Ectoparasites associated with the Bushveld gerbil (*Gerbilliscus leucogaster*) and the role of the host and habitat in shaping ectoparasite diversity and infestations

Amber T. Smith[1], Boris R. Krasnov[2] (iD), Ivan G. Horak[3], Eddie A. Ueckermann[4] and Sonja Matthee[1] (iD)

[1]Department of Conservation Ecology and Entomology, Stellenbosch University, 7602 Stellenbosch, South Africa; [2]Mitrani Department of Desert Ecology, Swiss Institute for Dryland Environmental and Energy Research, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Sede-Boqer Campus, 84990 Midreshet Ben-Gurion, Israel; [3]Department of Zoology and Entomology, Rhodes University, PO Box 94, Makhanda 6140, South Africa and [4]Unit for Environmental Sciences and Management, Potchefstroom Campus, North-West University, North-West, South Africa.

Abstract

Rodents are known hosts for various ectoparasite taxa such as fleas, lice, ticks and mites. South Africa is recognized for its animal diversity, yet little is published about the parasite diversity associated with wild rodent species. By focusing on a wildlife-human/domestic animal interface, the study aims to record ectoparasite diversity and levels of infestations of the Bushveld gerbil, *Gerbilliscus leucogaster*, and to establish the relationship between ectoparasite infestation parameters and host- and habitat factors. Rodents ($n = 127$) were trapped in 2 habitat types (natural and agricultural) during 2014–2020. More than 6500 individuals of 32 epifaunistic species represented by 21 genera and belonging to 5 taxonomic groups (fleas, sucking lice, ticks, mesostigmatan mites and trombiculid mites) were collected. Mesostigmatan mites and lice were the most abundant and fleas and mesostigmatan mites the most prevalent groups. Flea and mesostigmatan mite numbers and mesostigmatan mite species richness was significantly higher on reproductively active male than female rodents. Only ticks were significantly associated with habitat type, with significantly higher tick numbers and more tick species on rodents in the natural compared to the agricultural habitat. We conclude that the level of infestation by ectoparasites closely associated with the host (fleas and mites) was affected by host-associated factors, while infestation by ectoparasite that spend most of their life in the external environment (ticks) was affected by habitat type.

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Introduction

Small mammals including rodents play important roles in shaping ecological structure and species composition and diversity of plants within ecosystems (Nyirenda *et al.*, 2020). They are often referred to as bio-engineers (Cameron, 2000; Reichman, 2007) because they contribute to the chemical and physical properties of soil (Galiano *et al.*, 2014; Yong *et al.*, 2019) and facilitate seed dispersal (Midgley and Anderson, 2005; Flores-Peredo *et al.*, 2011) and pollination (Wiens *et al.*, 1983; Wester *et al.*, 2009). Small mammals also form an integral part of food webs by acting as a food source for predators as well as consumers of plant material and arthropods (Morand *et al.*, 2006). In addition, rodents are known hosts for a diverse range of ectoparasite taxa (e.g. fleas, lice, ticks and mites) (Morand *et al.*, 2006). Life history traits (e.g. group size, nesting behaviour and habitat use) of a rodent species often influences their exposure to parasites and therefore their parasite profiles (Vaumourin *et al.*, 2015). This is because ectoparasites vary in their level of host specificity, micro-habitat preference and mode of transmission (Hopla *et al.*, 1994; Paramasvaran *et al.*, 2009). For example, lice are host-specific permanent parasites with all life stages occurring on the host's body and are transmitted through direct body contact between hosts, while ticks generally have a broader host range and attaches to a host only once during a life stage (larval, nymphal or adult) to obtain a bloodmeal (Morand *et al.*, 2006). Several ectoparasite taxa are known vectors for disease-causing pathogens (e.g. *Yersinia pestis* for plague and *Rickettsia* species for various rickettsioses). Consequently, it is important to develop accurate parasite profiles for rodents that routinely move between natural (reserves) and anthropogenic (e.g. agriculture and village) habitats to prevent spillover of pathogens into human-associated habitats.

The occurrence of parasites and infestation within a host population are influenced by both host-associated and environment-associated factors (Krasnov and Matthee, 2010; Stanko *et al.*, 2015; Obiegala *et al.*, 2021). Host-associated factors include body size, age, sex and reproductive state (Morand and Poulin, 1998; Kołodziej-Sobocińska, 2019). For example, larger hosts can harbour more parasites due to larger total mass (more potential resources for parasites) and larger surface area (more space/niches for parasites) (Lindenfors *et al.*, 2007; Froeschke *et al.*, 2013). Body size is also indicative of host age and older hosts may accumulate

parasites over time (Moore and Wilson, 2002; Poulin, 2007). Host sex can also influence parasite infestations, which are often related to sexual size dimorphism characteristic for many host species (Moore and Wilson, 2002) and difference in home range sizes between male and female hosts (Krasnov et al., 2005). In addition, elevated hormone levels can facilitate host sex-associated differences in mammals during the breeding season (Lightfoot, 2008). Reproductively active males that experience elevated testosterone levels, may become more aggressive towards conspecifics (Zielinski and Vandenbergh, 1993; Simon and Lu, 2006; Gleason et al., 2009) and enlarge their home range size in search of females (Tew and Macdonald, 1994; Bergallo and Magnusson, 2004). Testosterone has immunosuppressive properties that can increase male susceptibility to parasites (Hughes and Randolph, 2001; Klein, 2004; Matthee et al., 2010), whereas lowered immune defences during gestation can render female mammals more susceptible to parasites (Christe et al., 2000; Viljoen et al., 2011). Larger home ranges increase contacts between male hosts increasing probability of encounter with ticks and chiggers (Scantlebury et al., 2010; Butler et al., 2020). In contrast, during the breeding season, reproductively active female hosts are more tolerant of conspecifics and engage in social grooming between group members (Meaney and Stewart, 1979; Ganem and Bennett, 2004). A higher contact rate between host individuals can facilitate parasite exchange (Bordes et al., 2007; Patterson and Ruckstuhl, 2013), though host-induced mortality of parasites due to grooming can benefit female hosts (Marshall, 1981; Krasnov et al., 2002). In many rodent species, females may have a stronger nest association during the breeding season (Choate, 1972; Zenuto et al., 2001), which can promote infestations by nidicolous parasites such as fleas and mites (Krasnov et al., 2010). The effect of environment (= habitat)-associated factors are first and foremost determined by high sensitivity of ectoparasites to air temperature and relative humidity in terms of, for example, development rate and survival (Krasnov et al., 2001; Herrmann and Gern, 2010; van der Mescht et al., 2013). This is particularly true for taxa with free-living life stages (fleas, mites and ticks). The vegetation structure (plant growth forms and vegetation cover) in a habitat can influence the microclimatic conditions by reducing the soil temperature and loss of soil moisture (He et al., 2010; Jucker et al., 2018; Lozano-Parra et al., 2018). Consequently, variation in the microclimatic conditions between habitat types (e.g. natural and transformed habitat types) can affect parasite occurrence and infestation levels (Lorch et al., 2007; Froeschke et al., 2013; Froeschke and Matthee, 2014; van der Mescht et al., 2016).

South Africa has a rich diversity of small mammals and, in particular, rodents (Skinner and Chimimba, 2005). Among the approximately 50 rodent species recorded in South Africa, many vary in geographic range and adaptability to habitat transformation (Skinner and Chimimba, 2005; Monadjem et al., 2015). Currently, most information on rodent parasites is limited to host-parasite lists in monographs of which some are outdated (Zumpt, 1961; Theiler, 1962; Ledger, 1980; Segerman, 1995; Horak et al., 2018). More recently, empirical studies based on large sample sizes have been conducted on a few rodent species (Matthee et al., 2007, 2010; Fagir et al., 2014, 2021; Stevens et al., 2022). These studies highlighted the potentially large ectoparasite diversity in locally abundant and regionally widespread species such as the four-striped mouse (Rhabdomys pumilio) (Matthee et al., 2007, 2010; Matthee and Krasnov, 2009), Namaqua rock mouse (Micaelamys namaquensis) (Fagir et al., 2014) and mole rats (Viljoen et al., 2011; Fagir et al., 2021) that readily adapt to agricultural habitats. In addition, the occurrence of undescribed ectoparasite species and new parasite-host and parasite-locality records in these studies suggested that the ectoparasite diversity in South African rodents is currently underestimated (Matthee et al., 2007; Matthee and Ueckermann, 2008, 2009; Fagir et al., 2014; Stevens et al., 2022). Moreover, ecological studies on factors that influence ectoparasite infestations and their species composition are sparse. In other words, ectoparasite communities of South African rodents and factors influencing structure of these communities remain to be further investigated.

The Bushveld gerbil (Gerbilliscus leucogaster) is a widespread, nocturnal rodent occurring mainly in the Grassland and Savanna biomes of southern Africa (Skinner and Chimimba, 2005; Odhiambo et al., 2008). These gerbils are also commonly found in agricultural areas where they are seen as pests of crops (Odhiambo et al., 2008; Von Maltitz et al., 2016). The species is medium in size (48–98 g) with no clear sexual dimorphism (Skinner and Chimimba, 2005; Lötter, 2010). It constructs burrows in sandy soils that are cleaned every night (Apps, 2012; Monadjem et al., 2015) and demonstrates communal living (De Graaff, 1981; Skinner and Chimimba, 2005), with family groups sharing burrows (Monadjem et al., 2015) and reproduce during spring-summer (Perrin and Swanepoel, 1987; Neal, 1991). Although the biology of this rodent is relatively well studied, limited data exist on the ectoparasite diversity associated with G. leucogaster. Current data for this species is, as mentioned above, restricted to historic monographs (Zumpt, 1961; Ledger, 1980; De Graaff, 1981; Segerman, 1995; Horak et al., 2018) and a single field study at a single locality in the Savanna biome (Braack et al., 1996). The latter study identified a number of louse, flea and tick species on G. leucogaster, but mite species identification was incomplete.

Here, we studied ectoparasite diversity and factors that drive their infestation on G. leucogaster. Our objectives were (a) to record ectoparasite (especially mite due to incomplete knowledge) species and their level of infestation (mean abundance and prevalence) and (b) to establish the relationship between host-related (sex, body size and reproductive state) and habitat-related (natural vs agricultural) factors on ectoparasite infracommunity structure, namely (a) diversity in terms of species richness and (b) abundance in terms of the number of ectoparasite individuals. Given the nest type, social behaviour and habitat use of G. leucogaster, we expected high ectoparasite, especially mite, diversity and abundance.

Materials and methods

Study area

The study is part of a larger on-going research programme conducted within the Mnisi OneHealth platform in Mpumalanga Province, South Africa (Berrian et al., 2016) (Fig. 1). The Mnisi community comprises several villages that are bordered by large, fenced nature reserves. Rodents were trapped in 4 villages and 4 crop fields within these villages' (Gottenburg 24°38′01″ S, 31°25′19″ E; Thlavekisa 24°37′51″ S, 31°22′42″ E, Athol 24°42′29″ S, 31°20′43″ E and Utah 24°50′14″ S, 31°02′45″ E). In general, subsistence farming is practiced within these settlements. Small vegetable patches and cattle occur on the property (village), while small crop fields (agricultural areas) often occur between the village and the nature reserve. Rodents were also trapped at 4 localities in the Manyeleti Nature Reserve (24°38′52″ S, 31°31′35″ E) that represents pristine natural Savanna vegetation.

Rodent trapping

Gerbilliscus leucogaster individuals were trapped at 3 villages and their respective crops in (August–October) of 2014 and 2015 and once in summer (January) of 2015 and at 4 villages and their respective crops in spring (August–October) 2019 and 2020 (Fig. 1). All localities were >1 km apart. In each habitat type, a standardized rodent trap design was used. Sherman-type
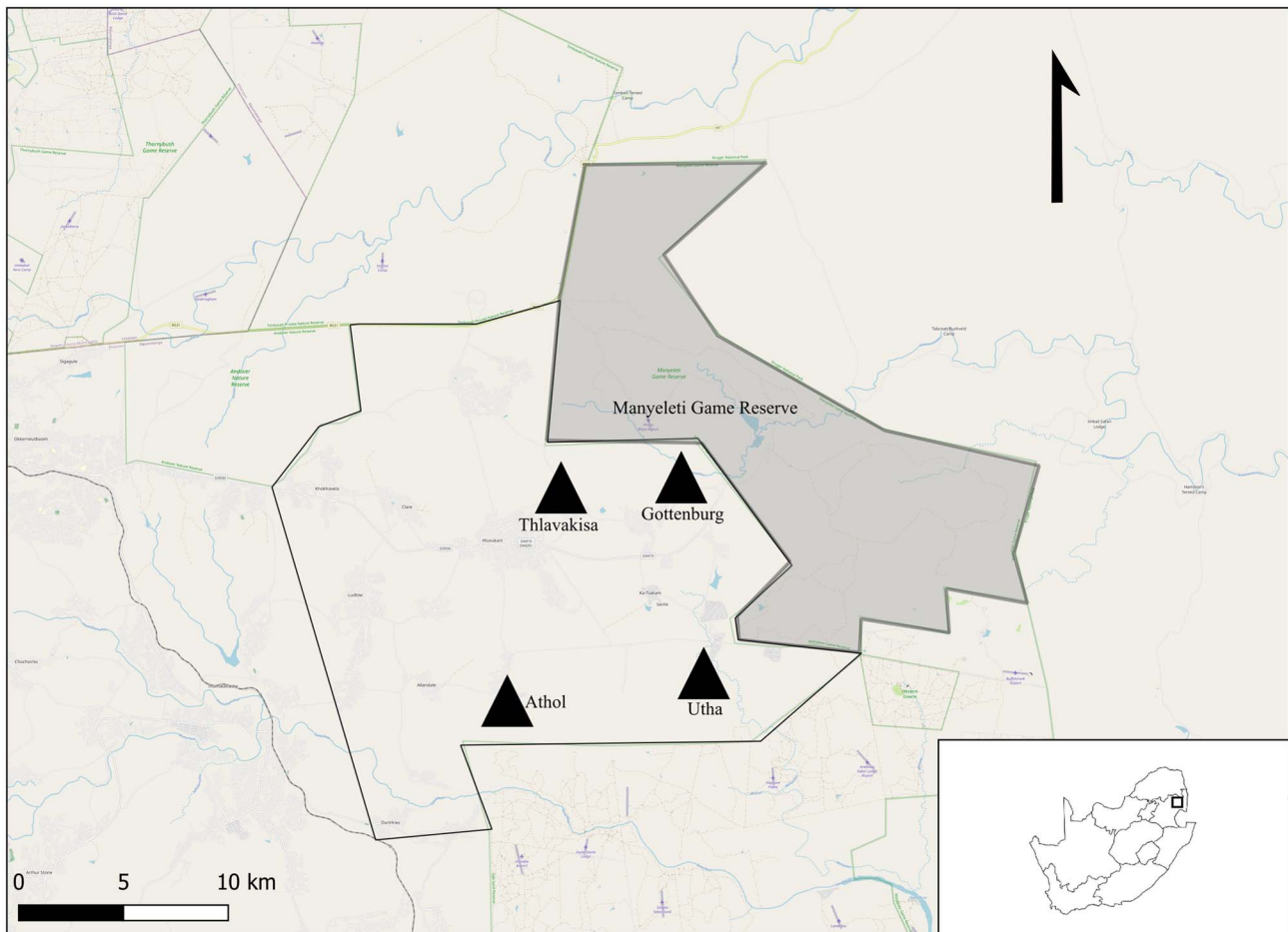
Figure 1. Locality map of the study area for *Gerbilliscus leucogaster* (*n* = 127) within the Mnisi OneHealth platform in the Mpumalanga Province, South Africa. The village sites are represented by black triangles (*n* = 4) and the shaded area is Manyeleti nature reserve.

live traps (80) were set in trap lines baited with a mixture of peanut butter and oats and set for 3–4 days per locality. Each locality was only trapped once during each trap period. During this time, traps were checked twice a day and closed in the heat of the day (10:00–15:00). Targeted rodents were removed from traps, placed in pre-marked plastic bags and euthanized with Isoflurane. Once labelled, the carcasses were frozen at −20°C (to preserve the integrity of the material and to kill the ectoparasites) for later examination. The study was approved by the Animal Ethics Committees of Stellenbosch University (Reference numbers: ACU 2016-00190; ACU 2018-4555; ACU 2020-17062), the Mpumalanga Tourism and Parks Agency (Permit number ES 5/14; MPB. 5694; MPB. 5663), Department of Agriculture, Forestry and Fisheries (Reference number 12/11/1/7/5) and Pretoria University (Reference number V046-14; VO23-19).

Laboratory procedures

Prior to ectoparasite removal, the carcasses were thawed. Each rodent body was systematically (anteriorly and posteriorly) examined for ectoparasites using a Zeiss Stemi DV4 stereomicroscope (Carl Zeiss Light Microscopy, Göttingen, Germany) and fine point forceps (used to separate hair shafts and to remove the ectoparasites). All rodents were preliminarily identified based on morphological and dental morphology using taxonomic references (De Graaff, 1981; Perrin and Swanepoel, 1987; Skinner and Chimimba, 2005; Monadjem *et al.*, 2015) and thereafter confirmed molecularly (cytochrome b gene) (Bastos *et al.*, 2011).

For each rodent individual, we recorded sex and body measurements (weight, total body length, tail length and hind foot length). Thereafter reproductive state (reproductively active females were characterized by a perforated vagina and reproductively active males were characterized by enlarged testes) was recorded. All fleas, lice, ticks and mesostigmatan mites (hereafter referred to as mites) were removed and transferred to sample tubes filled with 100% ethanol. All fleas were counted (male and female) but only male individuals were available for identification and used for the species abundance (this is because female fleas were used in a separate project). For each louse species counts of immature stages were combined and reported as nymphs. In the case of chiggers, only a sub-sample was collected and the parasitope (region on the body where chiggers occurred) recorded. Fleas (males), lice, mites and chiggers were cleared, and slide mounted (fleas in Canada balsam and the rest in Hoyer's mounting medium) using standard techniques, while ticks remained unmounted. Ectoparasite identification was conducted using taxonomic reference keys. Fleas were identified according to Segerman (1995) and lice were identified using various reference sources (Ledger, 1980; Durden and Musser, 1994). Ticks were identified according to Walker *et al.* (2000) and Horak *et al.* (2018). Mites were identified using various reference sources (Till, 1963; Herrin and Tipton, 1975; Matthee and Ueckermann, 2008), but species identification was not possible for all mites. Chiggers were identified following Zumpt (1961) and Stekolnikov and Matthee (2019). Identification of lice, fleas and chiggers was done using a Leica DM1000 light microscope (Leica Microsystems GmbH, Wetzlar, Germany) and that of

ticks using a Leica MZ75 high-performance stereomicroscope (Leica Microsystems GmbH, Wetzlar, Germany).

Data analysis

Rodent and ectoparasite data were pooled per locality within each of the habitat types (natural, agriculture and village) within a sampling year. We divided the ectoparasites into higher taxonomic groups (fleas, lice, mites and ticks) and pooled the different life stages (i.e. larvae, nymphs, males and females) within the respective ectoparasite taxa. For each higher ectoparasite taxon, we calculated mean abundance (mean number of parasites on an individual host) and prevalence (% of hosts infested). In addition, we considered total counts of ectoparasites of a given higher taxon and their species richness (the number of species) on an individual host (i.e. infracommunity). Analysis of species richness was not carried out for fleas and lice because these taxa were dominated by 1 and 2 species, respectively, even though more than one species were recorded. Because (a) the data were collected in different years and (b) some dependent variables (the number of ectoparasite individuals and ectoparasite species richness) were not normally distributed (Shapiro–Wilk tests), we applied generalized linear mixed-effect models with the *lme4* package (Bates *et al.*, 2015) in R (R Core Team, 2020) using year of sampling as a random factor and a negative-binomial error distribution. Thereafter, we applied model selection and model averaging using the R package *MuMIn* (Bartoń, 2018) to identify host-associated (sex, body size using tail length as a proxy and reproductive state) and habitat-associated (habitat type) variables and the interactions between them affecting the numbers of ectoparasite individuals and species. For each model averaging scenario, 95% confidence interval values are reported, and explanatory variables were considered significant when confidence intervals did not include zero. We also calculated conditional R^2 (the proportion of the variance explained by both fixed and random effects) and marginal R^2 (the proportion of the total variance explained by the fixed effects) of Nakagawa *et al.* (2017) for all models.

Results

A total of 127 *G. leucogaster* (77 males and 50 females) were captured and examined for ectoparasites (Table 1). The average tail length was 13.98 ± 0.20 cm in males and 14.02 ± 0.26 cm in females. Data on reproductive state were available for 123 rodents of which 74 were reproductively active (61 males and 13 females). We identified 21 genera that comprised of 28 ectoparasitic and 4 non-parasitic species (predatory mites: mites that predate on invertebrates in the nest of the host) (Table 2). Mites were represented by 14 species, followed by 9 chigger species, 5 tick species, 3 flea species and 2 louse species (Table 2). In total, 6758 epifaunistic individuals (excluding chiggers) were recorded of which mites and lice were the most abundant. Fleas were the most prevalent followed by mites (Table 3).

Epifaunistic diversity

Three flea species from the genus *Xenopsylla* were recovered from *G. leucogaster* (Table 3). Based on adult male fleas, *Xenopsylla frayi* was the most abundant and prevalent (>70%) flea species. The 2 remaining species (*Xenopsylla brasiliensis* and *Xenopsylla bechuanae*) occurred on <5% of the rodents (Table 3). Among lice, *Polyplax biseriata* was the most prevalent (74.80%) compared to *Hoplopleura biseriata* (2.67%) (Table 3). Five ixodid tick species, from 4 genera, were recorded (Table 3). *Hyalomma truncatum* was the most abundant and prevalent, followed by *Dermacentor*

Table 1. Sampling period and sample size for *Gerbilliscus leucogaster* ($n = 127$) trapped in Mpumalanga, South Africa (2014–2020)

Month and Year	No. of animals	Males	Females
August 2014	15	5	10
January 2015	14	7	7
September 2015	15	12	3
September 2019	23	16	7
October 2020	60	37	23
Total	**127**	**77**	**50**

rhinocerinus. Ticks were represented by nymph and larval life stages (Table 3). Fourteen mite species (excluding Trombiculidae) were found. *Androlaelaps oliffi* was the most abundant and prevalent species, followed by *Androlaelaps marshalli*. *Androlaelaps* mites represented 90% of the 14 mite species. Three unknown mite species were recorded (1 in the genus *Pachylaelaps* and 1 each from families Acaroidae and Uropodidae). *Cheyletus zumpti* was the most prevalent (22.05%) predatory mite. The adult female life stage was the most common life stage for 6 of the Laelapidae species (Table 3). Nine chigger species were recorded with an overall prevalence of 35.43% (Table 3). *Schoutedenichia lumsdeni* was the most prevalent species followed by *Gahrliepia nana*. Chiggers occurred on various parasitopes of which the pinna (external part of ear) was the most preferred followed by the front leg (Table 4).

Effects of host- and habitat-associated factors

The most abundant species in 4 of the higher taxa (excluding chiggers) were more abundant and prevalent on male compared to female rodents (Supplementary Table 1). The results of model selection and averaging are presented in Tables 5 and 6. None of the infestation parameters for any of the ectoparasite taxa was significantly associated with host body size. The number of flea and mite individuals were significantly related to host sex and the interaction between host sex and reproductive state (Table 5), with male hosts harbouring more flea and mite individuals than female hosts (Fig. 2A and 2B). Furthermore, the effect of the interaction of host sex and reproductive state on flea and mite numbers in infracommunities was manifested by higher parasite counts on reproductively active males followed by that on non-breeding females (Fig. 2A and 2B; Table 5). In addition, mite species richness was also significantly related to host sex, with a larger number of mite species occurring on males compared to females (Fig. 2C; Table 6).

Overall, a higher number of epifaunistic individuals were recorded on *G. leucogaster* in natural than agricultural habitats (3984 *vs* 2244, respectively) (Supplementary Table 2). However, a significant relationship was only recorded for ticks with more tick individuals (overall mean: 2.31 ± 0.66 *vs* 0.34 ± 0.16, respectively) and species (overall 5 *vs* 3 species, respectively) collected from rodents captured in natural as compared to agricultural habitats (Fig. 3A and 3B; Tables 5 and 6). The overall prevalence was also higher on *G. leucogaster* that occur in natural (48.53%) compared to agricultural (13.79%) habitat type (Supplementary Table 2).

Discussion

Epifaunistic diversity

The flea *X. frayi* was the most common species, which supports a close association between *X. frayi* and *G. leucogaster* as reported

Table 2. Epifaunistic arthropod taxa recorded on *Gerbilliscus leucogaster* (*n* = 127) in Mpumalanga, South Africa, 2014–2020

	Order	Suborder	Family/Subfamily	Taxon
Fleas	Siphonaptera		**Pulicidae**	
			Xenopsyllinae	*Xenopsylla bechuanae* de Meillon, 1947
				X. brasiliensis (Baker), 1904
				X. frayi de Meillon, 1947
Lice	Phthiraptera	Anoplura	**Hoplopleuridae**	*Hoplopleura biseriata* Ferris, 1921
			Polyplacidae	*Polyplax biseriata* Ferris, 1923
Ticks	Parasitiformes	Ixodida	**Ixodidae**	
			Haemaphysalinae	*Haemaphysalis elliptica* group
				Hae. spinulosa group
			Hyalomminae	*Hyalomma truncatum* Koch, 1844
			Rhipicephalinae	*Dermacentor rhinocerinus* (Denny, 1843)
				Rhipicephalus follis/simus group
Mites	Parasitiformes	Mesostigmata	**Laelapidae**	
			Laelapinae	*Androlaelaps marshalli* Berlese, 1911
				A. oliffi (Zumpt & Patterson, 1951)
				A. taterae (Zumpt & Patterson, 1951)
				A. theseus Zumpt, 1950
				Laelaps liberiensis Hirst, 1925
				L. muricola Trägårdh, 1910
				L. simillimus Zumpt, 1950
			Macronyssidae	*Ornithonyssus bacoti* (Hirst, 1930)
			Pachylaelapidae	*Pachylaelaps* sp.[P]
			Uropodidae	Uropodidae sp.[P]
	Sarcoptiformes	Acaridia	**Acaroidae**	Acaroidae sp.[P]
		Psoroptidia	**Atopomelidae**	*Listrophoroides (Afrolistrophoroides) mastomys* Radford, 1940
	Trombidiformes	Prostigmata	**Cheyletidae**	*Cheyletus zumpti* Fain, 1972[P]
			Myobiidae	*Austromyobia forcipifer* Lawrence, 1954
			Trombiculidae	
			Gahrliepiinae	*Gahrliepia nana* (Oudemans, 1910)
			Trombiculinae	*Ascoschoengastia ueckermanni* Stekolnikov and Matthee, 2019
				Microtrombicula mastomyia (Radford, 1942)
				Microtrombicula sp.
				Schoutedenichia dutoiti (Radford, 1948)
				S. horaki Stekolnikov and Matthee, 2019
				S. lumsdeni Vercammen-Grandjean, 1958
				S. morosi Vercammen-Grandjean, 1958
				Trombicula walkerae Stekolnikov and Matthee, 2019

Family name indicated in bold. Taxonomic authority included.
[P]Predatory feeding strategy.

by Segerman (1995) and Braack *et al.* (1996). The study area in the present study falls within the known distributional range of *X. frayi*, which spans the eastern and north-eastern Savanna bushveld areas of South Africa (Segerman, 1995). The low occurrence of *X. brasiliensis* may be due to the fact that other rodent species (e.g. *Rattus* spp. and *Mastomys* spp.) represent principal hosts for this flea (Segerman, 1995; Braack *et al.*, 1996). The presence of *X. bechuanae* on *G. leucogaster* in the present study could be accidental because (a) *X. bechuanae* is reported as host-specific to the pouched mouse (*Saccostomus campestris*) (Segerman, 1995) co-occurring with *G. leucogaster* and (b) only 2 individuals of *X. bechuanae* were recorded. In addition, a similar pattern was previously recorded for *X. bechuanae* on *G. leucogaster* and *S. campestris* in Namibia (Shihepo *et al.*, 2008).

The occurrence of 2 louse species, *H. biseriata* and *P. biseriata*, supports earlier findings (Ledger, 1980; Braack *et al.*, 1996). *Polyplax biseriata* was the most prevalent of the 2 species, and only 4 *H. biseriata* individuals were recorded. The dominance of *P. biseriata* is supported by Braack *et al.* (1996). Unfortunately,

Table 3. Epifaunistic arthropod taxa and their infestation parameters recorded from *Gerbilliscus leucogaster* (*n* = 127) in Mpumalanga Province, South Africa, 2014–2020

Ectoparasite taxa	Total Abundance	Adults (%)	Larvae (%)	Nymphs (%)	Adult Male (%)	Adult Female (%)	Sex Ratio (♂:♀)	Mean Abundance (±SE)	Prevalence (%)
Fleas[a]	**875**	**100**	**–**	**–**	**48.11**	**58.89**	**1:1.08**	**6.89 ± 0.69**	**87.40**
Xenopsylla bechuanae[b]	2	100	–	–	–	–	–	0.02 ± 0.01	1.57
X. brasiliensis[b]	7	100	–	–	–	–	–	0.06 ± 0.03	3.15
X. frayi[b]	412	100	–	–	–	–	–	3.24 ± 0.35	75.59
Lice	**1819**	**49.26**	**–**	**50.74**	**24.41**	**24.84**	**1:1.02**	**14.32 ± 1.93**	**76.38**
Hoplopleura biseriata	4	100	–	0	75	25	3:1	0.03 ± 0.01	2.67
Polyplax biseriata	1815	49.15	–	50.85	24.30	24.85	1:1.02	14.33 ± 1.93	74.80
Ticks	**177**	**–**	**43.50**	**56.50**	**–**	**–**	**–**	**1.39 ± 0.37**	**32.28**
Dermacentor rhinocerinus	3	–	33.33	66.67	–	–	–	0.02 ± 0.01	2.36
Haemaphysalis elliptica group	20	–	25	75	–	–	–	0.16 ± 0.05	9.45
Hae. spinulosa group	4	–	50	50	–	–	–	0.03 ± 0.02	1.57
Hyalomma truncatum	111	–	36.04	63.96	–	–	–	0.87 ± 0.30	22.05
Rhipicephalus follis/ simus group	39	–	74.36	25.64	–	–	–	0.31 ± 0.20	3.94
Mites	**3887**	**73.73**	**0**	**26.27[c]**	**29.74**	**43.99**	**1:1.48**	**30.61 ± 3.83**	**79.53**
Androlaelaps marshalli	458	91.48	0	8.52	13.54	77.95	1:6.05	3.61 ± 0.50	57.48
A. oliffi	2821	68.81	0	31.19	37.26	31.55	1.18:1	22.21 ± 3.49	69.29
A. taterae	13	100	0	0	7.69	92.31	1:12	0.10 ± 0.05	5.51
A. theseus	199	93.47	0	6.53	5.03	88.44	1:17.60	1.57 ± 0.31	32.28
Laelaps liberiensis	17	82.35	0	17.65	17.65	64.71	1:3.67	0.13 ± 0.08	4.72
L. muricola	1	100	0	0	0	100	–	0.01 ± 0.01	0.79
L. simillimus	19	78.95	0	21.05	26.32	52.63	1:2	0.15 ± 0.12	1.57
Ornithonyssus bacoti	1	0	0	100	0	0	–	0.01 ± 0.01	0.79
Pachylaelaps sp.[P]	12	100	0	0	16.67	83.33	1:7	0.09 ± 0.03	7.09
Uropodidae sp.[P]	27	55.56	0	44.44	0	55.56	–	0.42 ± 0.10	8.66
Acaroidae sp.[P]	61	0	0	100	0	0	–	0.95 ± 0.47	1.57
Listrophoroides (A.) mastomys	104	92.31	0	7.69	21.15	71.15	1:3.36	0.82 ± 0.45	4.72
Cheyletus zumpti[P]	149	100	0	0	0	100	–	1.17 ± 0.29	22.05
Austromyobia forcipifer	5	100	0	0	0	100	–	0.04 ± 0.02	3.15
Chiggers	–	–	–	–	–	–	–	–	**35.43**

Number/proportions for ectoparasite groups are indicated in bold.
[a]Taxon count includes all male and female individuals.
[b]Count for flea species based on male individuals only, lice nymphs: instars I, II and III combined.
[c]Mite nymphs represents proto- and deutronymphs.
[P]Predatory feeding strategy.

Braack *et al.* (1996) did not provide differential prevalence values for the 2 louse species, but rather an overall prevalence of 71.70%, which is comparable to the 76.38% recorded in our study.

The occurrence of *H. truncatum* on *G. leucogaster* in the present study supports the findings of Braack *et al.* (1996) who recorded the tick species on 20% of *G. leucogaster* at a locality in the same geographic region as the present study. According to Horak *et al.* (2018) the immature stages of *H. truncatum* seem to prefer *G. leucogaster* in addition to some other host species. *Dermacentor rhinocerinus* was the second most prevalent tick. Horak and Cohen (2001) also recorded this tick on *G. leucogaster* in the Mthethomusha Game Reserve in Mpumalanga

Province. It is thus possible that *G. leucogaster* is a preferred host of the immature stages of this tick. Morphological stasis of larval and nymph life stages often limits species-level identification for ticks in the genera *Rhipicephalus* and *Haemaphysalis* (see Walker *et al.*, 2000 for the genus *Rhipicephalus*).

Mites (including chiggers) represented the majority (23 of the 32 species) of the epifaunistic arthropods on *G. leucogaster*. The 3 most prevalent mite species are parasitic and belong to Laelapidae (*Androlalaps oliffi*, *A. marshalli* and *A. theseus*). Two species (*A. marshalli* and *A. theseus*) were previously recorded on *G. leucogaster* in the Savanna biome (Braack *et al.*, 1996). Zumpt (1961) also lists *A. oliffi*, *A. marshalli*, *A. taterae* and *A. theseus*

Table 4. Prevalence and parasitope for chigger species (Trombiculidae) recorded from *Gerbilliscus leucogaster* (*n* = 127) in Mpumalanga Province, South Africa, 2014–2020.

Chigger species	Prevalence (%)	Parasitope
Ascoschoengastia ueckermanni	0.79	pinna
Gahrliepia nana	7.87	tail base, perineum
Microtrombicula mastomyia	1.57	pinna
Microtrombicula sp.	0.79	front leg
Schoutedenichia dutoiti	3.15	pinna, front leg
S. horaki	3.15	face, front leg, hind leg
S. lumsdeni	10.24	pinna
S. morosi	6.30	pinna, front leg, face, perineum
Trombicula walkerae	1.57	pinna

on several *Gerbilliscus* species (including *G. leucogaster*). The dominance of *Androlaelaps* species, compared to *Laelaps* species, on *G. leucogaster* in the present supports earlier findings (Braack *et al.*, 1996) and this), gerbil seems to be the main host for *Androlaelaps* mites in southern Africa (Zumpt, 1961; Till, 1963). The predominance of a female-bias of Laelapidae in the present study is in accordance with previous studies on rodents in South Africa (Matthee *et al.*, 2007, 2010) and in other regions (Martins-Hatano *et al.*, 2002; Gettinger and Gardner, 2005, 2017). *Androlaelaps* and *Laelaps* females are generally found on the hosts' bodies whereas males and immature individuals are frequently in the nest (Radovsky, 1994). However, exceptions do occur, where male and immature life stages are more represented on the host's body; as seen in *Laelaps dearmasi* (Tipton *et al.*, 1966) and *A. oliffi* (this study). We provide the first record of *Listrophoroides (Afrolistrophoroides) mastomys* on *G. leucogaster* (4.75% prevalence). *Listrophoroides (A.) mastomys* was previously recorded on the Natal multimammate mouse (*Mastomys natalensis*) in north and west Africa (e.g. Rwanda, Uganda and Ivory Coast) (Fain, 1972; Dusbabek, 1983). Species in the fur mite genus *Listrophoroides* are associated with rodents, shrews and primates and are globally distributed (Fain and Bochkov, 2004). The presence of another fur mite, the myobiid *Austromyobia forcipifer* on *G. leucogaster* in our study is not surprising as mites in this genus are known exclusively from murid rodents (Bochkov, 2009). Members of the Myobidae are morphologically specialized to attach themselves firmly to the fur and hair of mammals (Wall and Shearer, 2001; Herrera-Mares *et al.*, 2021). The macronyssid mite, *Ornithonyssus bacoti* is a bloodsucking ectoparasite that only attaches to the host (birds and mammals) during feeding (Wall and Shearer, 2001). Although the presence of this species on *G. leucogaster* is the first record, it has been recorded on the four--striped mouse in the Western Cape Province of South Africa (Matthee *et al.*, 2007). Interestingly, although *A. forcipifer* and *O. bacoti* were recorded in low abundance and prevalence in the present study, they were both more common in the agricultural habitat type. The 4 predatory mite species that were recorded represent 4 families: Pachylaelapidae (*Pachylaelaps* sp.), Uropodidae, Cheyletidae (*C. zumpti*) and Acaroidae. The Pachylaelapidae are predators of micro-fauna (arthropods and soil-dwelling nematodes) in litter, humus, moss and are found in the nests of mammals, birds and insects (Lindquist *et al.*, 2009). Uropodidae are found in highly organic, insular deposits of manure and compost where they feed on bacteria, fungi, ants, nematodes and other mites

(Lindquist *et al.*, 2009). Approximately 78% of cheyletid species are predators, the remaining species are permanent parasites of mammals and birds. *Cheyletus zumpti* was previously recorded in the nests of rodents at various localities in South Africa and tropical African countries (Rwanda, Nigeria, Angola and the Democratic Republic of the Congo) (Fain and Bochkov, 2001). A single specimen was previously found on *G. leucogaster* in Skukuza in the Kruger National Park (Zumpt, 1961). Predacious individuals occupy a wide variety of habitats including plant and soil-litter and are mostly associated with nests of vertebrates or stored grains (Hughes, 1976; Bochkov and OConnor, 2004). The deutonymphs of the Acaroidae recorded in this study, attach themselves to insects or fur of animals, and use them as transport vehicles between habitats (also known as phoresy). Members of the Acaroidae are mainly fungivorous or saprophytic (Lindquist *et al.*, 2009).

The chigger, *S. lumsdeni*, is known from the Savanna biome where it was recorded on tree squirrels (*Paraxerus cepapi*) (Zumpt, 1961; Skinner and Chimimba, 2005; Stekolnikov, 2018) and the pouched mouse (Matthee *et al.*, 2020). *Gahrliepia nana* is known to parasitize the common mole rat (*Cryptomys hottentotus*), the lesser leaf-nose bat (*Hipposideros caffer*) and the Namaqua rock mouse in the Grassland biome in the central-eastern and eastern region of South Africa (Gauteng and Kwa-Zulu Natal) (Zumpt, 1961; Stekolnikov, 2018; Matthee *et al.*, 2020; Stevens *et al.*, 2022). *Schoutedenichia morosi* was previously recorded on the Cape gerbil (*Gerbilliscus afra*) and vlei rat (*Otomys irroratus*) in the south-eastern Grassland biome of Lesotho (Zumpt, 1961; Stekolnikov, 2018). Although *S. dutoiti* was described by Zumpt (1961) on the South African pouched mouse in the south-eastern part of South Africa, its presence on *G. leucogaster* has earlier been reported by Matthee *et al.* (2020) in the same locality. *Microtrombicula mastomyia* is known from Central and West Africa where it has a broad host range. Its presence in South Africa was marked as a new country locality by Matthee *et al.* (2020) but it was also reported on the Namaqua rock mouse in the Savanna biome by Stevens *et al.* (2022). The remaining chigger species, *A. ueckermanni*, *S. horaki* and *T. walkerae*, were recently described as new (Stekolnikov and Matthee, 2019). Stekolnikov and Matthee (2019) noted that *Trombicula walkerae* represented the first record of the genus *Trombicula sensu stricto* on the African continent. The *Ascoschoengastia* genus is known from 4 species in Africa. However, the recently described *A. ueckermanni* represents the first record for this genus in South Africa where it has been recorded on *Mastomys* sp. and the Tete veld rat (*Aethomys ineptus*). The genus *Schoutedenichia* is well represented in Africa (Stekolnikov, 2018) and the recently described species, *S. horaki*, has been recorded on *Mastomys* sp. and the pouched mouse.

In this study, the pinna was one of the preferred parasitopes for chiggers. This parasitope was also recorded for a *Leptotrombidium* species on the white-footed mouse (*Peromyscus leucopus*) in northern Michigan (Wrenn, 1974). Additionally, Goff (1979) noted that 96% of *Guntheria omega* were associated with the ear fringe of rodents in Papua New Guinea. In South Africa, this parasitope was previously recorded for chiggers on the Namaqua rock mouse in the Savanna (Fagir *et al.*, 2014; Stevens *et al.*, 2022) and the Grassland biome (Stevens *et al.*, 2022). Here, we found that the tail base was another preferred parasitope. The tail base and perineum of the host were also previously recorded for chiggers on rodents in South Africa (Barnard *et al.*, 2015; Stevens *et al.*, 2022).

Effects of host- and habitat-associated factors

Adult males (especially reproductively active) harboured significantly higher flea and mite counts. This pattern is supported by previous studies on ectoparasites associated with rodents in

Table 5. Summary of model-averaged (conditional average) coefficients for generalized linear mixed-effects models with negative binomial distribution on the effect of host sex (SX), reproductive state (RS) and habitat type (HBT) on the epifaunistic taxon abundance belonging to different higher taxa on *Gerbilliscus leucogaster* (n = 123[a])

Parasite Taxon	Explanatory variables	Estimate ± s.e.	95% CI	z	R^2c	R^2m
Taxon abundance						
Fleas	SX	0.10 ± 0.05*	0.005–0.20	2.05	0.42	0.13
	RS × SX	−0.11 ± 0.04*	−0.19 to −0.02	2.55		
Ticks	HBT	0.22 ± 0.08**	0.06–0.37	2.67	0.61	0.18
Mites	SX	0.01 ± 0.01*	0.001–0.02	2.29	0.77	0.05
	RS × SX	−0.01 ± 0.00**	−0.02 to −0.003	2.67		

The random factor in all models was year. R^2c and R^2m are – conditional and marginal R^2. Significance of estimates –.
[a]Data on reproductive state was only available for 123 individuals.
***$P < 0.001$, **$P < 0.01$, *$P < 0.05$.

Table 6. Summary of model-averaged (conditional average) coefficients for generalized linear mixed-effects models with poisson distribution on the effect of host sex (SX) and habitat type (HBT) on the epifaunistic taxon richness belonging to different higher taxa on *Gerbilliscus leucogaster* (n = 123[a])

Parasite Taxon	Explanatory variables	Estimate ± s.e.	95% CI	z	R^2c	R^2m
Taxon richness						
Ticks	HBT	0.84 ± 0.35*	0.15–1.52	2.38	0.27	0.15
Mites	SX	0.09 ± 0.04*	0.009–0.18	2.18	0.59	0.02

The random factor in all models was year. R^2c and R^2m are – conditional and marginal R^2. Significance of estimates – ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$.
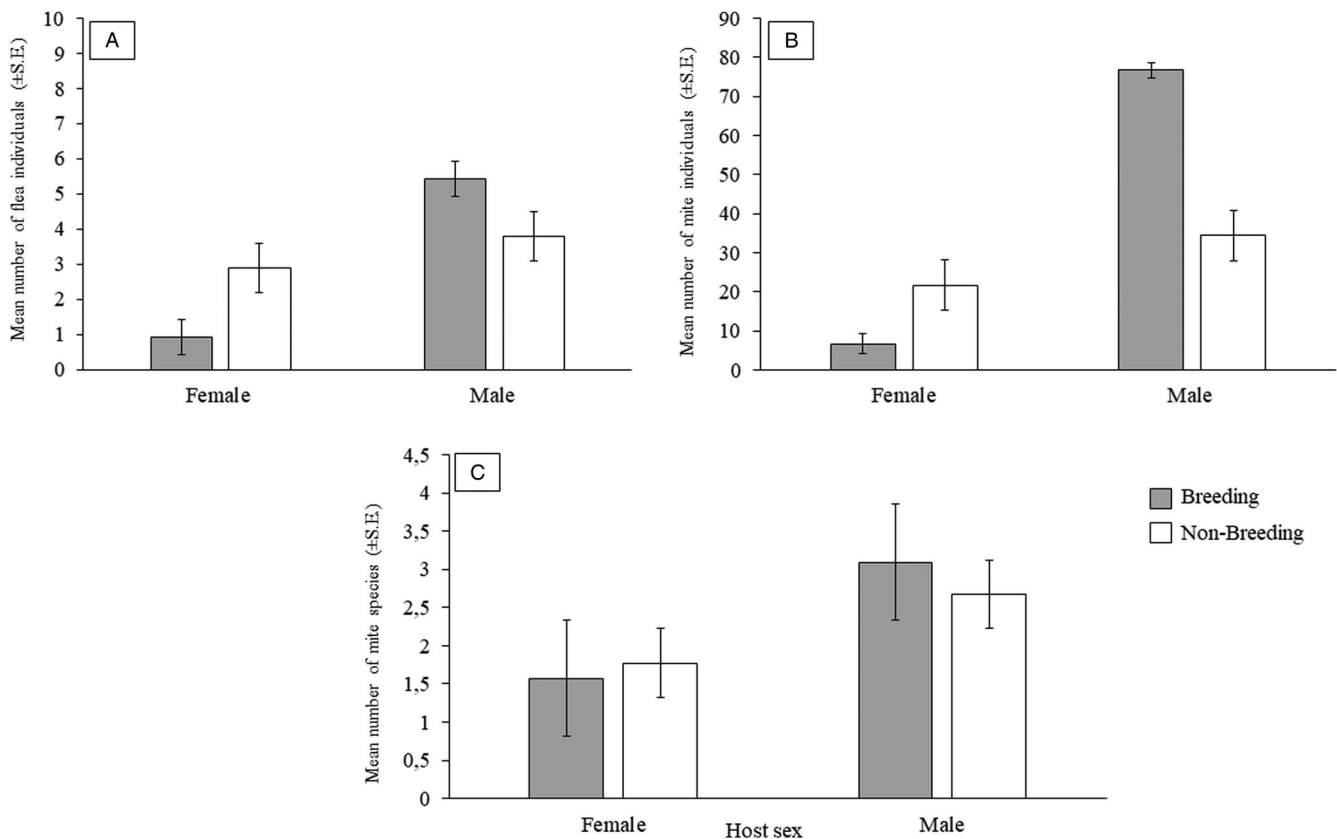[a]Data on reproductive state was only available for 123 individuals.

South Africa (Matthee *et al.*, 2010; Archer *et al.*, 2014; Fagir *et al.*, 2015) and elsewhere (Kowalski *et al.*, 2015; Hamidi and Bueno-Marí, 2021). As mentioned above, male biased ectoparasite infestation can be a result of several, not mutually exclusive, factors. Among them, sexual size dimorphism cannot explain sexual differences in ectoparasite infestation of *G. leucogaster* because males and females of this species are similar in size, as was also found in our study (Skinner and Chimimba, 2005). Consequently, these differences might be due to other mechanisms. For example, behavioural activities such as grooming and vagility (Krasnov *et al.*, 2012; Akinyi *et al.*, 2013). Indeed, Lötter and Pillay (2012) reported that female *G. leucogaster* groom more frequently than males. Given that grooming is an effective method to reduce ectoparasite infestations (Hawlena *et al.*, 2007, 2008), this may explain lower flea and mite counts and fewer mite species on females (Hart *et al.*, 1992; Mooring *et al.*, 2004). Regarding vagility, our sampling was mainly carried out during the breeding season (September and October) of *G. leucogaster*. It is thus possible that reproductively active males roamed more widely than females (Wang *et al.*, 2011; Gromov, 2012). Burdelov *et al.* (2007) demonstrated that starving fleas are positively phototactic and will therefore cluster at the openings of abandoned burrows and wait for a potential host (Darskaya and Besedina, 1961). More frequent roaming and larger home ranges by reproductively active males may result in higher visitation rates at burrows of other rodents, where they may encounter fleas and mites (Krasnov and Matthee, 2010). Although elevated testosterone levels during the breeding season may be another important contributing factor to male-biased infestations (Zuk and McKean, 1996; Hughes and Randolph, 2001; Ezenwa *et al.*, 2012), there is not consistent support for the association between high testosterone levels and parasite infestations (Grear *et al.*, 2009; O'Brien *et al.*, 2018).

In the present study, hosts captured in the natural compared to the agricultural habitat harboured more ticks. Several ixodid tick species require multiple host species and a favourable external environment, such as vegetation, to complete their life cycle (Cupp, 1991; Horak *et al.*, 2018). It is therefore not surprising that studies have reported a significant relationship between habitat type and tick occurrence (Gray, 1998; Jaenson *et al.*, 2009; Ledger *et al.*, 2019). The vegetation structure that is associated with a particular habitat type can have direct and indirect effects on ticks. Firstly, vegetation structure can directly affect the microclimatic conditions to which free-living tick life stages are exposed (Schulze and Jordan, 2005; Tack *et al.*, 2012; Ledger *et al.*, 2019). For example, canopies of woody plants alter the microclimate beneath and around them by intercepting precipitation and by shading, which increases soil moisture (Breshears *et al.*, 1998; Potts *et al.*, 2010; Lozano-Parra *et al.*, 2018). In addition, a layer of vegetation and leaf litter can insulate the soil and buffer it against extreme heat and cold temperatures (Pierson and Wight, 1991; Breshears *et al.*, 1997). Tick development and survival in the external environment is therefore facilitated in more sheltered habitats with a permanent vegetation layer and a more stable microclimate (Pfäffle *et al.*, 2013; Paul *et al.*, 2016). Tick genera recorded in the present study are 2- and 3-host ticks (i.e. those that need to find 2 or 3 different hosts, respectively, to complete their life cycle) (Horak *et al.*, 2018). Favourable microclimatic conditions seem to be particularly important for these taxa as their larval and nymphal life stages quest for hosts from the soil surface or from grass tufts (Horak and Cohen, 2001; Gallivan *et al.*, 2011). In addition, shrub and grass cover is important for ticks to quest and search for a host (Ledger *et al.*, 2019; Mathews-Martin *et al.*, 2020). Apart from *Hy. truncatum* nymphs, all the nymphs from the tick taxa are dependent on vegetation to quest and find a host (Horak *et al.*, 2018). In the present study, the pristine natural habitat had a higher proportion of grass (80 and 79%, respectively) than the agricultural habitat type (70 and 62%, respectively) during August 2014 and January 2015 (S. Matthee unpublished data). It is therefore possible that natural habitats provide a conducive microclimate and physical structures that facilitate tick development and survival (Dube *et al.*, 2018; Shilereyo *et al.*, 2022). Lastly, in the present study the natural habitat supports a larger diversity of vertebrate hosts and a larger

Figure 2. Mean number of: (A) flea individuals (±s.ε.), (B) mite individuals (±s.ε.) and (C) mite species (±s.ε.) per host sex and per reproductive state for *Gerbilliscus leucogaster* (*n* = 123*) in Mpumalanga, South Africa, 2014–2020. *Data on reproductive state was only available for 123 individuals.
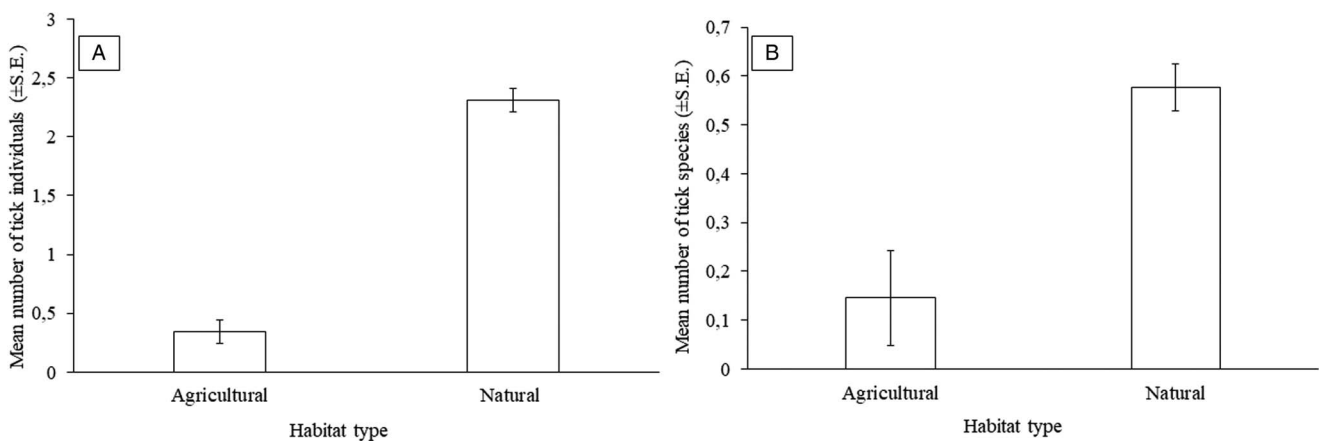
Figure 3. Mean number of: (A) tick individuals (±s.ε.) and (B) tick species (±s.ε.) per habitat type for *Gerbilliscus leucogaster* (*n* = 127) in Mpumalanga, South Africa, 2014–2020.

diversity of small and large-bodied vertebrate families (e.g. Bovidae, Canidae, Giraffidae and Rhinocerotidae) (Du Toit, 2003) of which the latter act as natural hosts for the adult life stages (Horak *et al.*, 2018). This contrasts with the agricultural habitat type that comprises small crop fields that generally harbour rodents and are infrequently visited by dogs, cattle and goats (personal observation). In addition, habitat types with a higher proportion of larger bodied vertebrate hosts have a higher abundance of ticks (Horak *et al.*, 2022) and more adult tick life stages (Esser *et al.*, 2016).

This study represents the first systematic long-term assessment of the ectoparasite species associated with *G. leucogaster*. We conclude that *G. leucogaster* is host to a large diversity of epifaunistic species of which mites represent a significant proportion. The

relationships recorded between ectoparasite infestations, and the host and habitat factors were life history specific. In particular, the level of infestation by ectoparasites closely associated with the host (fleas and mites) was affected by host-associated factors, while infestation by ectoparasites that spend most of their life in the external environment (ticks) was affected by habitat type. Although the study was limited to local conditions, it provides a valuable baseline for future broader scale studies on *G. leucogaster* in South and southern Africa.

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