A's was crucial as R Studio reads N/A's as zeros, however, the number zero represents a squirrel where parasites were counted, but none were found. Ectoparasites were quantified by using the measures of abundance and prevalence. Abundance measures the number of parasites on a host, whereas prevalence measures the proportion of hosts infected (Bush et al. 1997; Clay et al. 2018). Daily maximum and minimum temperatures (°C) were recorded from thermometers located on-site. The effects of temperature on parasite abundance and prevalence were evaluated from the years 2012 to 2019, and 2021. The effects of mass on parasite abundance and prevalence were also evaluated from the years 2012 to 2019, and 2021. Daily maximum and minimum temperatures were averaged for each year to represent the average temperature for each season. The average annual maximum and minimum temperatures were then evaluated for each tested variable. Statistical analyses of body condition measurements (spine length and body mass) from the years 2012 to 2019, and 2021 were performed by using an ordinary least squares regression. For an individual squirrel, all mass measurements were used to represent day-to-day variation, and spine length was averaged for one season to account for human error in a trapping season. Once an ordinary least squares regression was performed, body condition was averaged to represent how a female squirrel varies with each season. The package dplyr was used to manipulate the data and add the calculated average body condition values to the pre-existing dataset. The residuals from an ordinary least squares regression (measure of body condition) were then evaluated with parasite abundance using the glmmTMB package from the years 2012 to 2019, and 2021 and included individual tag number as a random effect. Residuals above zero represented above average body condition, and residuals below zero represented below average body condition from the years 2012 to 2019, and 2021. Models evaluated using a GLMM, required the package MumIn to extract the R^2 value. From there, the conditional R^2 value was used to determine the goodness of fit for each model tested using a GLMM.

Total ectoparasite abundance was calculated by combining the number of collected parasites observed in each category (ectoparasites seen and collected), including fleas and lice on a squirrel. To test the temperature effect hypothesis (H1), the body size effect hypothesis (H2) and the body condition hypothesis (H3), I used a negative binomial distribution using the glmmTMB package. Models for the temperature effect hypothesis (H1), the body size effect hypothesis (H2) and the body condition effect hypothesis (H3) were checked for normality using a normal quantile-quantile plot using the DHARMa package. Additionally, models for the temperature effect hypothesis (H1) were also checked by using a Levene Test for homogeneity of variance also using the DHARMa package.

The measure of ectoparasite prevalence (proportion of infected individuals) required differentiating individuals into two categories: infected and non-infected. In the dataset, individuals that had an abundance greater than one were classified as infected, and denoted with the number “1”, whereas individuals that had an abundance of zero were non-infected and denoted with the number “0”. From there, the number of infected individuals were compared to the total amount of individuals tested to provide a proportion of individuals infected for each year, mass range and average body condition. For prevalence data, the temperature effect hypothesis (H1) was evaluated using the annual proportion of infected individuals and the average annual maximum temperature. For the body size effect hypothesis (H2), the relative proportion of infected individuals within a given mass range was tested for significance by using an ANOVA test. For the body condition effect hypothesis (H3), average body condition and infected/non-infected individuals was also tested for significance by using an ANOVA test. Prevalence was then plotted using ggplot2 for the temperature effect hypothesis (H1), the body size effect hypothesis (H2) and the body condition effect hypothesis (H3).

Results

A total of 1256 adult female Cape ground squirrels were included in the analysis from 2012 to 2019, and 2021, with the annual total number of individuals per year as followed: 2012 (n = 111), 2013 (n = 66), 2014 (n = 46), 2015 (n = 128), 2016 (n = 63), 2017 (n = 63), 2018 (n = 193), 2019 (n = 365) and 2021 (n = 221). The average abundance of ectoparasites per female Cape ground squirrel was 2.15 ± 0.12, with an average abundance of fleas per squirrel of 1.52 ± 0.08, and an average abundance of lice per squirrel of 0.62 ± 0.08. The proportion of individuals that were infected by parasites from 2012 to 2019, and 2021 was 0.62.

When testing H1, ectoparasite abundance was not related to average annual maximum or minimum temperature (Table 2). We tested flea and lice abundance separately with average annual maximum and minimum temperatures and found that flea abundances was not related to either average annual maximum or minimum temperature (Table 2). Lice and both average annual maximum and minimum temperature were not related (Table. 2). Ectoparasite abundance has not increased over the past nine years (Table 2). Flea and lice abundance separately did not change over the past nine years (Table. 2).

Ectoparasite prevalence and average annual maximum temperature, as well as average annual minimum temperature, were evaluated using a linear model (Figs. 1-2). Ectoparasite prevalence over time (annually) was also evaluated using a linear model (Fig.3). Ectoparasite prevalence and average annual maximum temperature were not related (Table 2). Similarly, ectoparasite prevalence and average annual minimum temperature were not significantly related (Table 2). Lastly, ectoparasite prevalence did not change over time (Table 2).

Ectoparasite abundance and host body mass were not related (Table 2). Flea and lice abundance were not related to host body mass (Table 2). Ectoparasite prevalence and host body mass were negatively related (Fig.4; Table 2). Flea and lice prevalence were negatively related to host body mass (Fig.4; Table 2). Ectoparasite abundance and host body condition were not related (Table 2). Flea and lice abundance were not related to host body condition (Table 2). Ectoparasite prevalence between the body condition of infected and non-infected individuals were not significant (Fig.5; Table 2).

Table 2. Hypotheses and all variables tested with associated standard error, R^2, F Values and P-Values. An asterisk denotes an alpha of ≤ 0.05.

Hypothesis	**Variables Tested**	F Value	Estimate	**SE ±**	R^2	**P-Value**
H1	Abundance + Average Maximum Temperature		0.0196	0.01	0.13	0.0983
	Abundance + Average Minimum Temperature		0.0382	0.02	0.13	*0.0326
	Fleas + Average Maximum Temperature		0.0279	0.01	0.12	*0.0249
	Lice + Average Maximum Temperature		-0.0241	0.03	0.13	0.375
	Fleas + Average Minimum Temperature		0.0902	0.02	0.05	*0.0001
	Lice + Average Minimum Temperature		-0.1425	0.04	0.07	*0.0003
	Abundance + Year		0.0338	0.02	0.13	*0.0398
	Fleas + Year		0.0534	0.02	0.13	*0.0025
	Lice + Year		-0.0333	0.03	0.06	0.332
	Prevalence + Average Maximum Temperature		0.0011	0.01	0.00	0.9407
	Prevalence + Average Minimum Temperature		-0.0012	0.01	0.00	0.9528
	Prevalence + Year		-0.0058	0.02	0.01	0.7607
H2	Abundance + Mass		-0.0047	0.00	0.15	*0.0001
	Abundance (Fleas) + Mass		-0.0036	0.00	0.13	*0.0001
	Abundance (Lice) + Mass		-0.0071	0.00	0.08	*0.0001
	Prevalence + Mass	23.14	-0.0008	0.00	0.85	*0.0171
	Prevalence (Fleas) + Mass	21.44	-0.0005	0.00	0.84	0.0189
	Prevalence (Lice) + Mass	33.01	-0.0009	0.00	0.89	*0.0105
H3	Abundance + Body Condition		-1.5852	0.61	0.13	*0.0090
	Abundance (Fleas) + Body Condition		-1.6904	0.67	0.12	*0.0117
	Abundance (Lice) + Body Condition		-0.9429	1.14	0.05	0.408
	Prevalence + Body Condition	5.981	-0.4328	0.18	0.00	*0.0146

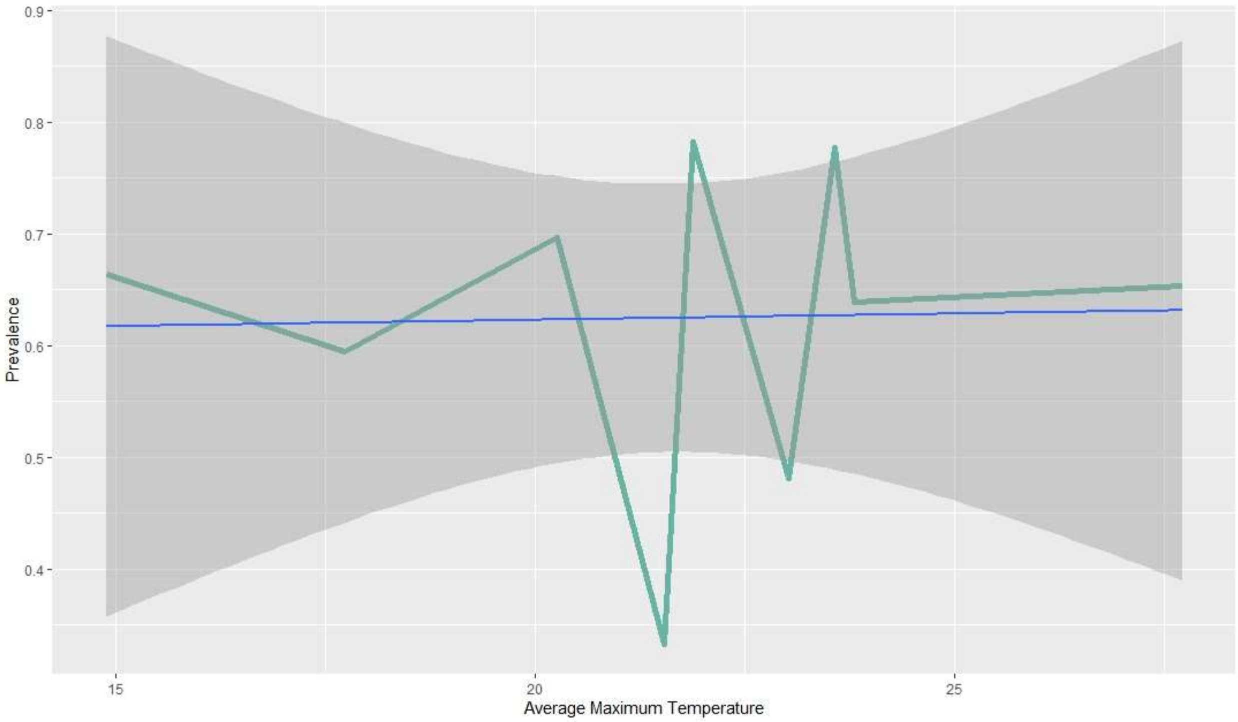

Figure 1. Total ectoparasite prevalence (flea and lice) and average maximum temperature (°C) of female Cape Ground Squirrels (*Xerus inauris*) from the years 2012 to 2019, and 2021. A linear model was used to test the two variables. The green line represents the changes in prevalence with average maximum temperature, whereas the blueline shows the overall direction of prevalence as a result of average maximum temperature.

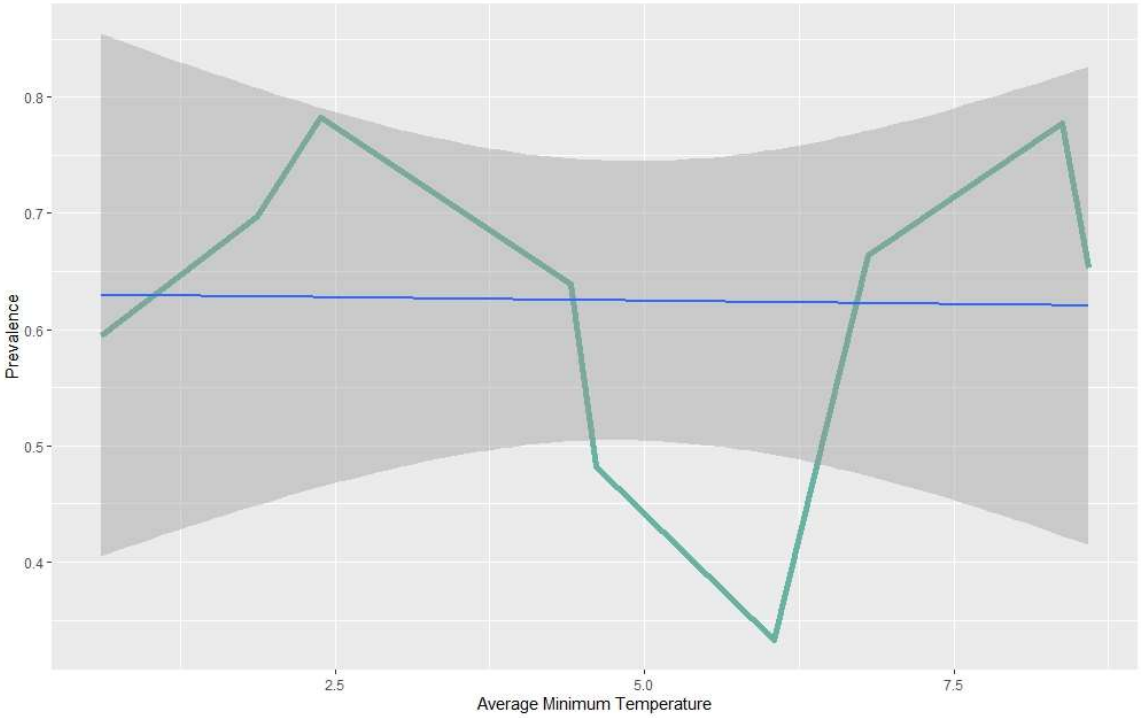

Figure 2. Total ectoparasite prevalence (flea and lice) and average minimum temperature (°C) of female Cape Ground Squirrels (*Xerus inauris*) from the years 2012 to 2019, and 2021. A linear model was used to test the two variables. The green line represents the changes in prevalence with average minimum temperature, whereas the blueline shows the overall direction of prevalence as a result of average minimum temperature.

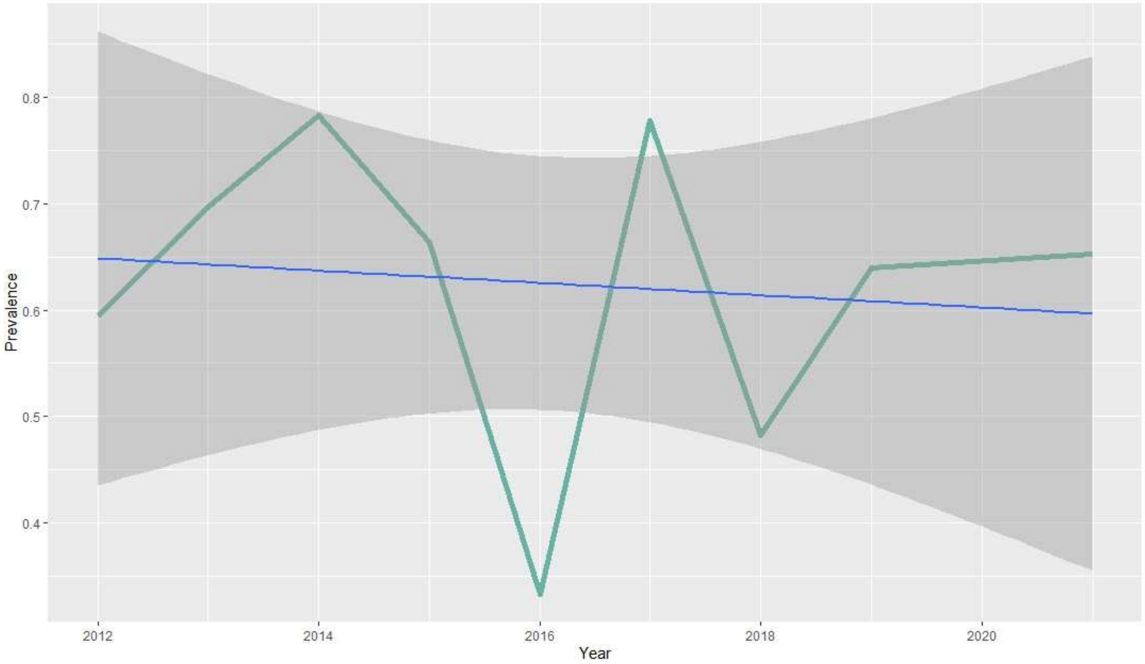

Figure 3. Total ectoparasite prevalence (flea and lice) and year of female Cape Ground Squirrels (*Xerus inauris*) from the years 2012 to 2019, and 2021. A linear model was used to test the two variables. The green line represents the changes in prevalence over time, whereas the blueline shows the overall direction of prevalence overtime.

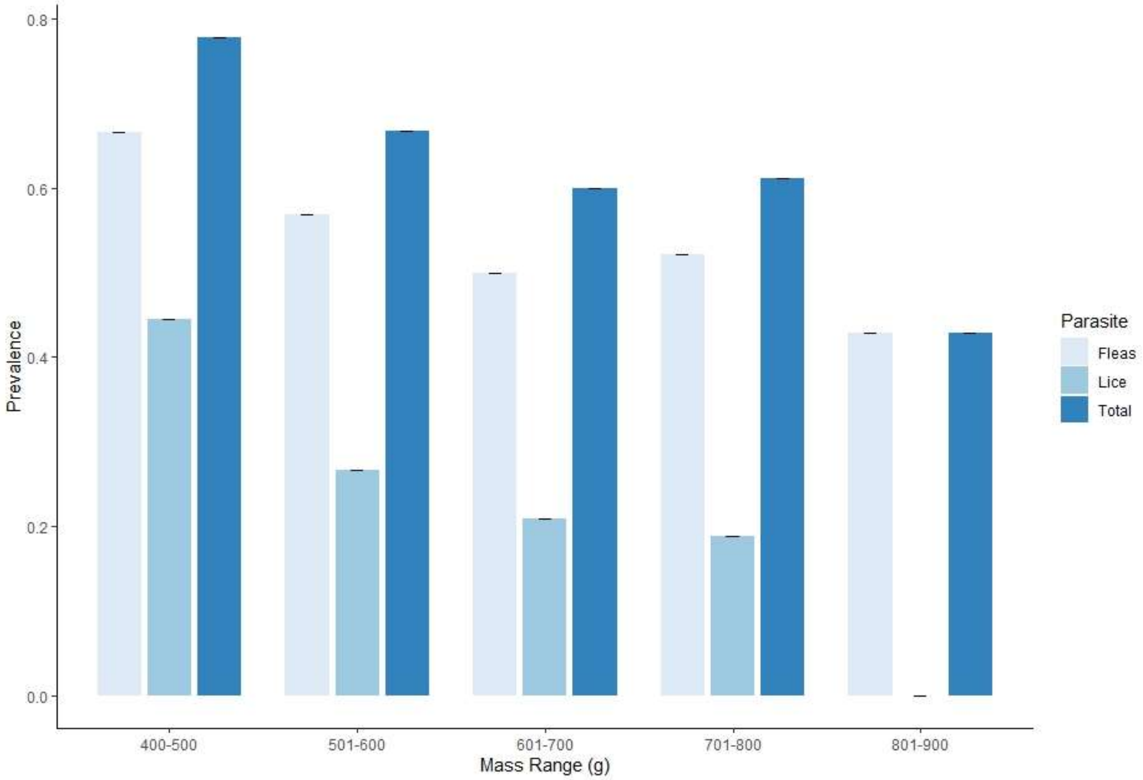

Figure 4. Parasite prevalence (total, flea, and lice) as a function of mass (g) of female Cape Ground Squirrels (*Xerus inauris*) from the years 2012 to 2019, and 2021. Total ectoparasite prevalence of infected individuals per body mass category is as follows: 400-500 (n = 6), 501-600 (n = 213), 601-700 (n = 450), 701-800 (n = 101), 801-900 (n = 3). Flea prevalence of infected individuals is as followed: 400-500 (n = 6), 501-600 (n = 182), 601-700 (n = 374), 701-800 (n = 86), 801-900 (n = 3). Lice prevalence of infected individuals is as followed: 401-500 (n = 4), 501-600 (n = 85), 601-700 (n = 157), 701-800 (n = 31), 801-900 (n = 0). An ANOVA was used to test the prevalence of total ectoparasites (fleas and lice), as well as fleas and lice separately. Total ectoparasites prevalence ($F_{1,3}$), flea prevalence ($F_{1,3}$), lice prevalence ($F_{1,3}$).

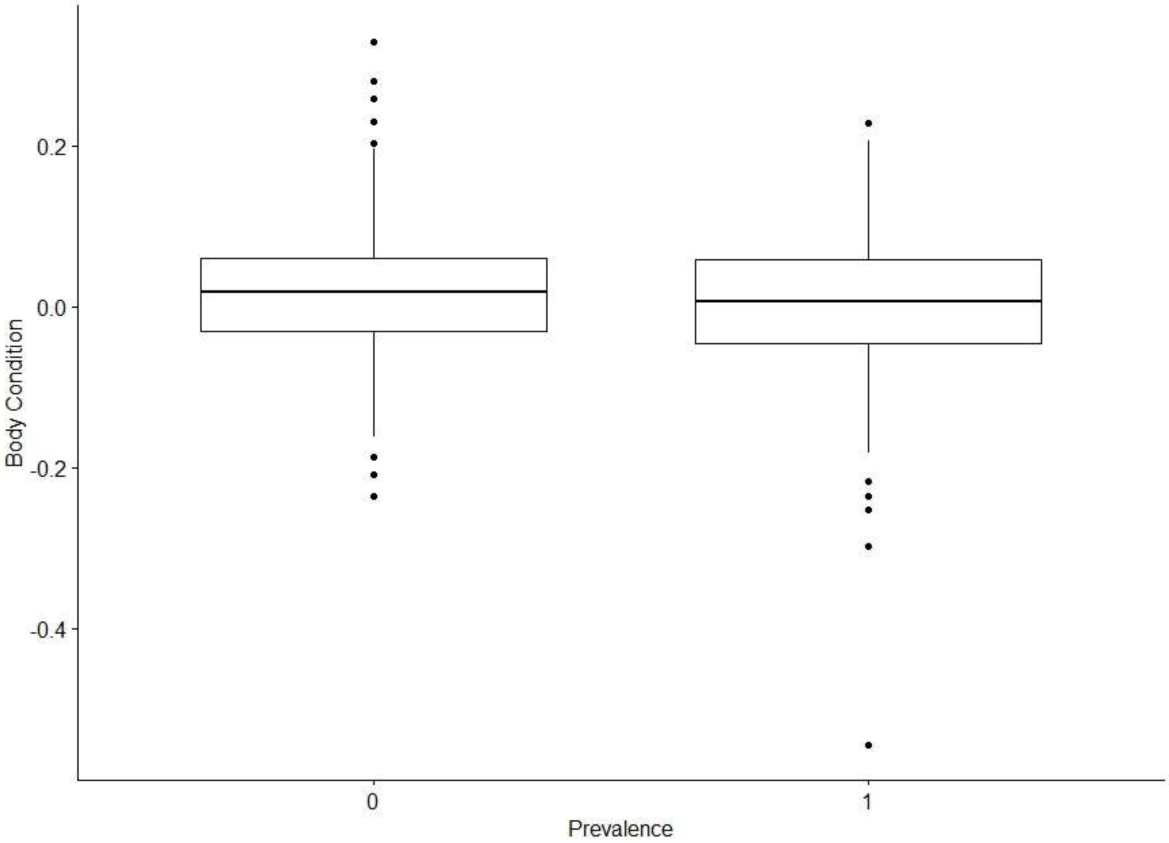

Figure 5. Prevalence and body condition of female Cape Ground Squirrels (*Xerus inauris*) from the years 2012 to 2019, and 2021. ($F_{1,1254}$). An ANOVA was used to test the difference in body condition between infected and non-infected individuals. The number zero represents non-infected individuals, whereas the number one represents infected individuals.

Discussion

Temperature effect hypothesis (H1)

Daily maximum and minimum temperature increase at the study site have been investigated with the shape-shifting phenomena of Cape ground squirrels (changes in morphology; Warrington and Waterman 2022). As ectoparasites are ectotherms and are dependent on external sources such as heat, we predicted that ectoparasite abundance and prevalence would also rise with increasing temperatures (Gehman et al. 2022). Studies have found similar relationships, such as the increased parasite abundance of cercariae with rising temperatures in amphipods (Studer et al. 2010). However, we did not find a relationship between rising temperatures (average annual maximum/minimum temperature) and ectoparasite abundance or prevalence. We also predicted that ectoparasite abundance and prevalence would increase over time (9 years) and did not find support for this prediction either. One possible explanation for the lack of a relationship between rising temperature and parasite loads (prevalence and abundance) is that hosts use their tails as parasols to regulate their body temperature (Bennett et al. 1984). As such, the tail of Cape ground squirrels provides shade to their bodies and reduces heat loads by an average of 5.6 °C (Bennett et al. 1984). Therefore, as tails serve as a means of thermoregulation for hosts, it is possible that they also function as a mechanism of thermoregulation for ectoparasites residing on hosts (Bennett et al. 1984). Tails could potentially reduce the heat load experienced by ectoparasites, thereby mitigating the effects of rising temperatures (Bennett et al. 1984). Another explanation could be that hosts might seek refuge underground to protect themselves from high daytime temperatures (Bolwig 1958). Furthermore, Cape ground squirrels forage actively throughout the day during the winter and seek refuge in their burrows when temperatures are high during the summer (Bolwig 1958; Herzig-Straschil 1979). As temperatures increase at the study site, Cape ground squirrels may seek refuge from rising temperatures in the winter to reduce heat loads, thus, alleviating the effect that temperature may have on ectoparasite loads (Bolwig 1958; Warrington and Waterman 2022).

Interestingly, a study that investigated the effects of temperature on Prairie dog (*Cynomys ludovicianus*) flea development found that flea development rate was strongly related to burrow temperature (Samuel et al. 2022). As such, the study modeled future trends that showed increasing ambient temperatures, could raise burrow temperatures, and shorten flea development time (Samuel et al. 2022). This finding could correspond to the burrow temperatures of Cape ground squirrels, such that as temperatures increase, burrow temperatures may also rise, causing flea development time to shorten and lead to higher parasite loads (abundance and prevalence; Samuel et al. 2022). As of current, our results show that the temperature effect hypothesis (H1) regarding the increase in ectoparasite loads (abundance and prevalence) with rising temperatures does not have support, suggesting that the current thermoregulatory behaviours of female Cape ground squirrels mitigate parasite loads.

Body size effect hypothesis (H2)

The relationship between host mass and parasite abundance is a commonly observed phenomenon. This phenomenon was confirmed by a study that analyzed parasite biomass and host mass across 131 species of vertebrates, which revealed a positive relationship between parasite biomass and host mass (Poulin and George-Nascimento 2007). As such, we predicted that there would be a positive relationship between both parasite abundance and prevalence concerning host body mass. Our results showed that body size (mass) did not affect parasite abundance. Although, we found a strong negative relationship between host body mass and parasite prevalence and discovered that fleas infect a higher proportion of hosts than lice. In turn, these findings produce the opposite effect of what was predicted for the body size hypothesis (H2). According to prior research, we already know that parasitized female Cape ground squirrels have reduced body fat when compared to parasite-free females (Scantlebury et al. 2007; Hillegass et al. 2008).

Additionally, previous studies on Cape ground squirrels found autogrooming and allogrooming decreased or almost stopped in the absence of parasites, suggesting that grooming behaviours may only function to control parasites and not for social dominance or other social reasons (Hillegass et al. 2008). Lice are true parasites (obligate) and remain on the host, whereas fleas are facultative parasites (occasionally living off the host); the two different life history traits could play a factor in how the two species respond to grooming behaviours (Medvedev and Krasnov 2006; Hillegass et al. 2008). As fleas occasionally live off the host, fleas may avoid some of the grooming behaviors of Cape ground squirrels (Medvedev and Krasnov 2006; Hillegass et al. 2008). This avoidance by fleas can be contrasted with lice that remain on the host and would have increased difficulty avoiding their grooming behaviours (Medvedev and Krasnov 2006; Hillegass et al. 2008). Furthermore, fleas have anatomical characteristics that enable them to cling to the hair of mammalian hosts, thereby withstanding the host’s attempts to groom them (Medvedev and Krasnov 2006). Perhaps, autogrooming and allogrooming effectively prevent higher proportions of infection of obligate parasites (lice) but ineffectively prevent higher proportions of infection of facultative parasites.

Contrary to the previous results (host body mass and parasite prevalence), when intermediate mass ranges (501-600, 601-700, 701-800) were compared to one another, host body mass did not affect parasite prevalence. The lack of individuals in the smaller mass range (401-500, n = 9) and the larger mass range (801-900, n = 7) skews the data due to the small sample sizes and disproportionately large and small proportions. Additionally, upon further investigation, within the smaller host mass range (401-500, n = 9), we found one lactating (not pregnant) individual that had shown a reduction in mass. As lactating females are in isolation (Waterman 1996), they are not allogroomed by other females and are more likely to have parasites (Waterman 2002; Hillegass et al. 2008). Nonetheless, the negative relationship between body mass and prevalence can also be reasoned by the fact that as animals grow older, the tensile strength of their skin tends to increase, as seen in a study that compared the collagen and tensile strength of juvenile and adult rabbits (*Oryctolagus cuniculus*; Marcel et al. 1966). As Cape ground squirrels tend to progressively gain weight as they mature (Shofstall, unpublished data), it is possible that heavier squirrels are also older in age. This possibility suggests that with older age and stronger skin ectoparasites would have increased difficulty breaking through their hosts' skin, thus reducing ectoparasite prevalence (Owen et al. 2009).

Body condition effect hypothesis (H3)

Studies have found strong negative relationships between ectoparasite abundance and body condition such as one that investigated the relationship in Galápagos Hawks (*Buteo galapagoensis*; Whiteman and Parker 2004). This study also found that ectoparasites reduced male mating success (Whiteman and Parker 2004). Our results did not support the body condition effect hypothesis (H3), as we did not find evidence that individuals in worse body condition had higher ectoparasite abundance or prevalence. One explanation for why body condition does not affect parasite prevalence or abundance, is that any available energy (fat reserves) in female Cape ground squirrels is invested in reproduction (Hillegass et al. 2010). The energetic costs associated with lactation can be quite high, thus abundant fat reserves (mass) are required for gestation and lactation to be successful (Hillegass et al. 2010). It was found that once parasites were removed from females, their energy was allocated towards reproduction, and as a result, parasite-free females had higher reproductive success compared to parasitized females (Hillegass et al. 2010). As average body condition includes the measures of body mass and spine length, if extra fat reserves (mass) is invested in reproduction, parasite-free females would not vary significantly in body condition compared to parasitized females (Hillegass et al. 2010).

Conclusion

Our results indicate that with rising temperatures (average annual maximum/minimum), the prevalence and abundance of infected hosts are staying the same over time. Suggesting that behaviours such as using one's tail to reduce heat loads or taking refuge underground mitigate parasite loads (Bolwig 1958; Herzig-Straschil 1979; Bennett et al. 1984). Body size is an important factor in determining parasite prevalence, as smaller individuals are more infected than larger individuals. As grooming is very effective at removing parasites, both allogrooming, and autogrooming could provide heightened group-level protection against ectoparasites (Wilson et al. 2020). Our results showed that a higher proportion of hosts are infected by fleas than lice, alluding to the fact that group-level protection against ectoparasites may effectively control lice numbers (Wilson et al. 2020). However, as fleas may avoid grooming behaviours in the burrow, group grooming may be less effective in controlling fleas (Wilson et al. 2020). Our results also suggest that ectoparasite prevalence and abundance do not vary with body condition as females allocate extra energy (mass) into reproduction (Hillegass et al. 2010).

As most of the data considered in the analysis displays weak relationships, more investigation should be done to compare parasite abundance between male and female Cape ground squirrels in response to temperature, body size, and body condition. As dispersed males show stronger responses to abiotic factors such as precipitation (O'Brien et al. 2021), it may be worth exploring the responses dispersed males have towards abiotic factors such as temperature, as the effects may be more significant to that of females. However, nine years of data may not be long enough to investigate changes in parasite abundance in response to climate change. Therefore, as the dataset expands, and if temperatures continue to rise, it would be worth revisiting the effects of temperature, body size, and body condition on the ectoparasites of Cape ground squirrels. Additionally, as an increase in burrow temperature with rising ambient temperature is plausible, it would be worth measuring the temperature of Cape ground squirrel burrows to test the effects of burrow temperature on ectoparasite prevalence and abundance over time (Samuel et al. 2022). Furthermore, investigating the reasons as to why parasite prevalence varies among parasite species in a non-dominant forming hierarchical species will help us understand the abiotic factors influencing parasite infections.

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Appendices

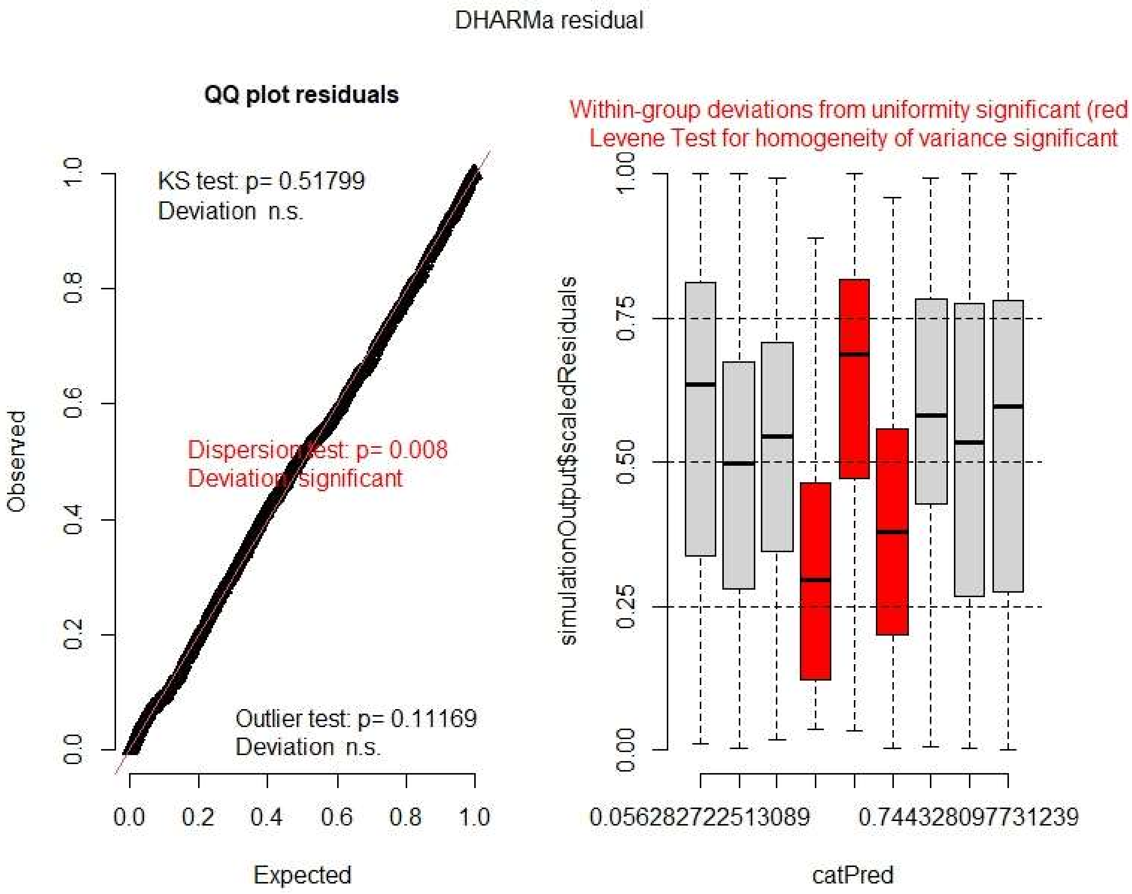

Figure A1 1. DHARMa residual fitting a Negative Binomial of total ectoparasite (flea and lice) numbers as a function of and average maximum temperature (°C). QQ plot residuals and Levene Test for homogeneity of variance were used to determine the fit of the model.

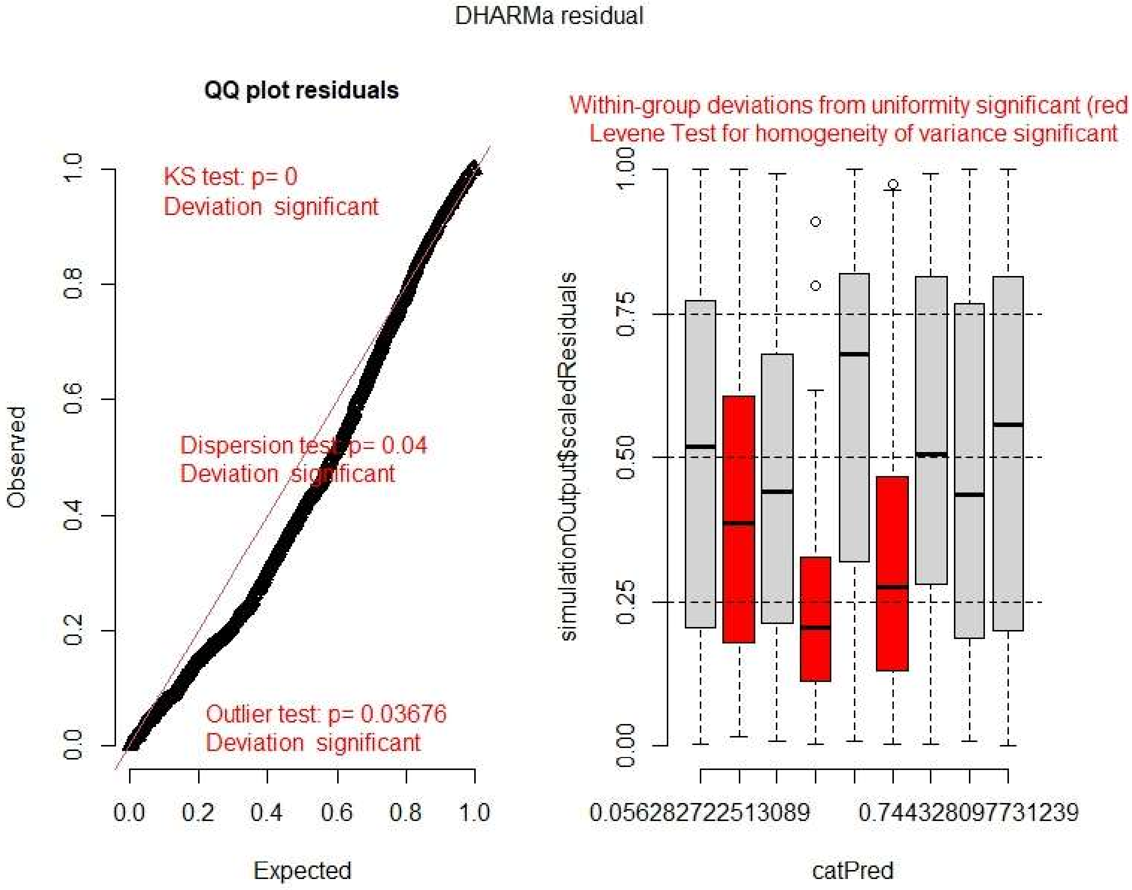

Figure A1 2. DHARMa residual fitting a Quassi-Poisson of total ectoparasite (flea and lice) numbers as a function of average maximum temperature (°C). QQ plot residuals and Levene Test for homogeneity of variance were used to determine the fit of the model.

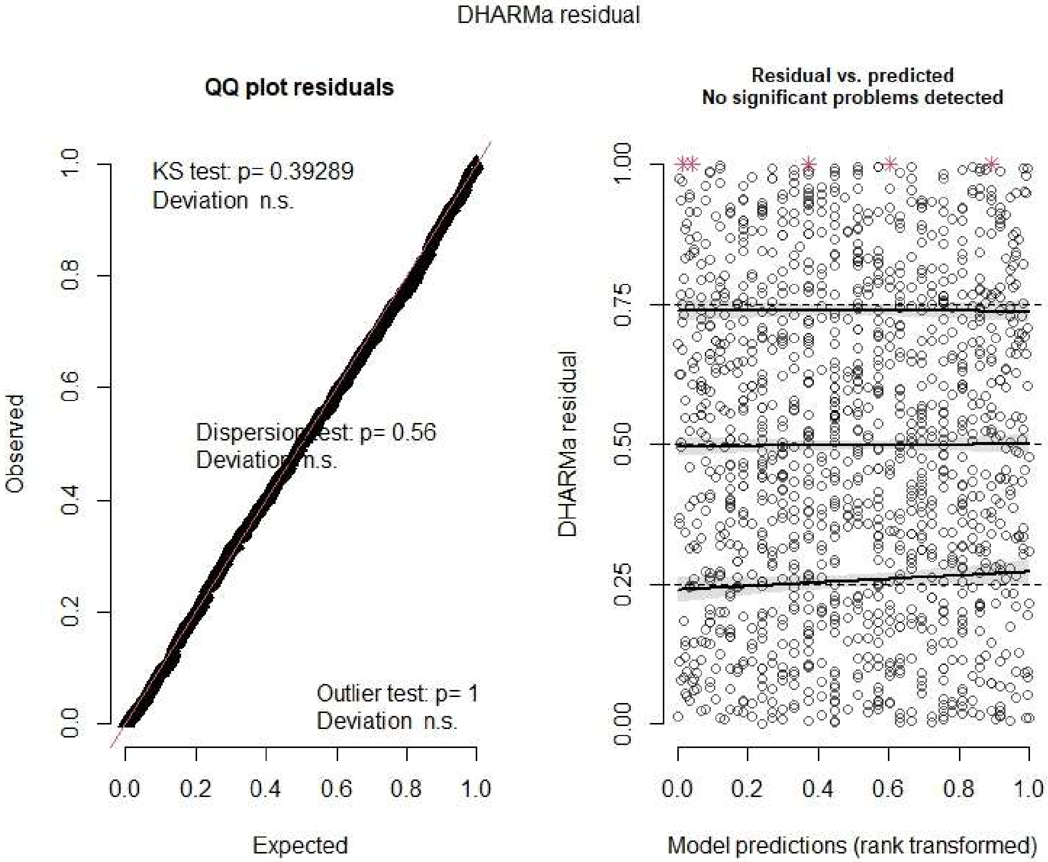

Figure A1 3. DHARMa residual fitting a negative binomial of flea abundance as a function of mass (g). QQ plot residuals were used to determine the fit of the model.

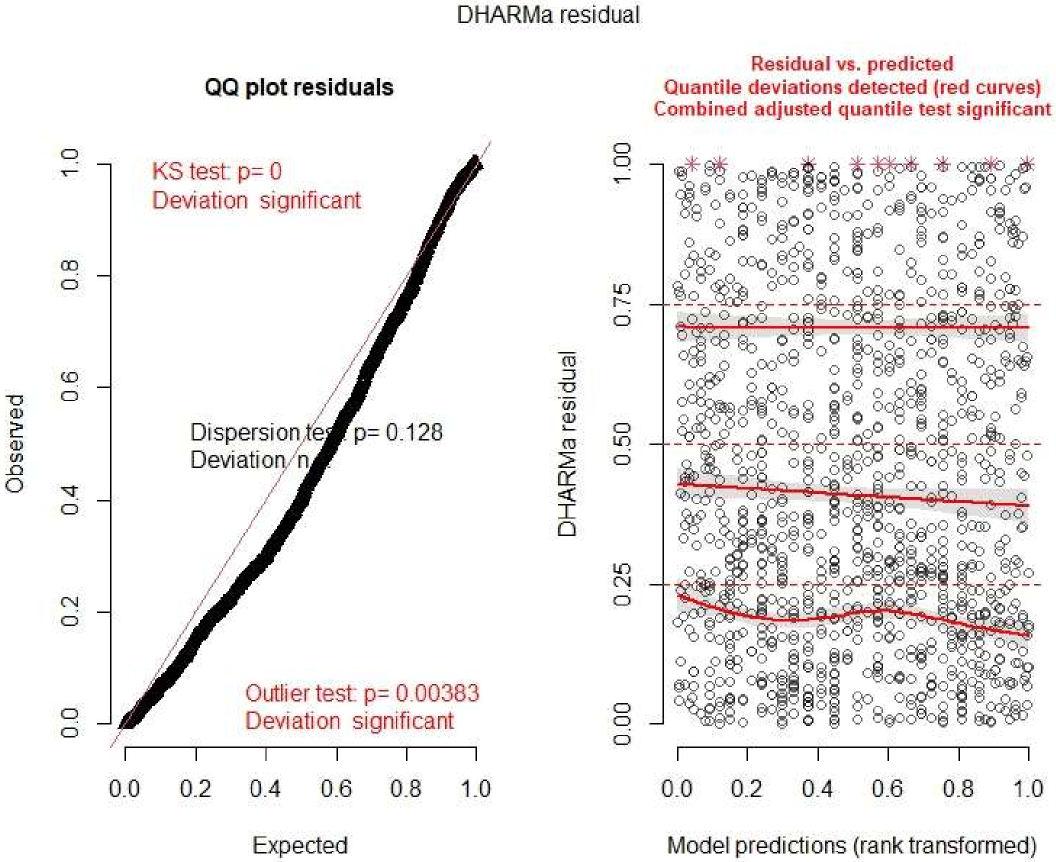

Figure A1 4. DHARMa residual fitting a Quassi-Poisson of flea abundance as a function of mass (g). QQ plot residuals were used to determine the fit of the model.