Host and habitat shape ectoparasite diversity on *Mastomys natalensis* and *Mastomys coucha* (Muridae)

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Abstract

Mastomys natalensis and *M. coucha* are commensal rodent species endemic to Africa. A recent taxonomic revision within *Mastomys* leaves the parasite–host list of *M. natalensis* questionable and that of *M. coucha* incomplete. The current study aimed to develop a better understanding of the ectoparasite diversity associated with the 2 distinct but closely related rodent species and to explore the influence of host and habitat type on ectoparasite infestations. Between 2014 and 2020, 590 rodents were trapped in 3 habitat types (village, agriculture and natural) across a wildlife-human/domestic animal interface. In total 48 epifaunistic species (45 ectoparasitic and 3 predatory) represented by 29 genera from 4 taxonomic groups (fleas, lice, mites and ticks) were recorded. Only 50% of the epifauna were shared between the 2 rodent species, with mites the most speciose taxon in both host species. The abundance of epifaunistic individuals, and also those of mites and fleas, were significantly higher on male *M. natalensis*, while ticks were significantly higher on reproductively active *M. natalensis*. For both rodent species, infestations by most epifaunistic taxa (on *M. natalensis*) and some taxa (on *M. coucha*) were significantly lower in the village as opposed to the less disturbed agricultural and natural habitat types. The study highlights the importance of host life history, even in closely related rodent species, in shaping parasite profiles and a loss of parasite diversity in more extreme anthropogenic habitats.

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Introduction

Rodentia is the largest mammalian order and have successfully colonized most of the globe (Wilson and Reeder, 2005). Their generally small size, vagility and adaptability enables them to occur in diverse habitats across the globe where they also encounter various parasites occurring in the external environments, in their nests and on the bodies of co-occurring hosts. For example, free-living immature life stages (larvae and/or nymphs) of most ixodid ticks and chiggers (trombiculid mites) attach to rodents when they move through vegetation, while lice are transferred between conspecifics through close body contact (e.g. during suckling, grooming and nest sharing) (Morand *et al.*, 2006). Given the diverse life-history characteristics displayed by rodents (e.g. sociality, body size, habitat preference and nest types) it is expected that their parasite profiles will be influenced by life-history traits (Krasnov *et al.*, 2010; Morand and Bordes, 2015). Indeed, higher parasite infestations are often associated with larger bodied hosts (providing more available niches and/or resources) (Kamiya *et al.*, 2014; Esser *et al.*, 2016) and high host population densities (providing more opportunity to encounter parasites) (Arneberg, 2001; Altizer *et al.*, 2003). In addition, rodents that are geographically widespread (occur in multiple vegetation types) encounter diverse parasite species mainly due to vegetation type associated parasite distributions (i.e. distance decay in species similarity) (Spickett *et al.*, 2017; Wells *et al.*, 2018; Stevens *et al.*, 2022).

Geographically widespread rodent species are often opportunistic in nature and take advantage of alternative resources available in anthropogenic habitats to the extent that they become pests (Drazo *et al.*, 2008; Makundi and Massawe, 2011; Welegerima *et al.*, 2020). Habitat transformation generally results in a change in the microclimatic conditions due to change in vegetation structure and reduced vegetation cover (Gehlhausen *et al.*, 2000; Newman *et al.*, 2013). Consequently, variation in the microclimatic conditions between habitat types (e.g. natural and transformed habitat types) is documented to affect parasite occurrence and infestation levels (Lorch *et al.*, 2007; Froeschke *et al.*, 2013; Froeschke and Matthee, 2014; van der Mescht *et al.*, 2016). The role of habitat-associated factors in shaping parasite infestations is mainly related to the susceptibility of free-living life stages to desiccation (Krasnov *et al.*, 2001a, 2001b; Herrmann and Gern, 2013; van der Mescht *et al.*, 2013). Parasite taxa with free-living

life stages (nematodes, fleas, mites and ticks) are particularly more sensitive to the microclimatic conditions (e.g. air temperature and relative humidity) compared to parasite taxa, such as lice, where all life stages occur permanently on the host's body (Krasnov et al., 2010; Viney and Cable, 2011; Härkönen et al., 2013).

To further investigate the role of abiotic factors (the environment) and host life history on parasite profiles of rodents, we herein study 2 multimammate mice species, *Mastomys natalensis* and *M. coucha*. In the 1970's, *M. natalensis* underwent taxonomic revision and a second species, *M. coucha*, was recognized based on differences in chromosome numbers, haemoglobin patterns, mtDNA sequencing, and subtle differences in the morphology of the cranium (Gordon, 1978; Green et al., 1980; Granjon et al., 1997). The 2 rodent species are widely distributed habitat generalists that overlap in occurrence in the north-eastern and eastern summer rainfall region (Savanna and Grassland biomes) in South Africa (Skinner and Chimimba, 2005; Monadjem et al., 2015). However, based on previous studies it appears that *M. natalensis* are more commensal (associated with houses) (Brouat et al., 2007; Mulungu et al., 2011, 2013), and that *M. coucha* could prefer less disturbed habitats. The latter may be mainly attributed to the higher breeding success of *M. natalensis* on a poor quality diet when compared to *M. coucha* (Jackson and van Aarde, 2004). *Mastomys* species are prolific breeders, live in family groups (Isaacson, 1975; Leirs et al., 1996a, 1996b) and can attain high population densities in anthropogenic habitats (Makundi and Massawe, 2011). In particular, *M. natalensis*, is regarded as an agricultural pest (Singleton et al., 2003; Prakash, 2018) where they frequently utilize abandoned burrows of other rodent species (Veenstra, 1958). *Mastomys natalensis* is also a reservoir host for disease causing pathogens such as Lassa virus that causes haemorrhagic fever, and *Yersinia pestis* which is the causative agent for bubonic plague (Isaacson, 1975; Singleton et al., 2003; Achtman et al., 2004; Lecompte et al., 2006). From a disease perspective, it is important to realize that the movement of commensal rodent species between habitat types and higher densities recorded in anthropogenic habitats, creates novel opportunities for parasite exchange and may pose a disease risk to domestic animals and humans (Lecompte et al., 2006; Brettschneider et al., 2012).

Although the ecology and taxonomy of *M. natalensis* and *M. coucha* is relatively well studied, information regarding their ectoparasite profiles is limited and biased towards parasite–host lists originally described for *M. natalensis* (Zumpt, 1961; Isaacson, 1975; Ledger, 1980; Segerman, 1995; Horak et al., 2018). Given the taxonomic revision of the host genus, and the fact that the 2 rodent species are cryptic, it is essential that the ectoparasite profile of *M. natalensis* is re-assessed and an ectoparasite profile established for *M. coucha*. More recent empirical studies documented a rich ectoparasite diversity associated with widely distributed rodents in South Africa (e.g. Matthee et al., 2007, 2010; Froeschke et al., 2013; Archer et al., 2014; Fagir et al., 2014, 2015; Stevens et al., 2022; Smith et al., 2023) and made a considerable contribution in updating parasite lists for these rodents. Several of the ectoparasite taxa recorded in these studies are known vectors for disease-causing pathogens such as *Y. pestis* (causative agent of plague) and *Rickettsia africae* (causative agent of African tick-bite fever) (Achtman et al., 2004; Ledger et al., 2022). To date only a few studies have explored the ecological factors (e.g. host and environment) that shape parasite infestations in South Africa (Froeschke et al., 2010, 2013; Froeschke and Matthee, 2014; van der Mescht et al., 2016; Smith et al., 2023). Although these studies confirm the importance of the host, habitat type and climate in shaping parasite infestations more studies on rodents with diverse life histories are needed before general patterns can be established.

The overall aim of the study was to develop a better understanding of the ectoparasite diversity associated with the 2 distinct but closely related rodent species and to explore the role of host and habitat type in shaping ectoparasite infestations. The objectives of the study were: (1) Record the ectoparasite diversity associated with *M. natalensis* and *M. coucha* across a wildlife-humans/ domestic animal interface, and (2) Explore the relationship between ectoparasite infestations, and host (sex, breeding state and body size) and habitat (village, agriculture and natural) factors in both rodents. Given the close evolutionary relationship between the rodents studied herein, it is predicted that the ectoparasite profile will largely overlap between *M. natalensis* and *M. coucha*. Further, it is predicted that ectoparasite infestations will be related to, (i) host sex, with higher infestations associated with larger-bodied male hosts, and (ii) habitat type, where ectoparasite taxa with free-living life stages (fleas, mites and ticks) will respond more strongly to habitat transformation.

Materials and methods

Study area

The study was conducted across a wildlife-human/domestic animal interface, located in the Mnisi rural community situated in the north-eastern Savanna biome of South Africa. The community comprises of several small villages that each have their own communal cattle grazing area and subsistence crop fields (also referred to as agriculture). Approximately 75% of the boundary surrounding the Mnisi rural community is shared with adjacent fenced nature reserves (Fig. 1). Rodents were trapped in the Manyeleti nature reserve (24°35′0.1″ S, 31°25′56″ E) and in 4 villages and their respective crop fields (Gottenburg 24°38′01″ S, 31° 25′19″ E; Hlavekisa 24°37′51″ S, 31°22′42″ E, Athol 24°42′29″ S, 31°20′43″ E and Utlha 24°50′14″ S, 31°02′45″ E) in 2014, 2015 and again in 2019 and 2020. The villages were >5 km apart from each other. Small vegetable patches, cattle and other domestic animals can be found on the property (in the village). Crop fields were planted with seasonal crops that were fenced with a combination of wire and dried tree branches that were stacked to form a fence. The crop fields were situated on the edge of the villages and often occurred between the village and nature reserve. Cattle could be found in the crop fields during the dry season. The nature reserve comprised of pristine natural Savanna vegetation and biome-associated wildlife species.

Rodent trapping and handling

Sherman-type live traps and Tomahawk live traps were used to trap rodents across 3 different habitat types namely, village (transformed), agriculture (semi-transformed), and natural (undisturbed). Rodents were trapped at 3 villages and their respective crop fields in spring (August–October) of 2014 and 2015, and once in summer (January) of 2015 and at 4 villages and their respective crop fields in spring (August–October) 2019 and 2020. A standardised trap design was followed every year, and each locality was only trapped once per trap session. Traps were placed at 10 m intervals along an 80 m-trap line that was replicated (3–4 times) at each sampling locality. The traps were left out for 3–4 days per locality. In the village, traps were set in and around the houses. In the agricultural habitat traps were placed along the fence of the crop fields, whereas in the nature reserve traps were set in trap lines in the natural vegetation. A mixture of oats and peanut butter was used as bait. Traps were checked twice daily and closed during the heat of the day (10:00–15:00). Targeted rodents were removed from the traps, individually placed into labelled plastic bags and euthanized
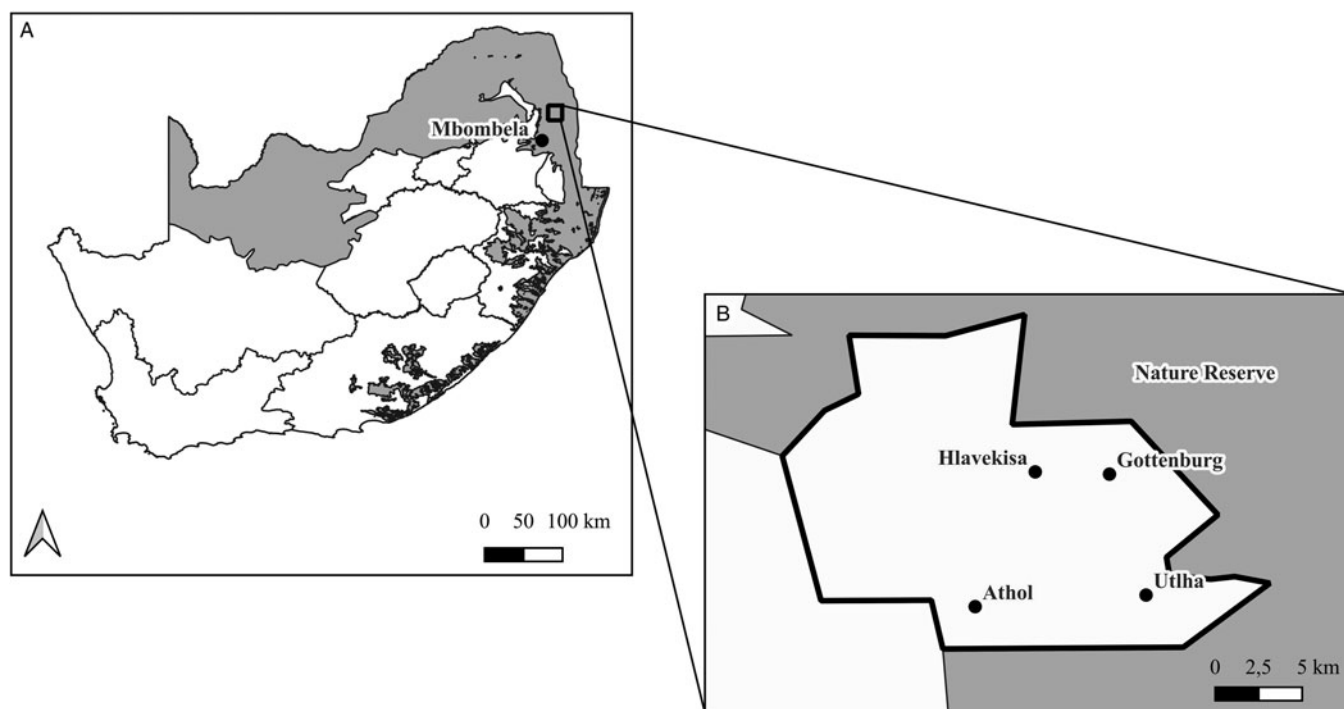
Figure 1. Study area where *Mastomys natalensis* (*n* = 375) and *Mastomys coucha* (*n* = 215) were trapped across a wildlife-human/domestic animal interface in Mpumalanga, South Africa. (a) Savanna biome (grey) in South Africa and the position of the sampling area (square on map). (b) position of the villages and the nature reserve.

with Isoflurane. All non-target rodent species were recorded and released at the trap sites. Targeted rodent species were frozen at −20°C to kill all ectoparasites. The rodents were initially morphologically identified to genus level using field guides (Stuart and Stuart, 2007) and thereafter species were confirmed molecularly using a species-specific mtDNA cytochrome-b multiplex PCR (Bastos *et al.*, 2005). For each rodent, their sex, reproductive state (breeding: males having a scrotum and females having a perforated vagina; or non-breeding: males with no visible scrotum and females with no perforated vagina), body weight, total-, tail- and hind foot- length was recorded. Rodents were dissected to further confirm rodent sex and reproductive state.

Laboratory procedures

Prior to ectoparasite removal rodents were thawed. All ectoparasites (fleas, lice, mites and ticks) and a subsample of trombiculid mites (chiggers) were systematically removed with fine point forceps while examining the body of the rodent under a Zeiss Stemi DV4 stereomicroscope (Carl Zeiss Light Microscopy, Göttingen, Germany). In the case of chiggers, the parasitope (region on the body where chiggers occurred) was recorded for each subsample. Ectoparasites were counted and placed into individual tubes containing 100% ethanol. All fleas (males and females) were counted, however only male individuals were available for species level identification and counts per species, as female fleas were used for a separate project and could not be identified to species level. The immature life stages of individual louse species remained undifferentiated and was reported as nymphs and counts presented per species. Fleas were mounted (in Canada balsam) as described by Segerman (1995) and van der Mescht *et al.* (2013). Lice and mites were cleared in lactic acid and mounted in Hoyer's or PVA (polyvinyl alcohol) on microscope slides. A subsample of the lice was kept for molecular examination. Chiggers were directly slide mounted in Hoyer's or PVA mounting medium. Ticks remained in 100% ethanol for morphological

identification. Identification of fleas, lice, mites and chiggers was done using a Leica DM1000 light microscope (Leica Microsystems GmbH, Wetzlar, Germany) and ticks were identified with a Leica MZ75 high-performance stereomicroscope (Leica Microsystems GmbH, Wetzlar, Germany). All ectoparasites were morphologically identified to species level where possible using taxonomic reference literature; fleas (Segerman, 1995); lice (Johnson, 1972; Ledger, 1980; Durden and Musser, 1994); mites (Till, 1963; Herrin and Tipton, 1975); chiggers (Zumpt, 1961; Stekolnikov, 2008, 2018) and ticks (Walker *et al.*, 2000; Horak *et al.*, 2018). In a few cases the differentiation between *Hoplopleura intermedia* and *H. ismailiae* louse individuals was troublesome and are referred to as *H. intermedia/ismailiae*.

Data analysis

The relative host density, for the 2 rodent species, was estimated on trapping success (%) (number of trapped animals divided by the number of trap nights multiplied by the number of traps) (Froeschke *et al.*, 2013). For descriptive statistics on epifaunistic infestations per rodent species, rodent and epifaunistic data were pooled per locality within each of the habitat types (village, agriculture and natural) for all sampling years (2014–2020 for all taxa except mites, as species-level abundance data for mites was only available for 2019–2020) and seasons. For each rodent species we divided the epifauna 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 taxa. The mean abundance (total epifaunistic abundance divided by the number of hosts) and prevalence (% of hosts infested) were calculated following Bush *et al.* (1997). Chigger prevalence was calculated using presence/absence data from 2019–2020, as chigger species identification per rodent species was only available for this sampling period.

To explore the relationship between epifaunistic infestations, host and habitat factors the following approach was used: total counts of epifaunistic individuals for a given taxon (overall

epifauna, fleas, lice, ticks and mites) were calculated for 2014–2020 (excluding January 2015) and species richness per taxon (overall epifauna, fleas and mites) was calculated for 2019–2020 on an individual host (i.e. infracommunity). Only rodents with confirmed reproductive state were used for regression analyses, which meant that a reduced sample size was used for these analyses. Epifaunistic count data (excluding chiggers) was modified (log + 1 transformed) prior to analyses as the data was highly skewed with an excess of zero's. All models were fit to examine the influence of host-related factors (sex, reproductive state, interaction between reproductive state and sex and body size (tail length as proxy)), habitat type (village, agriculture, natural) and sampling year on the total count for each ectoparasite taxon and species richness of each host species. A generalised linear model (GLM) was constructed for the overall epifauna and mite counts following a Poisson distribution for both rodent species (note, although a negative binomial distribution is often used for ectoparasite data, our preliminary analysis suggests a stronger support to the Poisson distribution). To account for the large number of zero's in flea, tick and louse counts, a zero-inflated Poisson (ZIP) and a zero-inflated negative binomial (ZINB) model were generated from 'pscl' package in R (R Core Team, 2023). The methodology and mathematics of the ZIP and ZINB models can be found in (Zeileis *et al.*, 2008; Zuur *et al.*, 2009; Zuur and Ieno, 2016). The ZIP or ZINB models, were compared using a Likelihood Ratio Test (LRT).

The relationship between epifaunistic, flea, mite species richness and host and habitat related factors were based on individual hosts of each rodent species. Species richness was not informative for lice (as the taxon was dominated by 1 or 2 louse species) and for ticks (due to low infestations: 4–5 individuals during the 2019–2020 sample period) for both rodent species. For the regression analyses of epifaunistic, flea and mite species richness a GLM with a Poisson distribution was used. A backward model selection was considered for all regression analyses (count and species richness), using a 'step' function for all models, whereby the models with the lowest Akaike information criterion (AIC) were presented as the final selected models (Burnham and Anderson, 2002; Snipes and Taylor, 2014). All statistical analyses were performed in R version 4.2.0 (R Core Team, 2023).

Results

Rodent density

In total 375 *M. natalensis* and 215 *M. coucha* individuals were trapped (Supplementary Table 1). The number of individuals trapped, and their relative densities varied between habitat types for both rodent species (Supplementary Table 2; Fig. 2). In particular, the total abundance of *M. natalensis* was higher in the village and agricultural habitat types compared to the natural habitat. In contrast, the total abundance of *M. coucha* was higher in the natural and agricultural habitat types compared to the village habitat type (Fig. 2).

Epifaunistic diversity

A total of 10 420 epifaunistic individuals (parasitic and nonparasitic) were recorded of which 5053 were recorded on *M. natalensis* and 5367 on *M. coucha* during the sampling period. Overall, 45 ectoparasitic and 3 non-parasitic species (predatory mites) were recorded on *M. natalensis* and *M. coucha* (Supplementary Table 3). Mites (excluding chiggers) were the most speciose taxon (23), followed by chiggers (8), fleas (7), ticks (6) and lice (4) (Supplementary Table 3). The 2 rodent species shared 23 of the 48 epifaunistic species (Supplementary Table 3). A larger number of epifaunistic species were recorded on *M. natalensis* (40) compared to *M. coucha* (31) (Supplementary Table 3).

Five flea species were recorded on *M. natalensis* and 6 species on *M. coucha*. However, fleas were more prevalent on *M. natalensis* (46.93%) compared to *M. coucha* (35.81%). *Xenopsylla brasiliensis* and *X. frayi* were the most prevalent fleas on both rodent species (Supplementary Tables 4 and 5). *Echidnophaga gallinacea* occurred on both rodent species, but the total abundance was higher on *M. natalensis* (9), while only 1 individual was recorded on *M. coucha*. Three louse species were recorded on *M. natalensis* and 2 on *M. coucha*. Lice were less prevalent on *M. natalensis* (33.33%) in comparison to *M. coucha* (54.42%). *Hoplopleura intermedia* was the most prevalent louse on both rodent species. *Polyplax biseriata* was only recorded on *M. coucha*, while *H. intermedia/ismailiae* and *P. spinulosa* was only recorded on *M. natalensis* (Supplementary Tables 4 and 5). Five tick taxa (species and species groups) were recorded on *M. natalensis* and 4 on *M. coucha*. However, ticks were overall less prevalent on *M. natalensis* (6.93%) as opposed to *M. coucha* (22.79%). *Dermacentor rhinocerinus* was shared between the 2 rodents, while *Amblyomma hebraeum* and *Haemaphysalis zumpti* was only recorded on *M. natalensis* whereas *Hyalomma truncatum* was only recorded on *M. coucha* (Supplementary Tables 4 and 5). There were 19 mite species (excluding chiggers) recorded on *M. natalensis* and 12 recorded on *M. coucha*. Mites were less prevalent on *M. natalensis* (81.01%) compared to *M. coucha* (92.50%). Two parasitic mites *Laelaps liberiensis* and *L. muricola* were the most prevalent mite species on both rodent species (Supplementary Tables 4 and 5). Eight chigger species were recorded on *M. natalensis* and 6 on *M. coucha*. Chiggers were less prevalent on *M. natalensis* (25.32%) compared to *M. coucha* (45.00%). *Microtrombicula mastomyia* occurred on both rodent species, but at a lower prevalence on *M. natalensis* (22.36%) compared to *M. coucha* (36.67%) (Supplementary Table 6). On both rodent species several chiggers occurred on the ear pinna (Supplementary Table 6).

Mastomys natalensis – Role of host- and habitat factors

The results of the final selected models are presented in Tables 1–3. Overall epifaunistic, mite and flea abundance were significantly related to host sex, with higher infestations on males compared to females (Tables 1 and 2; Fig. 3a–c). Tick abundance was significantly higher on breeding individuals, while louse occurrence was significantly higher on non-breeding rodents (Table 2). None of the infestation parameters (abundance or number of species) for overall epifauna, mites, fleas, lice and ticks on *M. natalensis* were significantly correlated with the interaction between sex and reproductive state and body size (Tables 1 and 2). In addition, none of the infestation parameters for overall epifauna, mites, fleas and ticks were significantly different between the agriculture and natural habitat types (Tables 1 and 2). However, overall epifaunistic, mite and tick abundances (Tables 1 and 2) were significantly lower in the village habitat type compared to the agricultural and natural habitat types (see Fig. 4a for epifaunistic abundance). Louse abundance was significantly higher on *M. natalensis* in the natural compared to the agricultural habitat type (Table 2; Fig. 4b). However, louse abundance did not differ between the agricultural and village habitat type, whereas louse occurrence was significantly higher on *M. natalensis* in the agricultural habitat compared to the village habitat type (Table 2). The number of epifauna, flea and mite species were significantly lower in the village compared to the agricultural habitat type (Table 3; Fig. 5a and b). Overall epifauna, tick abundance and the number of flea species were related to sampling year (Tables 1–3).
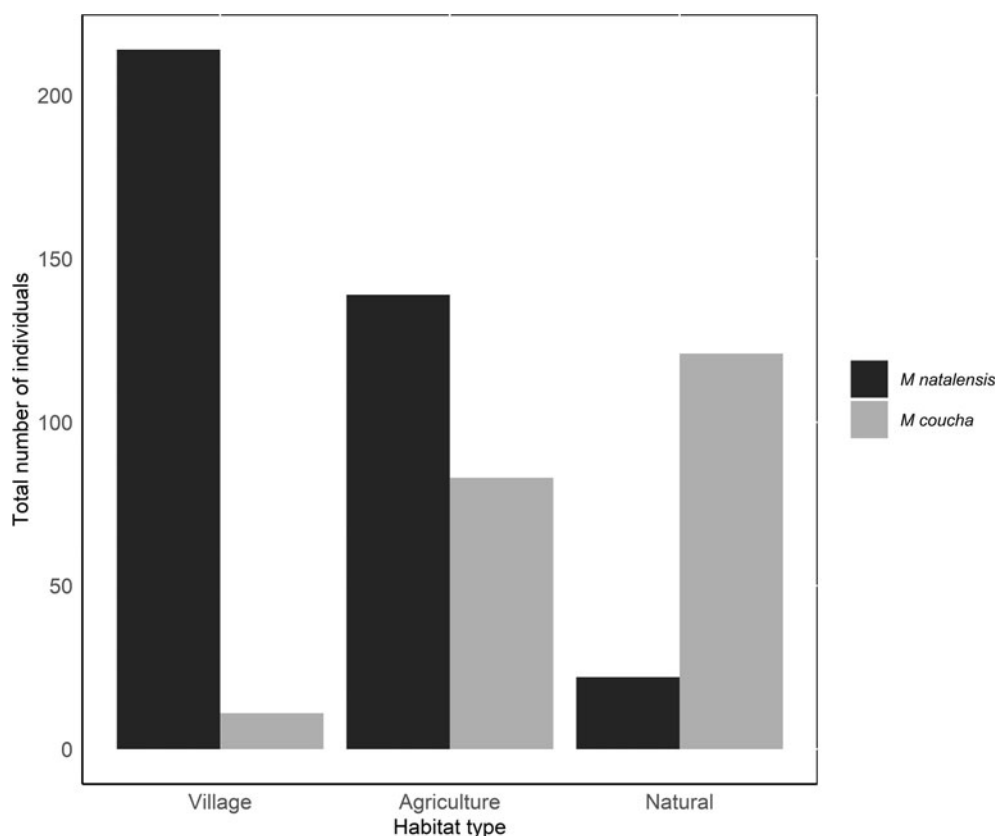
Figure 2. The total number of *Mastomys natalensis* (*n* = 375) and *Mastomys coucha* (*n* = 215), trapped in three habitat types across a wildlife-human/domestic animal interface in Mpumalanga, South Africa (2014–2020).

Mastomys coucha – *Role of host- and habitat factors*

The results of the final selected models are presented in Tables 4–6. Louse occurrence was significantly negatively related to host body size (i.e. higher occurrence on smaller-bodied rodents; Table 5). None of the infestation parameters for overall epifauna, mites, fleas and ticks on *M. coucha* were significantly associated with host sex, reproductive state, the interaction between sex and reproductive state and body size (Tables 4 and 5). Additionally, none of the infestation parameters for overall epifauna, mites, fleas and ticks were significantly

Table 1. Summary of the final selected generalized linear model with a Poisson distribution on the effect of host sex (SEX), reproductive state (BRS), year (Y) and habitat type (HBT) on the epifaunistic taxon abundance belonging to different higher taxa on *Mastomys natalensis* (*n* = 304, 2014–2020). Bold text indicate significant responses.

Taxon	Variable	Estimate	SE	*z*-value	*P* value
Overall epifaunistic individuals	BRS	0.284	0.165	1.721	0.085
	SEX	0.350	0.152	2.297	**0.022**
	HBT NAT: HBT AGR	0.180	0.146	1.230	0.219
	HBT VIL: HBT AGR	−0.466	0.106	−4.402	**<0.001**
	HBT NAT: HBT VIL	0.646	0.163	3.965	**<0.001**
	Y2015:Y2014	−0.069	0.178	−0.387	0.698
	Y2019:Y2014	−0.360	0.166	−2.163	**0.031**
	Y2020:Y2014	−0.307	0.169	−1.817	0.069
Mites	BRS	0.319	0.166	1.925	0.054
	SEX	0.324	0.158	2.052	**0.040**
	HBT NAT: HBT AGR	0.129	0.148	0.872	0.383
	HBT VIL: HBT AGR	−0.454	0.087	−5.199	**<0.001**
	HBT NAT: HBT VIL	0.583	0.156	3.742	**<0.001**
	BRS × SEX	−0.279	0.194	−1.440	0.150

Reference levels are male for SEX, non-breeding for BRS.
HBT NAT, natural habitat; HBT AGR, agricultural habitat; HBT VIL, village habitat.

Table 2. Summary of the final selected zero-inflation model with a Poisson distribution on the effect of host sex (SEX), reproductive state (BRS), tail length (TLL), year (Y) and habitat type (HBT) on the ectoparasite abundance belonging to different higher taxa on *Mastomys natalensis* (*n* = 304, 2014–2020). Bold text indicate significant responses.

Taxon	Variable	Estimate	SE	z-value	*P* value
Count model					
Fleas	SEX	0.471	0.179	2.641	**0.008**
	HBT NAT: HBT AGR	−0.422	0.330	−1.280	0.200
	HBT VIL: HBT AGR	−0.035	0.225	−0.153	0.878
	HBT NAT: HBT VIL	−0.388	0.369	−1.050	0.294
	Y2015:Y2014	−0.021	0.400	−0.053	0.957
	Y2019:Y2014	0.191	0.421	0.454	0.650
	Y2020:Y2014	−0.281	0.407	−0.691	0.490
Lice	BRS	−0.460	0.239	−1.922	0.055
	HBT NAT: HBT AGR	0.655	0.272	2.405	**0.016**
	HBT VIL: HBT AGR	0.392	0.265	1.479	0.139
	HBT NAT: HBT VIL	0.263	0.324	0.811	0.417
Ticks	TLL	0.412	0.356	1.158	0.247
	BRS	−3.161	1.117	−2.830	**0.005**
	HBT NAT: HBT AGR	0.973	1.198	0.812	0.417
	HBT VIL: HBT AGR	−3.039	1.074	−2.828	**0.005**
	HBT NAT: HBT VIL	5.316	1.108	4.798	**<0.001**
	Y2015:Y2014	−4.738	1.773	−2.672	**0.008**
	Y2019:Y2014	−2.267	1.251	−1.813	0.070
	Y2020:Y2014	−5.218	1.330	−3.923	**<0.001**
Zero model					
Fleas	SEX	1.498	1.322	1.133	0.257
	HBT NAT: HBT AGR	−0.569	1.156E3	0.000	1.000
	HBT VIL: HBT AGR	14.370	323.900	0.044	0.965
	HBT NAT: HBT VIL	−12.427	316.804	−0.039	0.969
	Y2015:Y2014	−0.298	1.53E6	0.000	1.000
	Y2019:Y2014	0.931	1.042	0.893	0.372
	Y2020:Y2014	−1.069	1.640	−0.651	0.515
Lice	BRS	−3.111	0.936	−3.323	**<0.001**
	HBT NAT: HBT AGR	−2.674	3.386	−0.494	0.621
	HBT VIL: HBT AGR	2.539	0.687	3.698	**<0.001**
	HBT NAT: HBT VIL	−4.212	3.397	−1.240	0.215
Ticks	TLL	0.388	0.590	0.657	0.511
	BRS	−20.433	188.366	−0.108	0.914
	HBT NAT: HBT AGR	11.154	67.298	−0.166	0.868
	HBT VIL: HBT AGR	29.468	129.561	−0.134	0.893
	HBT NAT: HBT VIL	15.999	93.113	−0.172	0.864
	Y2015:Y2014	43.901	212.537	−0.207	0.836
	Y2019:Y2014	−5.775	93.943	−0.061	0.951
	Y2020:Y2014	26.104	214.986	−0.121	0.903

Reference levels are male for SEX, non-breeding for BRS.
HBT NAT, natural habitat; HBT AGR, agricultural habitat; HBT VIL, village habitat.

different between the agriculture and natural habitat types. However, overall epifauna and mite abundance were significantly lower in the village habitat type compared to the agricultural and the natural habitat type (Table 4; Fig. 6a and b).

Further, louse occurrence was significantly higher on *M. coucha* in the agricultural habitat type compared to the natural and village habitat type and higher in the natural habitat type when compared to the village habitat type (Table 5). Flea and louse

Table 3. Summary of the final selected generalized liner model with a Poisson distribution on the effect of host reproductive state (BRS), tail length (TLL), year (Y) and habitat type (HBT) on number of epifaunistic, flea and mite species on *Mastomys natalensis* (n = 234, 2019–2020). Bold text indicate significant responses.

Taxon	Variable	Estimate	SE	*z*-value	*P* value
Epifaunistic taxa	TLL	−0.088	0.063	−1.410	0.158
	HBT NAT: HBT AGR	−0.116	0.218	−0.534	0.593
	HBT VIL: HBT AGR	−0.558	0.142	−3.938	**<0.001**
	HBT NAT: HBT VIL	0.442	0.237	1.867	0.062
Fleas	HBT NAT: HBT AGR	−1.522	1.046	−1.455	0.146
	HBT VIL: HBT AGR	−1.120	0.482	−2.323	**0.020**
	HBT NAT: HBT VIL	−0.402	1.061	−0.379	0.705
	Y2020	−1.265	0.442	−2.860	**0.004**
Mites	HBT NAT: HBT AGR	−0.249	0.243	−1.024	0.306
	HBT VIL: HBT AGR	−0.601	0.148	−4.057	**<0.001**
	HBT NAT: HBT VIL	0.352	0.261	1.347	0.178

Reference levels are male for SEX, non-breeding for BRS, 2019 for YEAR.
HBT NAT, natural habitat; HBT AGR, agricultural habitat; HBT VIL, village habitat.

abundance, and flea species were significantly related to sampling year (Tables 5 and 6).

Discussion

Epifaunistic diversity

The 2 rodent species only shared approximately 50% of the epifaunistic species. This is most probably the result of the observed variation in spatial occurrence between the rodents with *M. natalensis* occurring mainly in the agricultural and village habitats, while *M. coucha* occurred mainly in the agricultural and natural habitats (Stenseth *et al.*, 2001; Garba *et al.*, 2014; McCauley *et al.*, 2015). Habitat-type associated variance was also recorded in other co-occurring rodent species in the present study. In particular, *Rattus rattus* and *Rattus tanezumi* were trapped predominantly in the village habitat, while *Gerbilliscus leucogaster*, *Saccostomus campestris* and *Lemniscomys rosalia* overlapped

with *M. coucha* (Matthee *et al.*, 2020; Smith *et al.*, 2023). Based on this it is evident that the village habitat harboured fewer rodent species compared to the agricultural and natural habitats. The parasite diversity on *M. natalensis* and *M. coucha* may thus be directly related to variation in abundance and diversity of rodent hosts and their parasites in the different habitat types (also see Krasnov *et al.*, 2004; Morand *et al.*, 2006). Similarly, the variation in relative density across habitat types for both *Mastomys* species will influence their contact with conspecific and confamilial host species and ectoparasites in the environment (Cote and Poulin, 1995; Arneberg *et al.*, 1998). This is consistent with previous studies that recorded a positive relationship between host density and parasite infestations (Esch and Fernández, 1993; Tompkins *et al.*, 2001; Rifkin *et al.*, 2012). It is thus most likely that habitat type-related host diversity and relative abundance contributed to the fact that only 50% of epifaunistic species were shared between the 2 rodents (Haukisalmi *et al.*, 1987; Froeschke and Matthee, 2014).
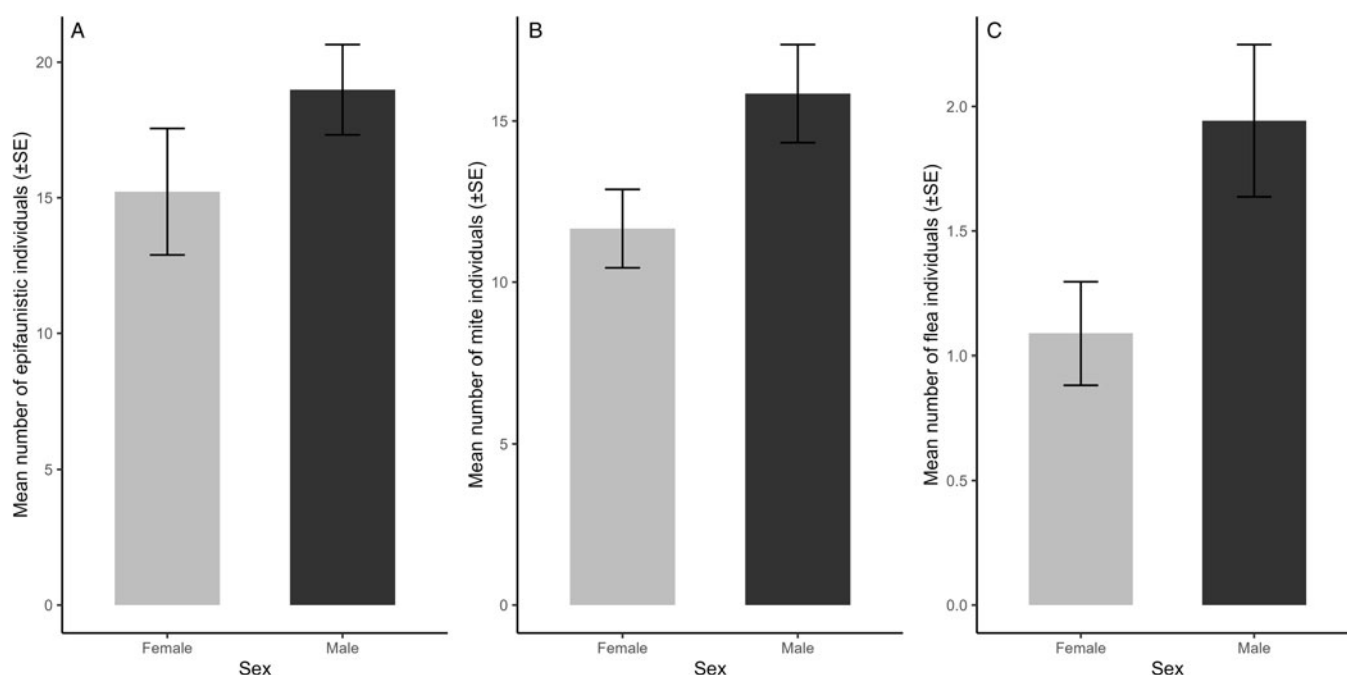

Figure 3. Mean number of: (a) epifaunistic, (b) mite and (c) flea individuals per host sex on *Mastomys natalensis* (n = 304) in Mpumalanga, South Africa (2014–2020).
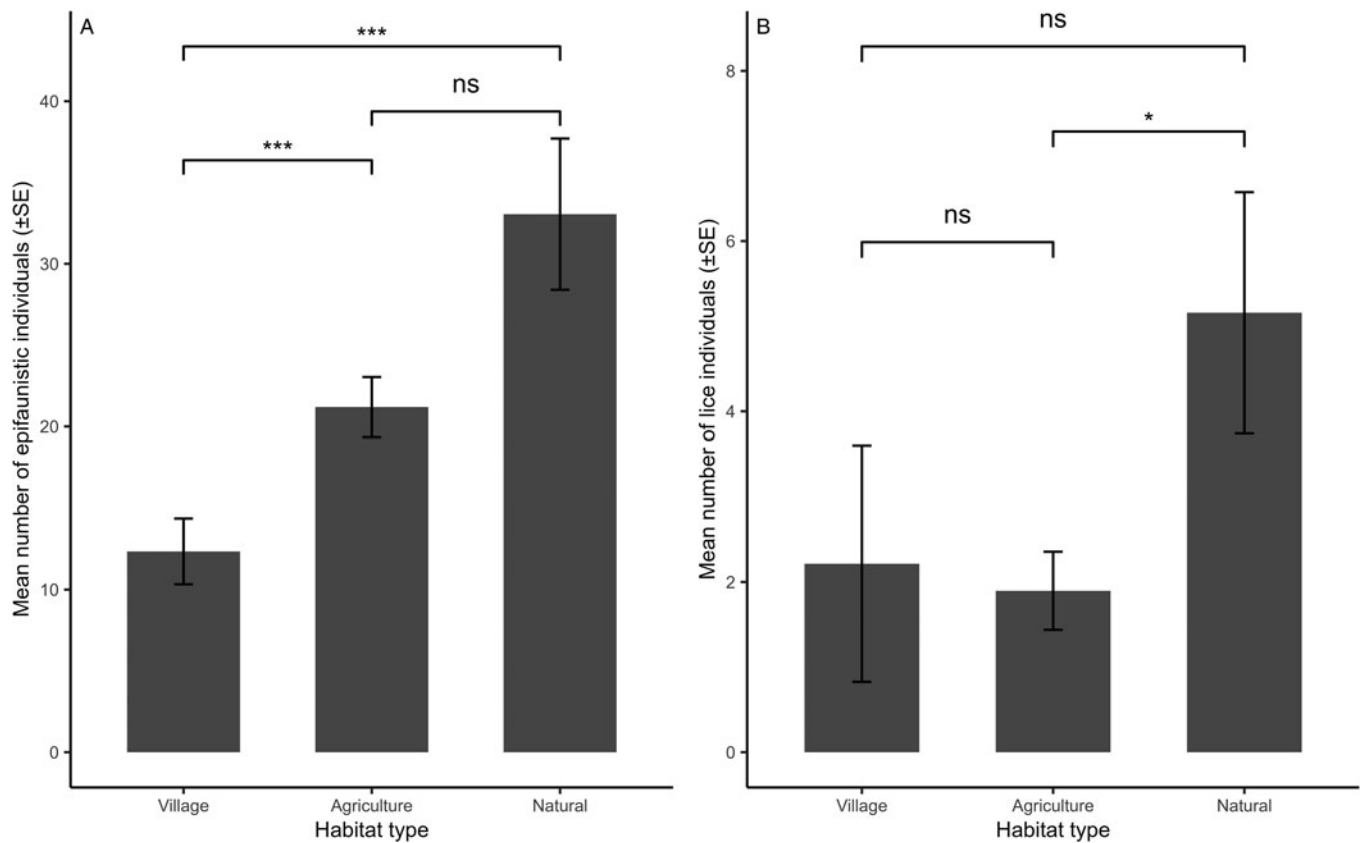
Figure 4. Mean number of: (a) epifaunistic and (b) lice individuals per habitat type on *Mastomys natalensis* ($n = 304$) in Mpumalanga, South Africa (2014–2020). Significant estimates: ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, ns-non-significant.
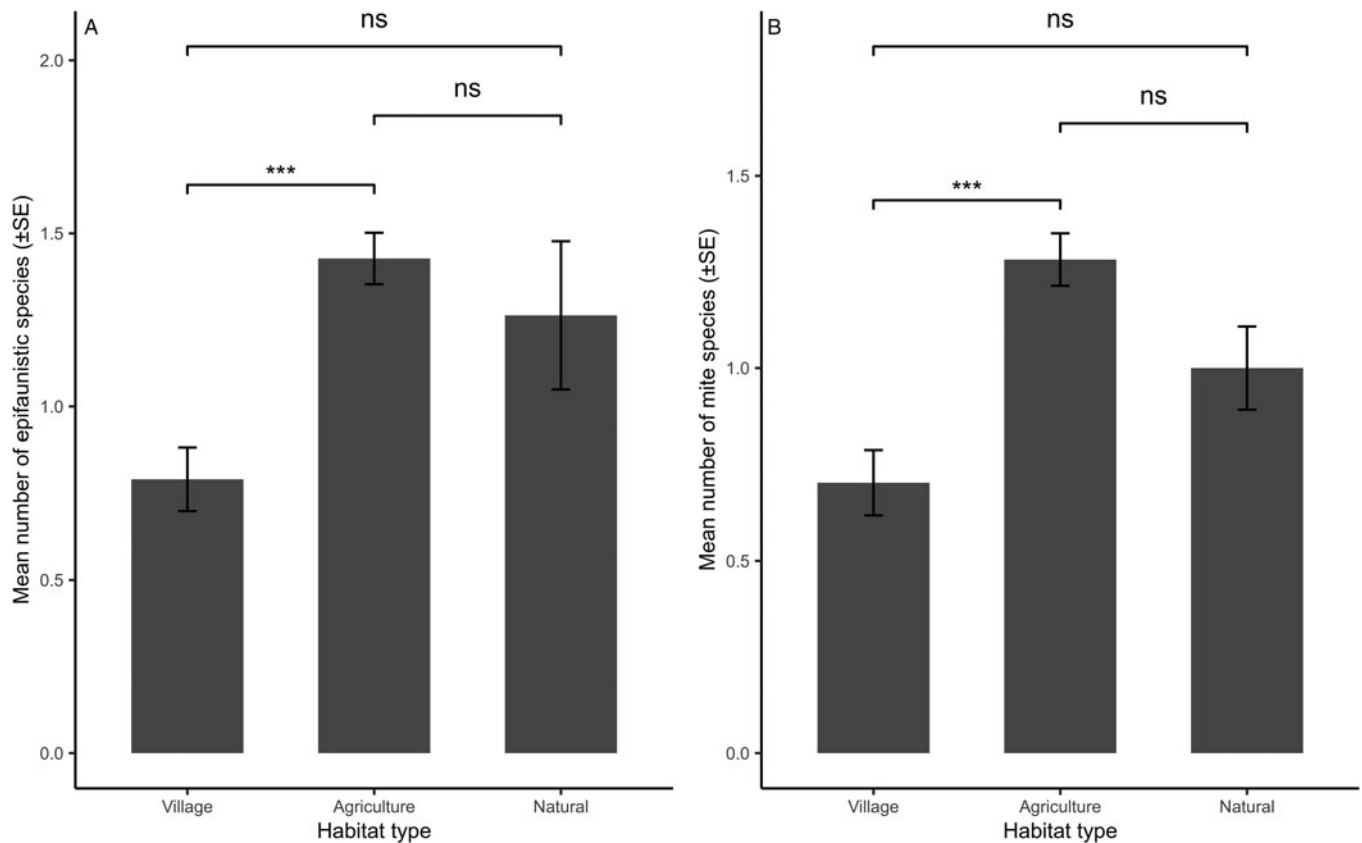

Figure 5. Mean number of: (a) epifaunistic, and (b) mite species per habitat type on *Mastomys natalensis* ($n = 234$) in Mpumalanga, South Africa (2014–2020). Significant estimates: ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, ns-non-significant.

Table 4. Summary of the final selected generalized linear model with a Poisson distribution on the effect of habitat type (HBT) on the epifaunistic taxon abundance belonging to different higher taxa on *Mastomys coucha* (*n* = 189, 2014–2020). Bold text indicate significant responses.

Taxon	Variable	Estimate	SE	*z*-value	*P* value
Overall epifaunistic individuals	HBT NAT: HBT AGR	−0.132	0.087	−1.511	0.131
	HBT VIL: HBT AGR	−0.820	0.285	−2.517	**0.004**
	HBT NAT: HBT VIL	0.688	0.283	2.375	**0.015**
Mites	HBT NAT: HBT AGR	0.030	0.094	0.314	0.754
	HBT VIL: HBT AGR	−0.762	0.311	−2.451	**0.014**
	HBT NAT: HBT VIL	0.791	0.307	2.578	**0.010**

HBT NAT, natural habitat; HBT AGR, agricultural habitat; HBT VIL, village habitat.

Table 5. Summary of the final selected zero-inflated model (count and zero model) with a Poisson distribution on the effect of host sex (SEX), reproductive state (BRS), tail length (TLL), year (Y) and habitat type (HBT) on the ectoparasite abundance belonging to different higher taxa on *Mastomys coucha* (*n* = 189, 2014–2020). Bold text indicate significant responses.

Taxon	Variable	Estimate	SE	z-value	*P* value
Count model					
Fleas	TLL	0.221	0.190	1.162	0.245
	BRS	0.474	0.414	1.143	0.253
	SEX	−0.350	0.265	−1.324	0.185
	Y2015:Y2014	1.561	0.455	3.435	**<0.001**
	Y2019:Y2014	1.605	0.429	3.740	**<0.001**
	Y2020:Y2014	0.749	0.531	1.410	0.158
Lice	TLL	0.058	0.107	0.547	0.585
	HBT NAT: HBT AGR	0.140	0.184	0.758	0.448
	HBT VIL: HBT AGR	0.355	0.865	0.410	0.682
	HBT NAT: HBT VIL	−0.215	0.857	−0.251	0.802
	Y2015:Y2014	−1.774	0.418	−4.249	**<0.001**
	Y2019:Y2014	−0.947	0.255	−3.687	**<0.001**
	Y2020:Y2014	−1.397	0.244	−5.721	**<0.001**
Ticks	TLL	0.118	0.243	0.486	0.627
	SEX	−0.524	0.361	−1.452	0.147
Zero model					
Fleas	TLL	−1.072	1.905	−0.563	0.574
	BRS	2.169	8.739	0.248	0.804
	SEX	−3.987	20.081	−0.199	0.843
	Y2015:Y2014	−10.796	204.626	−0.053	0.958
	Y2019:Y2014	−17.042	7805.506	−0.002	0.998
	Y2020:Y2014	1.859	3.478	0.535	0.593
Lice	TLL	−1.934	0.803	−2.409	**0.016**
	HBT NAT: HBT AGR	2.448	1.010	2.424	**0.015**
	HBT VIL: HBT AGR	6.961	2.434	2.859	**0.004**
	HBT NAT: HBT VIL	−4.513	1.970	−2.291	**0.022**
	Y2015:Y2014	−1.827	2.489	−0.734	0.463
	Y2019:Y2014	−1.904	1.325	−1.437	0.151
	Y2020:Y2014	−1.585	1.157	−1.370	0.171
Ticks	TLL	8.242	17.018	0.484	0.628
	SEX	15.862	29.328	0.541	0.589

Reference levels are male for SEX, non-breeding for BRS.
HBT NAT, natural habitat; HBT AGR, agricultural habitat; HBT VIL, village habitat.

Table 6. Summary of the final selected generalized linear model with a Poisson distribution on the effect of host sex (SEX), year (Y) and habitat type (HBT) on number of epifaunistic, flea and mite species on *Mastomys coucha* ($n = 118$, 2019–2020). Bold text indicate significant responses.

Taxon	Variable	Estimate	SE	*z*-value	*P* value
Epifaunistic species	HBT NAT: HBT AGR	−0.204	0.227	−0.899	0.369
	HBT VIL: HBT AGR	−0.981	0.540	−1.816	0.069
	HBT NAT: HBT VIL	0.777	0.510	−1.816	0.128
Fleas	Y2020	−3.273	1.054	−3.106	**0.002**
Mites	HBT NAT: HBT AGR	−0.116	0.247	−0.471	0.638
	HBT VIL: HBT AGR	−0.109	0.619	−1.754	0.079
	HBT NAT: HBT VIL	0.970	0.587	1.653	0.098

Reference levels are male for SEX, 2019 for YEAR.
HBT NAT, natural habitat; HBT AGR, agricultural habitat; HBT VIL, village habitat.

The occurrence of *X. brasiliensis* on *M. natalensis* is well documented (Isaacson, 1975; Segerman, 1995; Guerra *et al.*, 2016) and in fact *M. natalensis* together with *Rattus* spp. (also commensal) are the principal hosts for the flea (Segerman, 1995). The present study provides the first record of *X. brasiliensis* on *M. coucha* in South Africa. This flea is a known vector of several zoonotic pathogens such as the bacterium *Y. pestis* and *Bartonella* species in Africa (Zimba *et al.*, 2011; Billeter *et al.*, 2014). In the study, higher infestations of *X. frayi* were recorded on *M. coucha* compared to *M. natalensis*. This may be due to the fact that *G. leucogaster* is the principal host of *X. frayi* (Segerman, 1995) and the rodent co-occurred with *M. coucha* in the agricultural and natural habitat type (Smith *et al.*, 2023). Given that *M. natalensis,* and most likely *M. coucha,* often use the abandoned burrows of other rodent species (Veenstra, 1958; Coetzee, 1975; Isaacson,

1975) the occurrence of non-specific flea species on *Mastomys* is most likely facilitated through nest sharing.

Current taxonomic records list the louse *H. intermedia* on *M. natalensis* and *M. coucha* (Ledger, 1980; Durden and Musser, 1994). Important to realize, however, co-evolutionary divergence among lice and their hosts are often found (du Toit *et al.*, 2013; Bothma *et al.*, 2020, 2021; Durden *et al.*, 2020) and it is thus quite possible that *H. intermedia* comprises of 2 cryptic species. The presence of *P. biseriata* on *M. coucha* is possibly an accidental infestation, given that *G. leucogaster* is the principal host of this taxon (Ledger, 1980; Durden and Musser, 1994). Similarly, the presence of *P. spinulosa* on *M. natalensis* may also be accidental given that the principal host is *R. rattus* (Durden and Musser, 1994). Studies have recorded that *M. natalensis* (and possibly *M. coucha*) are rarely aggressive to conspecifics and/or other
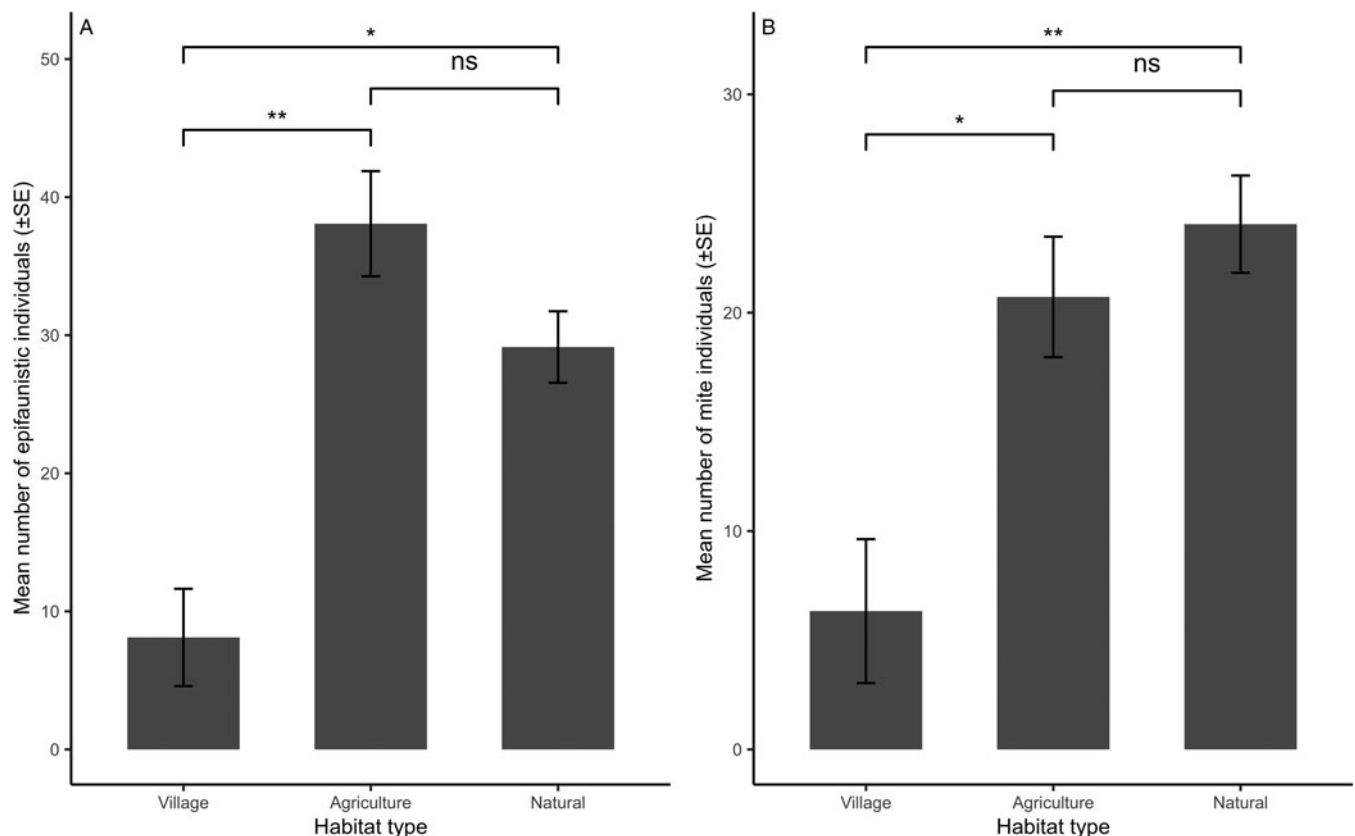

Figure 6. Mean number of: (a) epifaunistic, and (b) mite individuals per habitat type for *Mastomys coucha* in Mpumalanga, South Africa (2014–2020). Significant estimates: ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, ns-non-significant.

rodent species (Veenstra, 1958) and accidental parasite exchange is quite plausible.

Overall ticks were the least prevalent taxon on both rodent species studied herein. Many ixodid tick species, and especially the taxa recorded in the present study, require vegetation (e.g. grass) to attach to and wait for a host to pass (Horak *et al.*, 2018; Ledger *et al.*, 2019). In the present study, the village habitat lacked natural vegetation and had proportionally lower cover compared to the agricultural and natural habitat type (Matthee *et al.*, 2020; S. Matthee personal observation). This may contribute to the overall lower tick infestations on *M. natalensis*. The larvae and or nymphs of 3 of the 4 species that could be identified (*A. hebraeum, D. rhinocerinus,* and *H. truncatum*) are known to occur on murid rodents (Horak *et al.*, 2018). However, the single occurrence of *Hae. zumpti* (1 individual) is most probably related to the fact that the tick prefers Sciuridae and Carnivora (Horak *et al.*, 2018; Jongejan *et al.*, 2020).

Mites (excluding chiggers) were the most specious taxon with *L. liberiensis* and *L. muricola* (both parasitic species) being the most common on both rodents. *Mastomys natalensis* is a new host record for *Androlaelaps oliffi, A. rhodesiensis, A. taterae* and *L. simillimus*. The presence of the remaining *Androlaelaps* and *Laelaps* species on *M. natalensis* is supported by previous taxonomic records (Isaacson, 1975). Apart from *L. muricola* (previously recorded on *M. coucha*, Engelbrecht *et al.*, 2014) the remaining *Androlaelaps* and *Laelaps* species are new records for *M. coucha*. The presence of *Ornithonyssus bacoti,* known as the tropical rat mite, represents the first record of this mite species on *M. natalensis*. The mite was recorded on *M. natalensis* in the village and agricultural habitat types but was absent from conspecific individuals trapped in the natural habitat. The primary hosts of *O. bacoti* are *R. tanezumi* and *R. rattus*, and as mentioned before both rodent species co-occurred with *M. natalensis* in the village habitat. This mite can cause pruritic papular dermatitis (known as rat mite dermatitis) in humans (Feldman and Easton, 2005; Clancy *et al.*, 2022).

Chiggers were less prevalent on *M. natalensis* (25.32%) as opposed to *M. coucha* (45%). Six chigger species were shared between the 2 *Mastomys* species. Chiggers are regarded as habitat specialists and can occur on multiple unrelated host species in a particular habitat (Sasa, 1960). The present study provides the first list of chigger species recorded for *M. coucha* in South Africa. The ear pinna was the preferred attachment site for chiggers on both rodents. This parasitope was also recorded for several other rodents in South Africa (Fagir *et al.*, 2014; Matthee *et al.*, 2020; Stevens *et al.*, 2022). It is possible that this attachment site is preferred due to the protection that it provides against parasite removal through grooming.

Role of host- and habitat-associated factors on the epifauna of *M. natalensis* and *M. coucha*

Male-biased parasitism was recorded for overall epifauna, mite and flea abundance on *M. natalensis*. This pattern supports previous studies on other rodent species in South Africa (Archer *et al.*, 2014; Smith *et al.*, 2023) and elsewhere (Krasnov *et al.*, 2005). There are several, not mutually exclusive, factors that can contribute to this pattern. In particular, large-bodied male hosts encounter and can accommodate more ectoparasites due to their larger surface area and available niche space for parasites (Krasnov *et al.*, 1997; Ezenwa *et al.*, 2006), males are less likely to engage in grooming activities compared to females (Ferkin and Leonard, 2007; Hawlena *et al.*, 2007) and males of some rodent species increase their home range during the breeding season (in search for females) which increases their contact with ectoparasites (i.e. mites, fleas, ticks) (Perez-orella and

Schulte-hostedde, 2005; Morand *et al.*, 2006; Frafjord, 2016). Linked to this, during the breeding season elevated testosterone levels can facilitate immune suppression that may further increase their susceptibility to parasites (Klein, 2004; Stanko *et al.*, 2015). In the present study, male *M. natalensis* were larger (9.61 cm ± 0.05) compared to females (9.08 cm ± 0.06)) and more than 50% of the individuals were in the breeding state. Furthermore, from previous studies (Mlyashimbi *et al.*, 2019; Goyens *et al.*, 2020) male *M. natalensis* increase their home range during the breeding season, thereby increasing their exposure to free-living infective life stages in the environment. The above mentioned may also explain why tick counts were significantly higher on *M. natalensis* individuals that were in the breeding state compared to non-breeding individuals. In contrast to the tick pattern, lice were significantly more prevalent on non-breeding *M. natalensis* individuals compared to breeding individuals. Lice are transmitted through direct body contact and it is possible that non-breeding *M. natalensis* spend more time engaging with conspecifics in the nest (Choate, 1972).

From the study it seems that host-related parameters were less important in shaping epifaunistic infestations on *M. coucha*. It is possible that the fact that a higher proportion of *M. coucha* individuals were in the non-breeding state (83.07%) compared to the breeding individuals (16.93%) contributed to this. However, louse prevalence was significantly higher on smaller-bodied *M. coucha* compared to larger individuals. This pattern is in agreement with the pattern recorded for *M. natalensis* (higher louse prevalence on non-breeding individuals).

Epifaunistic abundance and particularly overall, flea, tick and mite abundance, on *M. natalensis* and *M. coucha* were not significantly different between the agricultural and natural habitat types. In contrast, the abundance of epifaunistic individuals, mites and ticks (the latter for *M. natalensis*) were significantly lower in the village compared to the agricultural and natural habitats. In addition, epifaunistic, flea and mite species richness on *M. natalensis* were also significantly lower in the village compared the agricultural habitat type. These patterns may be due to higher similarity in the vegetation structure (Matthee *et al.*, 2020) and rodent species in the agricultural and natural habitats compared to the village. Another contributing factor may be the fact that ectoparasite infestations were very low on the 2 *Rattus* species that co-occurred in the village habitat with *M. natalensis* (unpublished data). Depauperate parasite communities associated with *Rattus* species have also been recorded elsewhere (Murrel and Cates, 1970; Alonso *et al.*, 2020). Lower rodent diversity in addition in a poorer parasite community most probably contributes to the lower ectoparasite abundances and species richness in the village. It is interesting to note that lice were significantly more abundant on *M. natalensis* in the natural compared to the agricultural habitat type but was not significantly different from the village habitat when compared to the agricultural and natural habitat type. Although fewer *M. natalensis* individuals were trapped in the natural habitat (19) the total louse abundance was 98 individuals and 6 *M. natalensis* individuals harboured >10 louse individuals. Whereas the 136 *M. natalensis* individuals in the agricultural habitat harboured a total of 258 lice and only 8 individuals carried >10 louse individuals. Therefore, a higher proportion of *M. natalensis* had higher louse counts in the natural habitat type (31.57%) when compared to the agricultural habitat (5.88%). However, lice were more prevalent on *M. natalensis* and *M. coucha* in the agricultural habitat type compared to the village habitat. Higher host density can facilitate contact between conspecifics which may result in louse transfer (Arneberg *et al.*, 1998). However, in the present study, the densities of *M. natalensis* was the highest in the village (66.88%) followed by the agriculture habitat type (43.44%), while *M. coucha* had the highest

density recorded in the natural (37.81%) followed by the agriculture habitat type (25.94%). Regarding *M. natalensis*, the agricultural habitat type had a higher proportion of non-breeding individuals (53.70%) when compared to the village (36.90%), fitting the pattern that lice are more prevalent on non-breeding *M. natalensis* individuals compared to breeding individuals. In addition, Borremans *et al.* (2016) found that at high host densities *M. natalensis* spend less time in contact with each other, whereas at a lower host density they spend more time together. Similar to *M. natalensis*, a higher proportion of non-breeding compared to breeding individuals were recorded for *M. coucha* in the agriculture (86.80%) compared to village habitat (55.50%). This pattern is also in agreement with the abovementioned record that lice were significantly more prevalent on smaller bodied (and most possibly non-breeding) *M. coucha*. However, lice prevalence was also significantly higher on *M. coucha* in the agricultural habitat type compared to the natural habitat type. It is uncertain what drives this pattern as the proportion of non-breeding compared to breeding individuals and their respective body sizes were not distinctly different between the agricultural and natural habitat types. It is possible that host density played a role as the relative density of *M. coucha* was higher in the natural compared to the agricultural habitat type. It is however important to note that previous studies on rodents have suggested that high host density does not always indicate a higher rate of contact between rodents (Froeschke *et al.*, 2013; Stanko *et al.*, 2015), which also agrees with the study by Borremans *et al.* (2016).

Recording the between-sampling year variation in infestations was not the focus of the study, however, given that epifaunistic species are ectothermic and sensitive to climatic conditions (Altizer *et al.*, 2006; Paaijmans *et al.*, 2013) it is expected that infestations will be influenced by annual variation in climatic conditions, a scenario that is open for further investigation in the future.

This study represents the first systematic long-term assessment of the ectoparasite species associated with *M. natalensis* and *M. coucha*. The findings support previous studies in that widely distributed rodent species harbour a diverse set of parasite species. Evident from the study is that habitat preference and the diversity of the local rodent community play important determining roles in shaping ectoparasite infestations, even in closely related host species such as *M. natalensis* and *M. coucha*.

Data availability statement. All data generated or analysed during this study are included in this published article. The datasets used and/or analysed are available from the corresponding author upon reasonable request.

Authors' contributions. A. J. L. contributed to the field and laboratory work, performed the statistical analyses, and wrote the draft versions of the article. C. A. M. assisted in the field and commented on draft versions of the article. I. G. H. assisted with tick identification and E. A. U. identified the mites (excluding chiggers). C. H. supervised the statistical analyses and commented on draft versions of the article. S. M. conceived the study, supervised A. J. L. in the field and laboratory and commented on draft versions of the manuscript. All authors contributed to the final version of the article.

Competing interests. None.

References

Achtman M, Morelli G, Zhu P, Wirth T, Diehl I, Kusecek B, Vogler AJ, Wagner DM, Allender CJ, Easterday WR, Chenal-Francisque V, Worsham P, Thomson NR, Parkhill J, Lindler LE, Carniel E and Keim P (2004) Microevolution and history of the plague bacillus, *Yersinia pestis*. *Proceedings of the National Academy of Sciences of the United States of America* **101**, 17837–17842.

Alonso R, Ruiz M, Lovera R, Montes De Oca DP, Cavia R and Sánchez JP (2020) Norway rat (*Rattus norvegicus*) ectoparasites in livestock production systems from central Argentina: influencing factors on parasitism. *Acta Tropica* **203**, 105299.

Altizer S, Nunn CL, Thrall PH, Gittleman JL, Antonovics J, Cunningham AA, Dobson AP, Ezenwa V, Jones KE, Pedersen AB, Poss M and Pulliam JRC (2003) Social organization and parasite risk in mammals: integrating theory and empirical studies. *Annual Review of Ecology, Evolution, and Systematics* **34**, 517–547.

Altizer S, Dobson A, Hosseini P, Hudson P, Pascual M and Rohani P (2006) Seasonality and the dynamics of infectious diseases. *Ecology Letters* **9**, 467–484.

Archer EK, Bennett NC, Ueckermann EA and Lutermann H (2014) Ectoparasite burdens of the common mole-rat (*Cryptomys hottentotus hottentotus*) from the Cape provinces of South Africa. *The Journal of Parasitology* **100**, 79–84.

Arneberg P (2001) An ecological law and its macroecological consequences as revealed by studies of relationships between host densities and parasite prevalence. *Ecography* **24**, 352–358.

Arneberg P, Skorping A, Grenfell B and Read AF (1998) Host densities as determinants of abundance in parasite communities. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **265**, 1283–1289.

Bastos AD, Chimimba CT, von Maltitz E, Kirsten F and Belmain SR (2005) Identification of rodent species that play a role in disease transmission to humans in South Africa. *Proceedings of the Southern African Society for Veterinary Epidemiology and Preventive Medicine* **0**, 78–83.

Billeter SA, Borchert JN, Atiku LA, Mpanga JT, Gage KL and Kosoy MY (2014) *Bartonella* species in invasive rats and indigenous rodents from Uganda. *Vector-Borne and Zoonotic Diseases* **14**, 182–188.

Borremans B, Hens N, Beutels P, Leirs H and Reijniers J (2016) Estimating time of infection using prior serological and individual information can greatly improve incidence estimation of human and wildlife infections. *PLoS Computational Biology* **12**, e1004882.

Bothma JC, Matthee S and Matthee CA (2020) The evolutionary history of parasitic sucking lice and their rodent hosts: a case of evolutionary co-divergences. *Zoologica Scripta* **49**, 72–85.

Bothma JC, Matthee S and Matthee CA (2021) Comparative phylogeography between parasitic sucking lice and their host the Namaqua rock mouse, *Micaelamys namaquensis* (Rodentia: Muridae). *Zoological Journal of the Linnean Society* **192**, 1017–1028.

Brettschneider H, Anguelov R, Chimimba CT and Bastos AD (2012) A mathematical epidemiological model of gram-negative *Bartonella* bacteria: does differential ectoparasite load fully explain the differences in infection prevalence of *Rattus rattus* and *Rattus norvegicus*? *Journal of Biological Dynamics* **6**, 763–781.

Brouat C, Kane M, Diouf M, Bâ K, Sall-Dramé R and Duplantier JM (2007) Host ecology and variation in helminth community structure in *Mastomys* rodents from Senegal. *Parasitology* **134**, 437–450.

Burnham KP and Anderson DR (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd Edn. New York: Springer.

Bush AO, Lafferty KD, Lotz JM, Shostak A (1997) Parasitology on its own terms: Margolis *et al.* revisited. *The Journal of Parasitology* **83**, 575–583.

Choate TS (1972) Behavioural studies on some Rhodesian rodents. *Zoologica Africana* **7**, 103–118.

Clancy BM, Theriault BR, Schoenberger JM, Bowers CJ, Mitchell CM, Langan GP, Ostdiek AM and Luchins KR (2022) Identification and control of an *Ornithonyssus bacoti* infestation in a rodent vivarium by using molecular diagnostic techniques. *Comparative Medicine* **72**, 113–121.

Coetzee CG (1975) The biology, behaviour, and ecology of *Mastomys natalensis* in Southern Africa. *Bulletin of the World Health Organization* **52**, 637–644.

Cote IM and Poulin R (1995) Parasitism and group size in social animals: a meta-analysis. *Behavioral Ecology* **6**, 159–165.

Drazo NA, Kennis J, Leirs H and Migimiru DA (2008) Farmer survey in the hinterland of Kisangani (Democratic Republic of Congo) on rodent crop damage and rodent control techniques used. *Mammalia* **72**, 192–197.

Durden LA and Musser GG (1994) *The Sucking Lice (Insecta, Anoplura) of the World- A Taxonomic Checklist with Records of Mammalian Hosts and Geographical Distributions No. 218*. New York, USA: Bulletin of the American Museum of Natural History.

Durden LA, Matthee S, Bothma JC, Greiman SE and Matthee CA (2020) Two new species of sucking lice (Phthiraptera: Anoplura: Hoplopleuridae and Polyplacidae) from Grant's Rock Mouse, *Micaelamys granti*, in South Africa. *The Journal of Parasitology* **106**, 478–489.

du Toit N, Matthee S and Matthee CA (2013) The sympatric occurrence of two genetically divergent lineages of sucking louse, *Polyplax arvicanthis* (Phthiraptera: Anoplura), on the four-striped mouse genus, *Rhabdomys* (Rodentia: Muridae). *Parasitology* **140**, 604–616.

Engelbrecht A, Matthee CA, Ueckermann EA and Matthee S (2014) Evidence of cryptic speciation in mesostigmatid mites from South Africa. *Parasitology* **141**, 1322–1332.

Esch GW and Fernández JC (1993) *A Functional Biology of Parasitism: Ecological and Evolutionary Implications*. London: Chapman and Hall.

Esser HJ, Foley JE, Bongers F, Herre EA, Miller MJ, Prins HHT and Jansen PA (2016) Host body size and the diversity of tick assemblages on Neotropical vertebrates. *International Journal for Parasitology: Parasites and Wildlife* **5**, 295–304.

Ezenwa VO, Price SA, Altizer S, Vitone ND and Cook KC (2006) Host traits and parasite species richness in even and odd-toed hoofed mammals, Artiodactyla and Perissodactyla. *Oikos* **115**, 526–536.

Fagir DM, Ueckermann EA, Horak IG, Bennett NC and Lutermann H (2014) The Namaqua rock mouse (*Micaelamys namaquensis*) as a potential reservoir and host of arthropod vectors of diseases of medical and veterinary importance in South Africa. *Parasites and Vectors* **7**, 366.

Fagir DM, Horak IG, Ueckermann EA, Bennett NC and Lutermann H (2015) Ectoparasite diversity in the Eastern Rock Sengis (*Elephantulus myurus*): the effect of seasonality and host sex. *African Zoology* **50**, 109–117.

Feldman SH and Easton DN (2005) Occupational health and safety. In Suckow MA, Weisbroth SH and Franklin CL (eds), *The Laboratory Rat*, 2nd Edn. Burlington: Academic Press, pp. 565–586.

Ferkin MH and Leonard ST (2007) Age of the subject and scent donor affects the amount of time that voles self-groom when they are exposed to odors of opposite-sex conspecifics. In Hurst JL, Beynon RJ, Roberts SC and Wyatt TD (eds), *Chemical Signals in Vertebrates*, Vol. 11. New York: Springer, pp. 281–289.

Frafjord K (2016) Influence of reproductive status: home range size in water voles (*Arvicola amphibius*). *PLoS ONE* **11**, e0154338.

Froeschke G and Matthee S (2014) Landscape characteristics influence helminth infestations in a peri-domestic rodent – implications for possible zoonotic disease. *Parasites and Vectors* **7**, 393.

Froeschke G, Harf R, Sommer S and Matthee S (2010) Effects of precipitation on parasite burden along a natural climatic gradient in Southern Africa – implications for possible shifts in infestation patterns due to global changes. *Oikos* **119**, 1029–1039.

Froeschke G, van der Mescht L, McGeoch M and Matthee S (2013) Life history strategy influences parasite responses to habitat fragmentation. *International Journal for Parasitology* **43**, 1109–1118.

Garba M, Dalecky A, Kadaoure I, Kane M, Hima K, Veran S, Gagare S, Gauthier P, Tatard C, Rossi JP and Dobigny G (2014) Spatial segregation between invasive and native commensal rodents in an urban environment: a case study in Niamey, Niger. *PLoS ONE* **9**, e110666.

Gehlhausen SM, Schwartz MW and Augspurger C (2000) Vegetation and microclimatic edge effects in two mixed-mesophytic forest fragments. *Plant Ecology* **147**, 21–35.

Gordon DH (1978) Distribution of sibling species of the *Praomys* (*Mastomys*) *natalensis* group in Rhodesia (Mammalia: Rodentia). *Journal of Zoology* **186**, 397–401.

Goyens J, Reijniers J, Borremans B and Leirs H (2020) Density thresholds for Mopeia virus invasion and persistence in its host *Mastomys natalensis*. *Journal of Theoretical Biology* **317**, 55–61.

Granjon L, Duplantier JM, Catalan J and Britton-Davidian J (1997) Systematics of the genus *Mastomys* (Thomas, 1915) (Rodentia: Muridae): a review. *Belgian Journal of Zoology* **127**, 7–18.

Green C, Keogh H, Gordon DH, Pinto M and Hartwig EK (1980) The distribution, identification, and naming of the *Mastomys natalensis* species complex in Southern Africa (Rodentia: Muridae). *Journal of Zoology* **192**, 17–23.

Guerra AS, Eckerlin RP, Dowling APG, Durden LA, Robbins RG, Dittmar K, Helgen KM, Agwanda B, Allan BF, Hedlund T and Young HS (2016) Host–parasite associations in small mammal communities in semiarid savanna ecosystems of East Africa. *Journal of Medical Entomology* **53**, 851–860.

Härkönen L, Hurme E and Kaitala A (2013) Unexpected seasonal variation in offspring size and performance in a viviparous ectoparasite. *Parasitology* **140**, 229–236.

Haukisalmi V, Henttonen H and Tenora F (1987) Parasitism by helminths in the grey-sided vole (*Clethrionomys rufocanus*) in northern Finland: influence of density, habitat and sex of the host. *Journal of Wildlife Diseases* **23**, 233–241.

Hawlena H, Bashary D, Abramsky Z and Krasnov BR (2007) Benefits, costs and constraints of anti-parasitic grooming in adult and juvenile rodents. *Ethology* **113**, 394–402.

Herrin CS and Tipton VJ (1975) Spinturnicid mites of Venezuela (Acarina: Spinturnicidae). *Brigham Young University Science Bulletin, Biological Sciences* **20**, 1–72.

Herrmann C and Gern L (2013) Survival of *Ixodes ricinus* (Acari: Ixodidae) nymphs under cold conditions is negatively influenced by frequent temperature variations. *Ticks and Tick-Borne Diseases* **4**, 445–451.

Horak IG, Heyne H, Williams R, Gallivan GJ, Spickett AM, Bezuidenhout JD and Estrada-Peña A (2018) *The Ixodid Ticks (Acari: Ixodidae) of Southern Africa*. Scotland, UK: Springer.

Isaacson M (1975) The ecology of *Praomys* (*Mastomys*) *natalensis* in Southern Africa. *Bulletin of the World Health Organization* **52**, 629–636.

Jackson TP and van Aarde RJ (2004) Diet quality differentially affects breeding effort of *Mastomys coucha* and *M. natalensis*: implications for rodent pests. *Journal of Experimental Zoology* **301A**, 97–108.

Johnson PT (1972) *Hoplopleura intermedia* kellog and ferris and its allies, with the description of a new species. *Proceedings of the Entomological Society of Washington* **74**, 330–337.

Jongejan F, Berger L, Busser S, Deetman I, Jochems M, Leenders T, de Sitter B, van der Steen F, Wentzel J and Stoltsz H (2020) *Amblyomma hebraeum* is the predominant tick species on goats in the Mnisi Community Area of Mpumalanga Province South Africa and is co-infected with *Ehrlichia ruminantium* and *Rickettsia africae*. *Parasites and Vectors* **13**, 172.

Kamiya T, O'Dwyer K, Nakagawa S and Poulin R (2014) What determines species richness of parasitic organisms? A meta-analysis across animal, plant and fungal hosts. *Biological Reviews* **89**, 123–134.

Klein SL (2004) Hormonal and immunological mechanisms mediating sex differences in parasite infection. *Parasite Immunology* **26**, 247–264.

Krasnov BR, Shenbrot GI, Medvedev SG, Vatschenok VS and Khokhlova IS (1997) Host-habitat relations as an important determinant of spatial distribution of flea assemblages (Siphonaptera) on rodents in the Negev Desert. *Parasitology* **114**, 159–173.

Krasnov BR, Khokhlova IS, Fielden LJ and Burdelova NV (2001a) Development rates of two *Xenopsylla* flea species in relation to air temperature and humidity. *Medical and Veterinary Entomology* **15**, 249–258.

Krasnov BR, Khokhlova IS, Fielden LJ and Burdelova NV (2001b) Effect of air temperature and humidity on the survival of pre-imaginal stages of two flea species (Siphonaptera: Pulicidae). *Journal of Medical Entomology* **38**, 629–637.

Krasnov BR, Shenbrot GI, Khokhlova IS and Degen AA (2004) Relationship between host diversity and parasite diversity: flea assemblages on small mammals. *Journal of Biogeography* **31**, 1857–1866.

Krasnov BR, Morand S, Hawlena H, Khokhlova IS and Shenbrot GI (2005) Sex-biased parasitism, seasonality and sexual size dimorphism in desert rodents. *Oecologia* **146**, 209–217.

Krasnov BR, Matthee S, Lareschi M, Korallo-Vinarskaya NP and Vinarski MV (2010) Co-occurrence of ectoparasites on rodent hosts: null model analyses of data from three continents. *Oikos* **119**, 120–128.

Lecompte E, Fichet-Calvet E, Daffis S, Koulémou K, Sylla O, Kourouma F, Doré A, Soropogui B, Aniskin V, Allali B, Kan SK, Lalis A, Koivogui L, Günther S, Denys C and ter Meulen J (2006) *Mastomys natalensis* and Lassa fever, West Africa. *Emerging Infectious Diseases* **12**, 1971–1974.

Ledger JA (1980) *The Arthropod Parasites of Vertebrates in Africa South of the Sahara. Volume IV. Phthiraptera (Insecta).* Johannesburg, South African: Institute for Medical Research.

Ledger KJ, Keenan RM, Sayler KA and Wisely SM (2019) Multi-scale patterns of tick occupancy and abundance across an agricultural landscape in Southern Africa. *PLoS ONE* **14**, e0222879.

Ledger KJ, Innocent H, Lukhele SM, Dorleans R and Wisely SM (2022) Entomological risk of African tick-bite fever (*Rickettsia africae* infection) in Eswatini. *PLoS Neglected Tropical Diseases* **16**, e0010437.

Leirs H, Verhagen R, Verheyen W, Mwanjabe P and Mbise T (1996a) Forecasting rodent outbreaks in Africa: an ecological basis for *Mastomys* control in Tanzania. *Journal of Applied Ecology* **33**, 937–943.

Leirs H, Verheyen W and Verhagen R (1996b) Spatial patterns in *Mastomys natalensis* in Tanzania (Rodentia, Muridae). *Mammalia* **60**, 545–595.

Lorch D, Fisher DO and Spratt DM (2007) Variation in ectoparasite infestation on the brown antechinus, *Antechinus stuartii*, with regard to host, habitat and environmental parameters. *Australian Journal of Zoology* **55**, 169–176.

Makundi RH and Massawe AW (2011) Ecologically based rodent management in Africa: potential and challenges. *Wildlife Research* **38**, 588–595.

Matthee S, Horak IG, Beaucournu J, Durden LA, Ueckermann A and McGeoch MA (2007) Epifaunistic arthropod parasites of the four-striped mouse, *Rhabdomys pumilio*, in the Western Cape Province, South Africa. *The Journal of Parasitology* **93**, 47–59.

Matthee S, Horak IG, van der Mescht L, Ueckermann EA and Radloff FGT (2010) Ectoparasite diversity on rodents at de Hoop Nature Reserve, Western Cape Province. *African Zoology* **45**, 213–224.

Matthee S, Stekolnikov AA, van der Mescht L, Froeschke G and Morand S (2020) The diversity and distribution of chigger mites associated with rodents in the South African Savanna. *Parasitology* **147**, 1038–1047.

McCauley DJ, Salkeld DJ, Young HS, Makundi R, Dirzo R, Eckerlin RP, Lambin EF, Gaffikin L, Barry M and Helgen KM (2015) Effects of land use on plague (*Yersinia pestis*) activity in rodents in Tanzania. *American Journal of Tropical Medicine and Hygiene* **92**, 776–783.

Mlyashimbi ECM, Mariën J, Kimaro DN, Tarimo AJP, Machang RS, Makundi RH, Isabirye M and Massawe AW (2019) Home ranges, sex ratio and recruitment of the multimammate rat (*Mastomys natalensis*) in semi-arid areas in Tanzania. *Mammalia* **84**, 336–343.

Monadjem A, Taylor PJ, Denys C and Cotterill FPD (2015) *Rodents of Sub-Saharan Africa: A Biogeographic and Taxonomic Synthesis.* Berlin, Germany: De Gruyter.

Morand S and Bordes F (2015) Parasite diversity of disease-bearing rodents of Southeast Asia: habitat determinants and effects on sexual size dimorphism and life-traits. *Frontiers in Ecology and Evolution* **3**, 110.

Morand S, Krasnov BR and Poulin R (2006) *Micromammals and Macroparasites: From Evolutionary Ecology to Management.* Berlin, Germany: Springer.

Mulungu LS, Mahlaba TA, Massawe AW, Kennis J, Crauwels D, Eiseb S, Monadjem A, Makundi RH, Katakweba AAS, Leirs H and Belmain SR (2011) Dietary differences of the multimammate mouse, *Mastomys natalensis* (Smith, 1834), across different habitats and seasons in Tanzania and Swaziland. *Wildlife Research* **38**, 640–646.

Mulungu LS, Ngowo V, Mdangi M, Katakweba AS, Tesha P, Mrosso FP, Mchomvu M, Sheyo PM and Kilonzo BS (2013) Population dynamics and breeding patterns of multimammate mouse, *Mastomys natalensis*

(Smith 1834), in irrigated rice fields in Eastern Tanzania. *Pest Management Science* **69**, 371–377.

Murrel BKD and Cates MD (1970) Seasonal periodicity of ectoparasites of *Rattus rattus tanezumi* Temminck from Taiwan. *Journal of Medical Entomology* **7**, 367–370.

Newman BJ, Ladd P, Brundrett M and Dixon KW (2013) Effects of habitat fragmentation on plant reproductive success and population viability at the landscape and habitat scale. *Biological Conservation* **159**, 16–23.

Paaijmans KP, Heinig RL, Seliga RA, Blanford JI, Blanford S, Murdock CC and Thomas MB (2013) Temperature variation makes ectotherms more sensitive to climate change. *Global Change Biology* **19**, 2373–2380.

Perez-orella C and Schulte-hostedde AI (2005) Effects of sex and body size on ectoparasite loads in the northern flying squirrel (*Glaucomys sabrinus*). *Canadian Journal of Zoology* **83**, 1381–1385.

Prakash I (2018) *Rodent Pest Management*, 1st Edn. Boca Raton, USA: CRC Press.

R Core Team (2023) *R: A Language and Environment for Statistical Computing.* Vienna, Austria: R Foundation for Statistical Computing. Available at https://www.R-project.org/

Rifkin JL, Nunn CL and Garamszegi LZ (2012) Do animals living in larger groups experience greater parasitism? A meta-analysis. *American Naturalist* **180**, 70–82.

Sasa M (1960) Biology of chiggers. *Annual Review of Entomology* **6**, 221–244.

Segerman J (1995) *Siphonaptera of Southern Africa: Handbook for the Identification of Fleas.* Johannesburg, South Africa: Publications of the South African Institute for Medical Research.

Singleton GR, Hinds LA, Krebs CJ and Spratt DM (2003) *Rats, Mice and People: Rodent Biology and Management.* Australia: Australian Centre for International Agricultural Research.

Skinner JD and Chimimba CT (2005) *The Mammals of the Southern African Subregion*, 3rd Edn. Cape Town, South Africa: Cambridge University Press.

Smith AT, Krasnov BR, Horak IG, Ueckermann EA and Matthee S (2023) Ectoparasites associated with the Bushveld gerbil (*Gerbilliscus leucogaster*) and the role of the host and habitat in shaping ectoparasite diversity and infestations. *Parasitology* **150**, 792–804.

Snipes M and Taylor DC (2014) Model selection and Akaike information criteria: an example from wine ratings and prices. *Wine Economics and Policy* **3**, 3–9.

Spickett A, Junker K, Krasnov B, Haukisalmi V and Matthee S (2017) Intra- and interspecific similarity in species composition of helminth communities in two closely-related rodents from South Africa. *Parasitology* **144**, 1211–1220.

Stanko M, Fričová J, Miklisová D, Khokhlova IS and Krasnov BR (2015) Environment-related and host-related factors affecting the occurrence of lice on rodents in Central Europe. *Parasitology* **142**, 938–947.

Stekolnikov AA (2008) Two new species of chigger mites (Acari: Trombiculidae) close to *Neotrombicula minuta*, application of nonlinear multivariate statistics. *Acarina* **16**, 21–29.

Stekolnikov AA (2018) Taxonomy and distribution of African chiggers (Acariformes, Trombiculidae). *European Journal of Taxonomy* **395**, 1–233.

Stenseth NC, Leirs H, Mercelis S and Mwanjabe P (2001) Comparing strategies for controlling an African pest rodent: an empirically based theoretical study. *Journal of Applied Ecology* **38**, 1020–1031.

Stevens L, Stekolnikov AA, Ueckermann EA, Horak IG and Matthee S (2022) Diversity and distribution of ectoparasite taxa associated with *Micaelamys namaquensis* (Rodentia: Muridae), an opportunistic commensal rodent species in South Africa. *Parasitology* **149**, 1229–1248.

Stuart C and Stuart T (2007) *Field Guide to Mammals of Southern Africa*, 4th Edn. Cape Town, South Africa: Struik Nature.

Till WM (1963) Ethiopian mites of the genus *Androlaelaps* Berlese s. lat. (Acari: Mesostigmata). *Bulletin of the British Museum (Natural History) Zoology* **10**, 1–104.

Tompkins DM, Dobson AP, Arneberg P, Begon ME, Cattadori IM, Greenman JV, Heesterbeek JAP, Hudson PJ, Newborn D, Pugliese A, Rizzoli AP, Rosa R, Rosso F and Wilson K (2001) Parasites and host population dynamics. In Hudson P, Rizzoli A, Grenfell BT, Heesterbeek H and Dobson AP (eds), *The Ecology of Wildlife Diseases* (online edn.). Oxford: Oxford University Press, pp. 45–62.

van der Mescht L, le Roux PC and Matthee S (2013) Remnant fragments within an agricultural matrix enhance conditions for a rodent host and its fleas. *Parasitology* **140**, 368–377.

van der Mescht L, le Roux PC, Matthee CA, Raath MJ and Matthee S (2016) The influence of life history characteristics on flea (Siphonaptera) species distribution models. *Parasites and Vectors* **9**, 178.

Veenstra AJF (1958) The behaviour of the multimammate mouse *Rattus (Mastomys) natalensis* (A. Smith). *Animal Behaviour* **6**, 195–206.

Viney M and Cable J (2011) Macroparasite life histories. *Current Biology* **21**, R767–R774.

Walker TB, Keirans JE and Horak IG (2000) *The Genus Rhicephalus (Acari: Ixoididae): A Guide to the Brown Ticks of the World.* Cambridge, UK: Cambridge University Press.

Welegerima K, Meheretu Y, Haileselassie TH, Gebre B, Kidane D, Massawe AW, Mbije NE and Makundi RH (2020) Abundance and microhabitat use of rodent species in crop fields and bushland in Ethiopia. *Journal of Vertebrate Biology* **69**, 20054.

Wells K, Gibson DI, Clark NJ, Ribas A, Morand S and McCallum HI (2018) Global spread of helminth parasites at the human–domestic animal–wildlife interface. *Global Change Biology* **24**, 3254–3265.

Wilson DE and Reeder DM (2005) *Mammal Species of the World: A Taxonomic and Geographic Reference*, 3rd Edn. Baltimore, MD: Johns Hopkins University Press.

Zeileis A, Kleiber C and Jackman S (2008) Regression models for count data in R. *Journal of Statistical Software* **27**, 1–25.

Zimba M, Pfukenyi D, Loveridge J and Mukaratirwa S (2011) Seasonal abundance of plague vector *Xenopsylla brasiliensis* from rodents captured in three habitat types of periurban suburbs of Harare, Zimbabwe. *Vector-Borne and Zoonotic Diseases* **11**, 1187–1192.

Zumpt F (1961) *The Arthropod Parasites of Vertebrates in Africa South of the Sahara (Ethiopian Region)*, Vol. **I** (Chelicerata). Johannesburg, South African: Institute for Medical Research.

Zuur AF and Ieno EN (2016) *Beginner's Guide to Zero-Inflated Models with R*. Newburg, UK: Highland Statistics Limited.

Zuur AF, Ieno EN, Walker NJ, Saveliev AA and Smith GM (2009) *Mixed Effects Models and Extensions in Ecology with R*. Netherlands: Springer.