Digging for answers: contributions of density- and frequency-dependent factors on ectoparasite burden in a social mammal

[1]Elizabeth K. Archer, [1]Nigel C. Bennett, [2]Chris G. Faulkes & [1]Heike Lutermann:

[1]Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Private Bag X20, Hatfield 0028, South Africa, [2]School of Biological and Chemical Sciences, Queen Mary University of London, Mile End Road, London E1 4NS, UK.

Abstract

Due to the density-dependent nature of parasite transmission parasites are generally assumed to constrain the evolution of sociality. However, evidence for a correlation between group size and parasite burden is equivocal, particularly for mammals. Host contact rates may be modified by mobility of the host and parasite as well as social barriers. In the current study, we used the common mole-rat (*Cryptomys hottentotus hottentotus*), a social subterranean rodent, as a model system to investigate the effect of host density and frequency of contact rates on ectoparasite burdens. To address these factors we used a study species that naturally varies in population densities and intergroup contact rates across its geographic range. We found that ectoparasite prevalence, abundance and species richness decreased with increasing host density at a regional scale. At the same time, measures of parasite burden increased with intergroup contact rates. Ectoparasite burdens decreased with colony size at the group level possibly as a result of increased grooming rates. Equating group size with population density might be too simplistic an approach when assessing parasite distributions in social mammals. Our data suggest that frequency-dependent mechanisms may play a much greater role at a population level than density-dependent mechanisms in determining parasite distributions in social species. We suggest that future studies should explicitly consider behavioural mechanisms that may affect parasite distribution.

Keywords: *Cryptomys*, ectoparasite, group size, parasite transmission, sociality

Background

A central objective of ecology is to identify traits that govern species distribution. This includes parasite species that tend to exhibit highly aggregated distributions across host populations (Wilson et al. 2002; Poulin 2007). One determinant of parasite distribution is social interactions between conspecifics as direct contact between hosts facilitates parasite transmission. Consequently social host species are expected to suffer from a greater parasite prevalence, abundance and/or species richness due to higher host densities (Altizer et al. 2003). Although density-dependent transmission is frequently assumed for social hosts (Anderson and May 1978), not all social host species appear to suffer higher parasitism as a result of increased proximity to conspecifics irrespective of whether ecto- or endoparasites are considered (Arnold and Lichtenstein 1993; van Vuren 1996; Hillegass et al. 2008; Viljoen et al. 2011; Lutermann et al. 2013; Lopez et al. 2013).

Nevertheless, three meta-analyses have demonstrated across a broad range of host species and parasite taxa that hosts living in larger groups generally suffer higher levels of parasitism (Côté and Poulin 1995; Rifkin et al. 2012; Patterson and Ruckstuhl 2013). The strength of these patterns depends on the mode of transmission of the parasite with positive correlations being more apparent for directly transmitted parasites (Côté and Poulin 1995; Rifkin et al. 2012; Patterson and Ruckstuhl 2013). In addition, it has been suggested that host mobility may be important with group size-dependent increases in parasite burden being more pronounced for sedentary host species than those that range over large areas. However, Rifkin et al. (2012) show that the relationship between group size and parasite burden is weakest with regard to mammalian hosts. Since the strong effects of group size observed among sedentary species was largely due to colonially breeding birds, which greatly exceeded mammal

group sizes, they hypothesise that the nature and frequency of social interactions within groups may counteract a density-dependent transmission (i.e. result in frequency-dependent transmission). A comparative study in rodents that explicitly considered the degree of sociality did not find a clear relationship between sociality and endoparasites while it was negative for ectoparasites (Bordes et al. 2007). In addition, behavioural mechanisms such as clustering into sub-groups may reduce parasite transmission within larger social groups (Wilson et al. 2003; Griffin and Nunn 2012; Manlove et al. 2014). The significance of social barriers such as xenophobia and high group integrity to parasite transmission has already been pointed out several decades ago (Freeland 1976; Freeland 1979; Loehle 1995). Although Freeland's observations of group specific endoparasite infracommunities could not be reproduced in a recent study on the same primate population (Chapman et al. 2012), several other studies in primates and carnivores have provided theoretical and empirical evidence for a role of intergroup contact rates for endoparasite transmission (Walsh et al. 2009; Drewe 2010; Nunn et al. 2015; Rimbach et al. 2015). Furthermore, a number of recent studies show that group membership is an important determinant of parasite burden suggesting that parasite burden is more similar among group members than between members of different groups in several mammal taxa (Viljoen et al. 2011; Lutermann et al. 2013; Leclaire and Faulkner 2014; Manlove et al. 2014). Consequently, both density- and frequency dependent mechanisms may affect the relationship between parasite burden and sociality, meaning group size alone may be a poor predictor of these mechanisms. Furthermore, social interactions tend to be highly dynamic and species that form large breeding aggregations may range solitarily during the remainder of the year suggesting that host contact rates and parasite transmission can exhibit large seasonal variation. Similarly, seasonal variation in parasite burdens (both endo and ectoparasites), that might be linked to climate variables, has been reported for a wide range of social mammal taxa (Huffman et al.

2009; Gillespie et al. 2010; Viljoen et al. 2011; Cizauskas et al. 2014; Klompen et al. 2015).

We evaluated the contributions of density- and frequency-dependent mechanisms on the prevalence, abundance and species richness of ectoparasitic arthropods in the common mole-rat (*Cryptomys hottentotus hottentotus*). This species of the hystricomorph family of African mole-rats (Bathyergidae) is known to be distributed along the western part of South Africa from the Cape Peninsula northward to Steinkopf near the Namibian border (Bennett and Faulkes 2000). Colonies of this herbivorous rodent can reach sizes of up to 14 individuals (Spinks et al. 1997; Spinks et al. 1999). Common mole-rats are cooperative breeders with a single breeding female and one, perhaps two, resident breeding males (Bishop et al. 2004). The subterranean life-style greatly limits dispersal in mole-rats since the costs of digging have been estimated to be up to be 3600 times the energetic requirements for above-ground dispersal (Vleck 1979). Rainfall, that softens the soil and reduces energy expenditure for burrowing, determines dispersal patterns in the study species. Consequently, while contact rates between colony members remain constant throughout the year inter-colony contact rates vary seasonally as well as regionally with rainfall (Spinks et al. 2000b). On South Africa's west coast dispersal patterns differ along a latitudinal gradient with increasing annual rainfall from north to south and dispersal being greater in mesic areas (Spinks et al. 2000b; Bishop et al. 2004). The resulting differences in colony integrity coincides with a markedly increased xenophobia in arid compared to mesic sites (Spinks et al. 1998). At the same time, the population densities of common mole-rats at the rainfall extremes differ by an order of magnitude and can reach densities of 18.7 ±1.2 individuals/ha in mesic compared to 1.8 ±0.2 individuals/ha in arid sites while mean colony size (5.1 ±0.2 individuals) is comparable (Spinks et al. 2000b; Bishop et al. 2004). These regional differences in population density are likely to further affect inter-colony contacts and have been shown to be higher in high density populations irrespective of rainfall (Spinks et al. 2000b). This combination of ecological and behavioural traits makes common mole-rats an ideal model system to tease apart

the contributions of density- and frequency-dependent mechanisms on parasite burdens. Additionally, the number of ectoparasite species is limited in common mole-rats (Archer et al. 2014), allowing monitoring all of their ectoparasite species simultaneously.

Abiotic factors, such as rainfall and temperature, may influence the prevalence and abundance of parasites in a community directly and result in seasonal fluctuations in parasite burdens (Altizer et al. 2006). This may be particularly apparent in arthropod ectoparasites where increased temperature can accelerate the life-cycle and moderate to high humidity is necessary for survival (Marshall 1981). However, burrow-dwelling ectoparasites are likely to be less affected by seasonal fluctuations in climate due to the attenuated temperature amplitude and constantly high humidity found in sealed burrow systems (Roper et al. 2001; Sumbera et al. 2004). Previous work on social bathyergids including the study species have revealed that ectoparasite prevalence and abundance tends to increase during the wet season irrespective of whether they inhabit a summer- or winter-rainfall area (Viljoen et al. 2011; Archer et al. 2014; Lutermann et al. 2015).

The geographic and seasonal variance in rainfall patterns that determine inter-colony encounter rates in the study species provide a unique natural experiment without the need for experimental manipulation. In the current study, we examined the prevalence, abundance and species richness of the ectoparasite community sustained by common mole-rats from two localities representing the extreme mesic and arid conditions inhabited by the study species over a period of two years. We hypothesised that ectoparasite burdens increase with (i) host density (i.e. greater in mesic vs. arid site and/or increases with colony size) and (ii) inter-colony contact rates (i.e. increases with rainfall: regionally and seasonally). Through this work we show that density-dependent mechanisms appear to be of minor importance compared to frequency-dependent and social mechanisms in determining the ectoparasite burden of a social host.

Methods
Study sites and animal capture

Trapping was carried out at two sites approximately 440km apart near the western coast of South Africa between February 2011 and August 2012. The mesic site, Darling, Western Cape (33.25^{o}S, 18.25^{o}E) has approximately 457mm of rainfall per annum while the arid site, Kamieskroon, Northern Cape (30.13^{o}S, 17.57^{o}E), was located in the Namaqualand habitat with an average annual rainfall of 234mm (approx. 50-year averages (Romanach 2005)). Both sites were located on farms with grazing cattle and sheep at low densities. Trapping occurred at both sites during summer (January-March) and winter (June-August). Animals were captured using live traps (Hickman 1979) baited with sweet potato. Trap sites were at least 30m apart to prevent multiple traps capturing the same colony. Traps were checked every two to three hours from first light until just after dark. A colony was considered complete when no activity was recorded at a trap site for 36h after the last animal capture (Spinks et al. 1998). Once captured, individuals of the same colony were housed together in plastic crates provided with at least a 3cm layer of soil and air holes in the lid. Sweet potato was used to feed the mole-rats daily. Animals were kept in crates for a maximum of two weeks until all colony members were captured before being processed.

Parasite collection and quantification
Each individual was euthanized with an overdose of halothane. Immediately after expiration the animals were sexed and weighed with scales (SNUG-III precision balance, Jadever) accurate to 0.05g. Breeding status of individuals (breeder or non-breeder) was determined (Spinks et al. 1999). Ectoparasites were removed by washing (see Archer et al. (2014) for washing protocol) and any ectoparasites recovered were stored, mounted and identified as described in Archer et al. (2014). Prevalence and abundance was recorded for each species, with species richness for each host individual as measures of parasite burden.

Statistical analyses
Colony sizes were compared between the two localities using a Mann-Whitney-U test. As a test of the effects of clustering into groups on

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ectoparasite measures, we applied generalized linear models (GLMs) containing colony identity as the only predictor variable. We evaluated the contributions of locality, the probability of seasonal dispersal and colony size employing generalized linear mixed-effects models (GLMMs). Measures of parasite burden were used as dependent variables. Ectoparasite prevalence models were fitted with a binomial distribution ('lmer' function, lme4 package, Bates et al. 2012) while ectoparasite abundances were explored fitting a negative binomial distribution ('glmmadmb' function, glmmADMB package, Fournier et al. 2012). Zero inflation was specified in abundance models for three ectoparasite species due to low prevalence (see Results). The low abundances of *Androlaelaps capensis* found (see Results) lead to the two species of *Androlaelaps* mites being combined for analyses. Species richness models were fitted to a Poisson distribution ('glmer' function, lme4 package, Bates et al. 2012). Colony ID was included as a random effect in all GLMMs. Locality, rainfall and colony size were used as independent predictor variables. In addition, host sex, breeding status (breeder vs. non-breeder) and host body mass were included in the model. Rainfall was a cumulative total over a period of two months prior to the capture period and was used as proxy for inter-colony dispersal. Mean temperature was included to confirm that climatic effects on the host (i.e. rainfall) rather than effects of abiotic factors on the parasite accounted for observed patterns. Climatic data were obtained from the South African Weather Service. Since highly complicated models were unlikely to be statistically viable (Burnham and Anderson 2002; Symonds and Moussalli 2011) all possible models with all possible combinations were run with up to 4 predictors, with 2 and 3-way interactions between categorical variables included. Lack of flea infections in summer (see Results) prevented the inclusion of climate variables and colony size in the models for this taxon. Similarly, the absence of lice in one locality (see Results) excluded the consideration of this variable in the analyses. Only complete colonies for which colony size was known were included in the analyses. However, model results

were similar for the full data set excluding colony size as predictor (data not shown).

Due to a large number of possible predictors we chose an information-theoretic (IT) approach to assess patterns of ectoparasite infection, using the Akaike information criterion (AIC) to identify the best model fit (Burnham and Anderson 2002; Symonds and Moussalli 2011; Burnham et al. 2011; Garamszegi 2011). This is a method that compares models with all possible combinations of factors via the Akaike information criterion (AIC) as a measure of goodness-of-fit (Symonds and Moussalli 2011). This makes it extremely useful for analyses that involve a large number of factors (Burnham and Anderson 2002; Symonds and Moussalli 2011).

Although many GLMMs were run, there was a possibility that omitting the most complicated models may lead to a small amount of bias in the data and making the best model alone not necessarily reliable. Therefore the significance of a specific predictor was inferred by using the cumulative Akaike weight (w_i) (Burnham and Anderson 2002; Symonds and Moussalli 2011). The w_i was calculated for each model as a measure of the significance of that specific model. Cumulative w_i of a specific predictor was then calculated by totalling the w_i of the models that include the predictor. These are expressed as percentages by multiplying this number by 100 (Burnham and Anderson 2002). Cumulative w_i of above 90% are generally considered high (Burnham and Anderson 2002; Symonds and Moussalli 2011) however, we considered predictors with a cumulative w_i above 80% as important for our study. The evidence ratio (ER) was also calculated. This provides a measure of how much more likely the best model is compared other models (Symonds and Moussalli 2011). Models that account for a total of 95% of cumulative w_i are reported here. The tables include the w_i and ER for each model. Corrected AIC values were calculated (AICc) to account for limited sample size (Burnham and Anderson 2002; Symonds and Moussalli 2011). All models were run in R2.15.1 (2012).

Results

Two sampling trips per site and season were conducted with the exception of summer in the arid site which was sampled once. During the

study period rainfall differed markedly both with season and locality. In contrast, mean temperature profiles were fairly similar in both localities (Online resource 1 Fig. ESM 1). In total, 268 *C. h. hottentotus* were collected during the study period (Online resource 1 Table ESM 1). Of these, 151 individuals were from complete colonies. There was no significant difference in the average size of colonies between locations (mean ±SE; mesic = 5.9 ±0.3, arid = 5.6 ±0.3, MWU: U = 0.998, P = 0.318).

A total of five species of ectoparasite were found to infect *C. h. hottentotus*. The three mite species collected (*Androlaelaps scapularis*, *A. capensis,* and *Radfordia ensifera*) were the most prevalent and abundant ectoparasites at both locations with *Androlaelaps* spp. being the most prevalent and abundant mites (Table 1). In addition, a single flea species (*Cryptopsylla ingrami*) was harboured by common mole-rats at both localities. This species was only collected during the winter months and occurred at low prevalence and abundance (Table 1). Exclusive to hosts at the arid site was an anopluran louse species (*Eulinognathus hilli*). Though less prevalent than *C. ingrami*, it was much more abundant (Table 1).

Effects of population density and group integrity
Locality was an important determinant of ectoparasite prevalence and abundance for all species for which this variable could be considered, as well as for species richness. With the exception of *C. ingrami* abundance the cumulative w_i for locality never dropped below 99% (Table 2) However, contrary to predictions ectoparasite burdens were lower at the mesic site (Table 1). The ER suggested that the effect of locality on ectoparasite burden was more pronounced for ectoparasite abundance than for prevalence while the opposite was true for *C. ingrami* (Online Resource 1 Tables ESM 2-10). Though we were unable to explore this statistically, the observation that *E. hilli* was absent in the mesic habitat suggests that locality is also an important predictor of louse abundance and prevalence. This is corroborated by the high cumulative w_i of locality for species richness and that richness was higher at the arid site (Table 2).

Density-dependent effects at the group level

Colony size was an important predictor of prevalence and abundance for *Androlaelaps* spp. with a cumulative w_i of ≥90% (Table 1). Unexpectedly *Androlaelaps* spp. prevalence and abundance decreased with increasing colony size (estimate ±SE: -0.429 ±0.4288 and -0.706 ±0.2935, respectively, Fig. 1a and b). In contrast, the influence of colony size on the prevalence and abundance of *R. ensifera* appeared to be limited and cumulative w_i was low for both measures of parasite burden (Table 1). Though colony size is present in the best fitting models for species richness (Online Resource 1 Table ESM 10), the cumulative w_i was below 80% (Table 2). However, the results of the GLMs indicate that colony identity is a significant predictor for the prevalence (*Androlaelaps* spp.: estimate ±SE: 0.104 ±0.017, P < 0.0001 and *R. ensifera*: estimate ±SE: 0.030 ±0.010, P = 0.003) and abundance (*Androlaelaps* spp.: estimate ±SE: 0.040 ±0.008, P < 0.0001 and *R. ensifera*: estimate ±SE; 0.030 ±0.007, P = 0.015) of both mite taxa. Colony identity was similarly significant for ectoparasite species richness (estimate ±SE: 0.020 ±0.003, P < 0.0001).

Frequency-dependent effects on ectoparasite burdens
Seasonal variation in cumulative rainfall affected the prevalence and abundance of mites, however, this effect was stronger for the more prevalent and abundant mite genus. The cumulative w_i for rainfall exceeded 98% for the prevalence and abundance of *Androlaelaps* spp. (Table 2). Both measures increased with increasing rainfall (estimates ±SE: 0.049 ±0.017 and 0.017 ±0.004, respectively, Fig. 2a and b). In contrast, rainfall was not included in the best model for *R. ensifera* prevalence (Online Resource 1 Table ESM 4) and the cumulative w_i was just below 50% (Table 1). Rainfall was included in the best model for the *R. ensifera* abundance and the cumulative w_i was 81.5%. The abundance of *R. ensifera* increased with rainfall (estimate ±SE: 0.015 ±0.006, Fig. 2c). Fleas were absent during the dry summer while louse prevalence and abundance was greater in winter (Table 1) suggesting that rainfall also affects the prevalence and abundance of *C. ingrami* and *E. hilli*. This is substantiated by the high cumulative w_i for rainfall in the model for ectoparasite

species richness and species richness increased with rainfall (estimate ±SE: 0.008 ±0.002, Table 2, Fig. 2d). In contrast, there was low support for temperature as a predictor of mite prevalence and abundance as well as ectoparasite species richness. Temperature did not exceed a cumulative w_i of 39.3% (Table 3). Additionally, ER for the best models including temperature were high (Online Resource, Table ESM 2-10) supporting the hypothesis that host dispersal rather than the climate effect of on ectoparasites affected parasite distribution.

Influence of other biotic factors
Overall host factors such as sex, breeding status and body mass appeared to have little influence on the ectoparasite prevalence, abundance and species richness (Table 1). Support for sex-biases in ectoparasite burden was only apparent for lice with a cumulative w_i of 91.6% and male common mole-rats (6.36±3.09) had a greater abundance of *E. hilli* than females (4.62±1.44). Lice were also the only ectoparasite taxon encountered that showed evidence for effects of body mass (Table 1). The cumulative w_i for body mass effects on *E. hilli* abundance was 80.2% and it increased with increasing body mass (estimate ±SE: 0.038 ±0.013). However, none of the factors considered were indicated as a good predictor for the variation in *E. hilli* prevalence as the intercept model had the lowest AICc (Online Resource 1, Table ESM 8). The breeding status of the host individuals had an effect on the abundance of *C. ingrami* but none of the other parasites collected. Breeding status had a cumulative w_i of 86% and breeders (0.29±0.12) had a lower abundance of *E. hilli* than non-breeders (0.40±0.09). Although host factors such as host sex, breeding status and body mass were included in the best models for several of the mite species and species richness, the cumulative w_i did remain below 80% and ER was high for these factors (Table 2; Online Resource 1, Tables ESM 1-4, 10).

Discussion
Contrary to predictions based on population densities all measures of the ectoparasite community sustained by *C. h. hottentotus* were greater in the arid than the mesic habitat. This finding contrasts markedly with the positive correlation between ectoparasite burden and population density of a solitary subterranean rodent, the Talas tuco-tuco (*Ctenomys talarum*), in Argentina (Cutrera et al. 2014). It suggests that density-dependent mechanisms are unlikely to explain the observed patterns although all ectoparasites collected in the current study are directly transmitted. Although theoretical models provide good support for a density-dependent parasite transmission, particularly for directly transmitted parasites such as the ones in the current study (Anderson and May 1978; Altizer et al. 2003), empirical studies across mammalian and parasite taxa provide mixed support for this assumption even within the same host species (Arneberg et al. 1998; Morand and Poulin 1998; Vicente et al. 2007; Winternitz 2012; Renwick and Lambin 2013; Luong et al. 2014) suggesting that equating host density with contact rates might be an oversimplification. However, host density has been shown to be negatively correlated with home range size (Bordes et al. 2009; Morand 2015) and hence the burrow systems of *C. h. hottentotus* in the arid site may have been larger than those in the mesic site. Although burrows were not excavated for the current study a previous assessment of burrow architecture of the study species corroborates this hypothesis and *C. h. hottentotus* burrows from an arid population extended over a larger area than those of the mesic population (Spinks et al. 2000a). Hence, the greater ectoparasite burden observed in arid populations of *C. h. hottentotus* may be a result of larger home ranges and the associated greater exposure potential in this population. In contrast, a number of studies found a negative correlation between home range size and parasite diversity in various mammal taxa (Nunn et al. 2003a; Nunn et al. 2003b; Lindenfors et al. 2007; Bordes et al. 2009) and it has been suggested that this may be attributable to lowered transmission rates of directly transmitted parasites with increases in home range at lower host densities (Morand 2015).

Comparable colony sizes among populations preclude density-dependent effects based on group sizes creating differences in ectoparasite burden between locations. Conversely, the dispersal constraints posed by the subterranean lifestyle of the study species that lead to an impaired mobility of the host in

the arid habitat are likely to account for the greater ectoparasite burden as has been suggested previously (Côté and Poulin 1995; Patterson and Ruckstuhl 2013). Hence, colony stability seems to maintain higher parasite burdens at the population level. This corresponds to increases in parasite burden as a result of a more intensive use of home ranges suggested for ungulates and primates (Ezenwa 2004a; Nunn and Dokey 2006). Additionally, social barriers are likely to have contributed to this pattern since colony identity was an important predictor of ectoparasite prevalence, abundance and species richness. Similar effects of group membership have previously been found for closely related social bathyergids (Viljoen et al. 2011; Lutermann et al. 2013) and other social mammals (Freeland 1979; Leclaire and Faulkner 2014; Manlove et al. 2014), supporting the hypothesis that segregation into clusters can reduce parasite transmission rates within a host population (Wilson et al. 2003; Rifkin et al. 2012; Griffin and Nunn 2012). Further corroborating evidence for significant effects of such social barriers and actual contact rates rather than group size on parasite transmission comes from a several studies in primates (Walsh et al. 2009; Griffin and Nunn 2012; Nunn et al. 2015; Rimbach et al. 2015). They furthermore suggest that larger groups may form more social sub-units which may in turn counter any density-dependent parasite propagation (Chapman et al. 2009). In the common mole-rat the heightened xenophobia in arid populations (Spinks et al. 1998) is a social mechanism likely to be responsible for maintaining group integrity and decreasing transmission rates (Freeland 1976; Loehle 1995).

The effectiveness of such social mechanisms and consequently the temporal stability of social subunits may vary seasonally. In the study species, rainfall facilitates dispersal and increased inter-colony dispersal ensues that ultimately increases contact rates between colonies (Spinks et al. 2000b; Bishop et al. 2004). Our results indicate that this breakdown of colony integrity coincides with increases in all measures of parasite burden considered in this study. Although abiotic factors such as rainfall may also act on arthropod ectoparasites directly (Marshall 1981) the stable abiotic conditions within mole-rat burrows make this an unlikely mechanism in the study species (Roper et al. 2001; Sumbera et al. 2004). This is corroborated by the lack of temperature effects in the current study. Furhtermore, ectoparasites associated with the closely related highveld mole-rat (*C. h. pretoriae*), which inhabit a summer rainfall area, also increase in abundance during the wet season when temperatures are high (Viljoen et al. 2011). Hence, the seasonal changes in ectoparasite burden observed are more likely linked to increases in dispersal activity. Thus our data provide evidence for frequency-dependent parasite transmission as would be expected in directly transmitted ectoparasites as those considered in the current study (Côté and Poulin 1995; Rifkin et al. 2012; Patterson and Ruckstuhl 2013). Seasonal variation in parasite burden is an ubiqous feature of parasite populations including those of social mammals (Wilson et al. 2002; Ezenwa 2004b; Altizer et al. 2006; Huffman et al. 2009; Viljoen et al. 2011; Cizauskas et al. 2015; Klompen et al. 2015; Lutermann et al. 2015). Consequently, our understanding of the prevalence of density vs. frequency-dependent drivers of host-parasite interactions might be improved by considering seasonal changes in both host and parasite traits.

At a colony level we found evidence for density-dependent patterns of ectoparasite burdens. Contrary to our hypothesis, parasite prevalence and abundance decreased with increasing group size. A similar negative correlation between group size and ectoparasite burden has been reported for other social rodents (Bordes et al. 2007; Viljoen et al. 2011). Bordes et al. (2007) suggested that increases in allogrooming frequency may account for decreases in ectoparasite burden. This mechanism is also likely to account for the patterns observed in the study species. However, negative correlations between group size and parasite burden are not restricted to ectoparasites in cooperatively breeding mammals and increases in group size may also affect the susceptibility to parasites (Lutermann et al. 2013; Leclaire and Faulkner 2014). It should be noted that patterns at the group level differed between ectoparasite species. Variation in parasite transmission (Côté and Poulin 1995; Rifkin et al. 2012; Patterson and Ruckstuhl

2013) or abundance may account for such differences. In addition, for directly transmitted parasites the directionality of social interactions may strongly affect transmission and in meerkats (*Suricata suricatta*) individuals initiating social interactions rather than those receiving them had a greater risk of transmission (Drewe 2010). This suggests that detailed long-term behavioural observations of social interactions may further help to disentangle the contributions of density- vs. frequency-dependent mechanisms operating in social mammals. However, such data are currently only available for a limited number of social mammals (e.g. primates, some carnivores and sciurids).

Social factors appeared to be more important than other host factors as determinants of ectoparasite burdens in common mole-rats. This may be partially attributable to the shared environment between colony members and the use of a central nest by all colony members (Thomas et al. 2013) that results in similar parasite exposure. Nevertheless breeding status did affect the abundance of *C. ingrami* and breeders sustained lower abundances than non-breeders. Based on the observation that reproductive investment tends to be associated with an increased susceptibility to parasites (Christe et al. 2000; Ezenwa et al. 2012) this was unexpected. Several mutually non-exclusive mechanisms may account for this observation. The division of labour found in mole-rats may allow breeders to invest more time in autogrooming while non-breeders spend more time foraging. Breeders may also receive more allogrooming than non-breeders (Bennett and Faulkes 2000). This division of labour also allows for energy conservation in breeders and a greater immune investment in breeders compared to non-breeders has been observed for closely related Natal mole-rats (*C. h. natalensis*, Lutermann and Bennett 2008). The comparatively high prevalence and abundance of mites may have negated a similar effect in this taxon. Lice are the only ectoparasite taxon encountered in the current study that spends its entire life-cycle on the host (Marshall 1981). Consequently host size is likely to correlate more strongly with resource availability for *E. hilli* than for the other ectoparasite taxa. Since the study species exhibits sexual dimorphism

(Spinks et al. 2000b) food patch limitations would account for the effects of sex and body mass on the abundance of *E. hilli* (Moore and Wilson 2002). It should be noted that the effects of host factors on the lice and fleas were calculated without considering colony size and these biotic factors may not be as important once colony size is considered.

Conclusion
The combination of constraints of the subterranean life-style, rainfall effects on inter-colony contact rates and similar group sizes irrespective of rainfall provided a unique opportunity to evaluate the contributions of density- and frequency-dependent mechanisms on ectoparasite prevalence, abundance and species richness in a social mammal. We found evidence that all measures of parasite burden are largely independent of local host population density but linked to dispersal barriers. Thus host mobility and behavioural mechanisms appear to be more important determinants of parasite burden than host density. At the group level, ectoparasite burdens decreased with group size suggesting that benefits of group-living may reduce susceptibility and/or exposure to ectoparasites. We suggest that explicitly considering social mechanisms is necessary to establish general mechanisms that govern the relationship between sociality and parasite burden.

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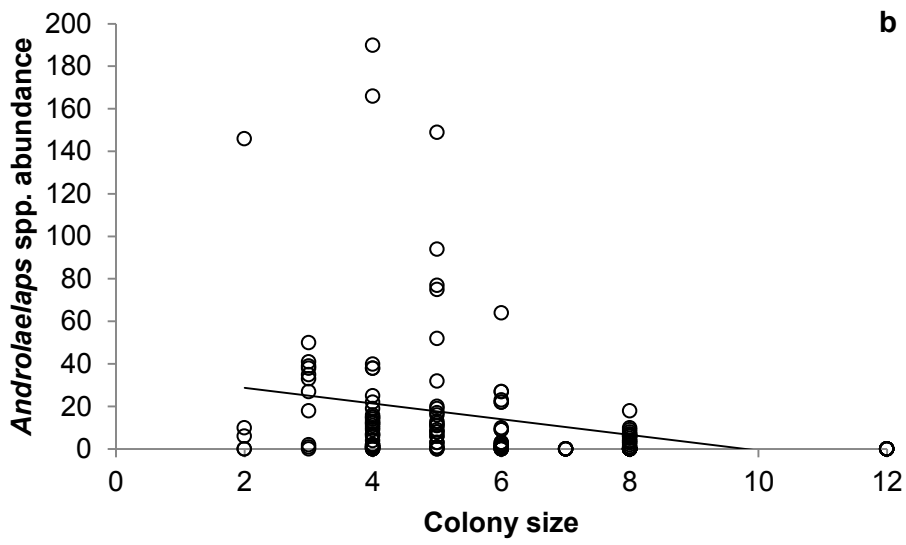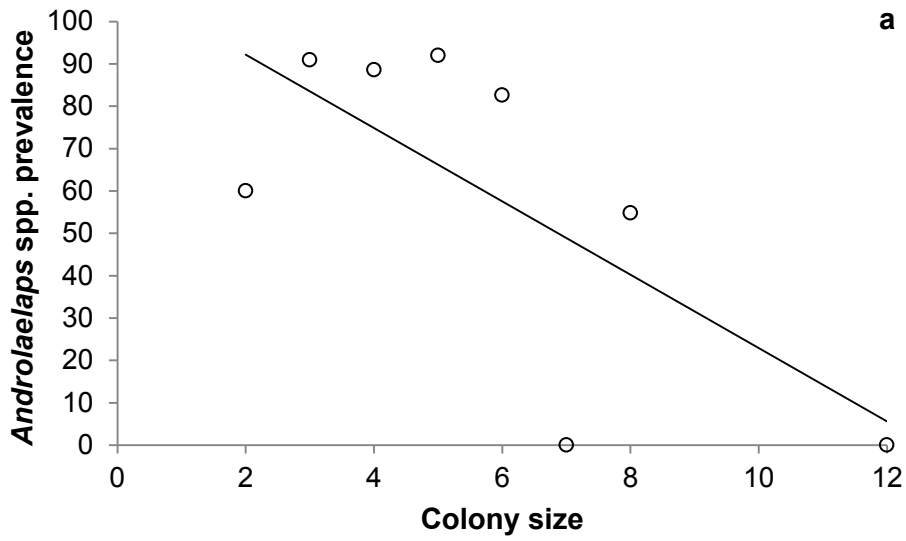
Fig. 1. Relationship between colony size and the a) prevalence and b) abundance of *Androlaelaps* spp.
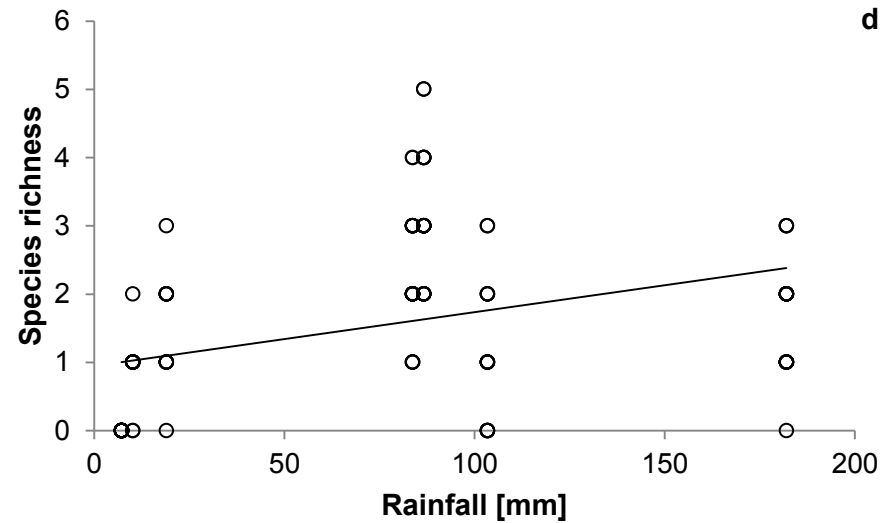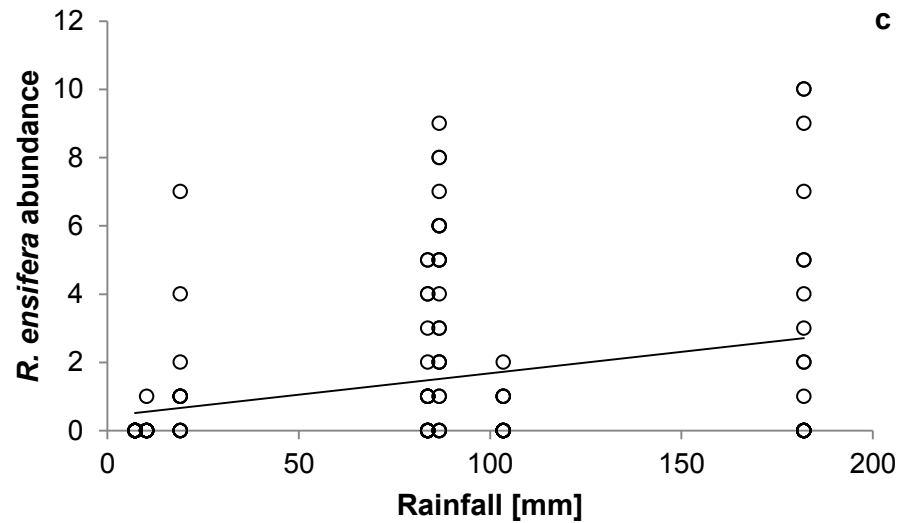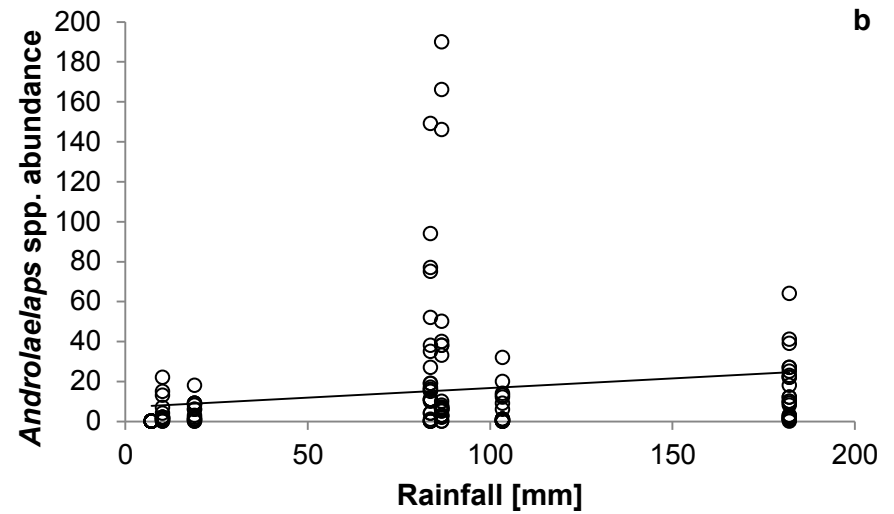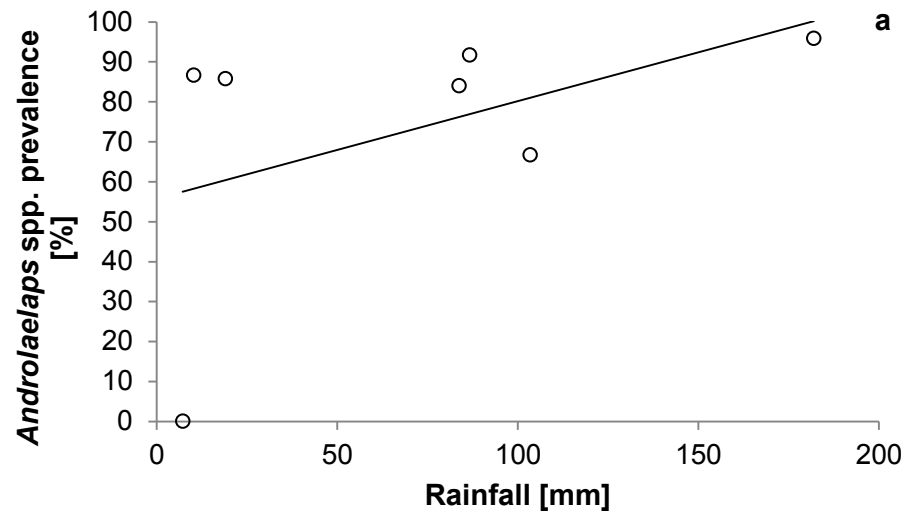
Fig. 2. Relationship between cumulative seasonal rainfall and the a) prevalence and b) abundance of *Androlaelaps* spp., c) the abundance of *R. ensifera* and d) species richness.

Table 1. Prevalence and total abundance (in brackets) of ectoparasite species infesting *C. h. hottentotus* by location and season.

		Androlaelaps spp.	*Radfordia ensifera*	*Cryptopsylla ingrami*	*Eulinognathus hilli*	Species richness
arid	Summer	85.0% (169)	45.0% (21)	-	5.0% (6)	1.40 ± 0.18
	Winter	89.2% (2567)	63.5% (235)	34.6% (64)	20.2% (421)	2.51 ± 0.10
mesic	Summer	29.1% (84)	5.5% (5)	-	-	0.35 ± 0.08
	Winter	78.9% (1139)	33.3% (86)	7.8% (12)	-	1.34 ± 0.09

Table 2. The cumulative weights (w_i) of the predictors from the GLMMs for prevalence and abundance of parasite taxa found on *Cryptomys h. hottentotus*. Predictors with w_i above 80% are in bold.

	Androlealaps spp.		*Radfordia ensifera*		*Cryptopsylla ingrami*		*Eulinognathus hilli*		Species richness
	Prevalence	Abundance	Prevalence	Abundance	Prevalence	Abundance	Prevalence	Abundance	
Location	**0.990**[a]	**0.999**[a]	**0.997**[a]	**0.997**[a]	**0.995**[a]	0.778[a]	-	-	**0.999**[a]
Rainfall	**0.979**[a]	**0.983**[a]	0.498	**0.815**[a]	-	-	-	-	**0.998**[a]
Temperature	0.393[a]	0.048	0.249	0.287	-	-	-	-	0.123
Colony size	**0.913**[a]	**0.900**[a]	0.158	0.256	-	-	-	-	0.663[a]
Sex	0.376	0.064	0.548[a]	0.258	0.773[a]	0.046	0.271	**0.916**[a]	0.266
Breeding status	0.077	0.705[a]	0.450[a]	0.317	0.391	**0.855**[a]	0.277	0.427	0.209
Body mass	0.150	0.229	0.455[a]	0.373[a]	0.321	0.076	0.265	**0.802**[a]	0.331[a]

[a]: predictor was included in the best model.