The effect of group size on ectoparasite load and physiological markers of health in a communally-roosting bird

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Abstract

Group living in animals can provide individuals with many fitness benefits, but also increases their exposure to parasites. However, the relationship between group size and parasite load both across and within species is highly variable, potentially due to selection acting on adaptations to reduce infection risks and costs, as well as species-specific variation in the type and frequency of social behaviours. Information about the risks and physiological costs of parasitic infection along a gradient of sociality and in different ecological settings is currently limited. Here, we explored how ectoparasite load and physiological markers of health are associated with group living in speckled mousebirds, *Colius striatus*. We found that group size had a non-linear effect on ectoparasite load: individuals in medium-sized groups were most infested. In addition, infested individuals in medium-sized groups showed the greatest signs of reduced health. We speculate that social immunity mechanisms such as allogrooming, and the physiological costs of group living might play important roles in mediating this relationship, where larger groups suffer increased risk of infection but also provide higher levels of anti-parasite behaviour or immunity. Our results suggest the existence of various mechanisms by which group-living

animals can mediate increased ectoparasite transmission and the negative health consequences of infestation, and highlight the need for further research on mechanisms of social immunity in a broad range of taxa.

Significance statement

In this study, we measured the ectoparasite loads of over 200 speckled mousebirds (Colius striatus). Birds living in medium-sized groups harbour the greatest number of parasites and the physiological costs of infection are also highest for individuals in medium-sized groups. This is, as far as we are aware, the first evidence of a non-linear relationship between group size and parasite load in a wild bird species, and it raises exciting new questions about how individuals in larger groups are able to offset the costs of increased parasite exposure. We speculate that social immunity mechanisms like allogrooming and the physiological benefits of group living might play important roles in mediating this relationship. Further, we argue that expanding the application of social immunity concepts to birds and other vertebrate taxa may reveal exciting new insights into host-parasite evolution in social species.

Keywords

Parasites, sociality, communal roosting, immunity, disease, mousebird

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Author contribution

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Introduction

The widespread occurrence and repeated evolution of sociality across animal taxa demonstrates that, under the right circumstances, social coordination and cooperation among selfish entities can offer many benefits (Rubenstein 1978; Nowak 2006; Silk 2007). However, living in groups also increases transmission of, and individual exposure to, pathogens and parasites (hereafter "parasites" refers to multicellular parasites and microparasites, including pathogenic bacteria and viruses; Freeland 1976; Coté and Poulin 1995; Godfrey et al. 2005; Ritchie et al. 2021). The heightened risk of transmission and infection associated with group living has been cited as a major constraint in the evolution of sociality (Alexander 1974; Hamilton 1987; Udiani and Fefferman 2020) and, as such, might be key to explaining why there is so much variation in the occurrence of group living as well as in social structure and social behaviours across the animal kingdom (Poulin and Filion 2021). However, while increased exposure to parasites might be inevitable in group-living species, the relationship between group size and actual parasite load is inconsistent, with mixed or even negative associations in many species and populations (e.g. Arnold and Lichtenstein 1993; Viljoen et al. 2011).

The apparent inconsistency of the link between group size and parasite load likely derives from two main sources. First, this link might be confounded by other co-varying factors related to social behaviour, cohesion and network structure, parasite type, or host ecology (Poiani 1992; Wilson et al. 2003; Ezenwa et al. 2016; Lucatelli et al. 2021). Second, given the additional selection pressure imposed by parasites on individuals living in groups, social species are predicted to have evolved adaptations to directly reduce the risks and negative impacts of infection (Stow et al. 2007; van Meyel et al. 2018). In eusocial insects in particular and to some extent in primates, evidence points to a broad panel of adaptations that arguably evolved in response to increased parasite exposure and infection in groups (Cremer et al. 2007). These adaptations include not only behavioural strategies such as strict group territoriality, social distancing and auto- and allogrooming (Nunn and Alitzer 2006; Cremer et al. 2018; Stockmaier et al. 2021), but also physiological traits such as social immunisation of group members and heighted production of natural antibodies and antimicrobial substances that can also reduce disease intensity (reviewed in Cremer et al. 2018). Such traits may obscure the expected positive relationship

between group size and parasite load, but our understanding of when these traits are expressed is almost entirely limited to the social insects. The combined effect of such direct immunological adaptations and indirect inter- or intraspecific variation in group structure, ecology and behaviour could be key in explaining the complex link between parasites and sociality, but further study in a wider range of taxa is needed.

Here, we study the relationship between group size and parasite load in an avian system. Although the evolution of sociality in birds is well-studied, comparatively little is known about the link between group living and parasite exposure in this taxon. The general prediction that parasite exposure should increase with group size has received some support in colonial (non-territorial) birds, where host parasite loads typically increase with colony size and density (e.g., Hoi et al. 1998; Møller et al. 2001; Brown and Brown 2004), but this pattern is far from universal (Gregory et al. 1991). The relationship between group size and parasite load has only been examined once in a territorial, group-living bird species as far as we are aware (Whiteman and Parker 2004). Furthermore, while there is evidence that immune defences are up-regulated in social bird species (Møller et al. 2001; Spottiswoode 2008), little is known about how (a) parasite load, (b) the health implications of infection and (c) the potential for social immunity traits to mitigate (a) and (b), vary with group size. To understand how concepts of social immunity apply to bird societies, more detailed work is needed.

Ectoparasites, or parasites living exclusively on the body surface, are well-studied in birds (Proctor and Owens 2000; Owen et al. 2010). Mites, lice and fleas are commonly found in the plumage of birds and many of them have been shown to reduce host fitness (Møller et al. 1990). Although some ectoparasites, such as feather mites, may incur little to no demonstratable cost to a host (Proctor and Owen 2000; Galván al. 2012; Dona et al. 2019), they are nevertheless transmitted through close body contact, which is commonly observed in group-living birds (Beauchamp 1999). Thus, ectoparasites, regardless of their health impacts, can serve as a useful model for testing ideas about sociality and disease ecology (e.g., parasite transmission and load). Importantly, there is evidence that cooperatively-breeding species harbour higher ectoparasite loads than pair-breeders (Poiani 1992), but information on intra-specific variation in ectoparasite load and sociality in birds is limited to a single study on

Galapagos hawks *Buteo galapagoensis* (Whiteman and Parker 2004). In addition, there is ample information documenting the effectiveness of a behavioural trait, preening, in reducing ectoparasite loads (Bush and Clayton 2018). In social bird species, allopreening, or preening of other group members, has been shown to play a role in group hygiene (Radford and Du Plessis 2006; Villa et al. 2016) and is presumably analogous to the allogrooming of infected workers in social insect colonies (Cremer et al. 2007). This behavioural mechanism may allow social birds to mitigate costs of increased ectoparasite transmission and could therefore potentially influence the relationship between group size and ectoparasite load. The selective pressure parasites exert on social species, combined with evidence that social species are able to evolve mechanisms to tolerate parasite infection on remarkably short timescales (Brown et al. 2021), suggests that relationships between parasites and social animals are likely to be diverse and highly complex, warranting further study.

In this study, we explored the link between group size, ectoparasite load and biomarkers of health status in the speckled mousebird, *Colius striatus*. Speckled mousebirds are medium-sized (mean ± SE = 46.96g ± 0.27, this study), exclusively herbivorous birds endemic to sub-Saharan Africa (Fry 2001). This species has a temporally split social structure: in the cooler non-breeding season, large groups (median = 8 individuals, range = 1-17; this study) forage together and roost communally in a tightly packed circle, while in the warmer breeding season, communal roosting is less common, and groups typically break up into breeding pairs and small groups (median = 4 individuals, range = 1 - 10; Decoux 1982; this study).

Communal roosting at low temperatures is crucial for thermoregulation in this species (Bartholomew and Trost 1970; McKechnie et al. 2009) but also likely facilitates parasite transmission among group members (Laughlin et al. 2019). However, ectoparasite prevalence is typically highest during the warmest months of the year (Martin II et al. 2007; Salam et al. 2009), suggesting that individuals might be at greater risk during the breeding season. In either season, we predict that larger groups have greater ectoparasite loads because they are at higher risk of ectoparasite infestation (*H1: high risk-high load*). However, speckled mousebirds frequently engage in allopreening (Rowan 1967; Brown and Foster 1992). With more individuals available to engage in allopreening, large groups might

be able to offset the increased risk of parasite exposure through behavioural immunity (*H2: high risk-low load*) (Villa et al. 2016). Alternatively, if sociality provides physiological benefits that allow individuals to counteract the negative health consequences increased parasite transmission, for example because communal roosting increases the available energy budget to dedicate towards immune defences, then parasite load and biomarkers of health status should be less strongly correlated in highly social settings (*H3: high risk-low impact*).

We first evaluated the relationship between social group size and ectoparasite load and tested whether this relationship differed between the non-breeding season, when communal roosting is common, and the warmer breeding season. We then evaluated the relationships between ectoparasite load and three biomarkers of health status and tested whether group size influenced these relationships.

Methods

We studied adult speckled mousebirds (hereafter: mousebirds) in Mbuluzi Game Reserve, part of the Lubombo Biosphere Reserve in northern Eswatini (-26.1603°, 32.0014°). Mousebirds live year-round and breed in the acacia savanna that covers the majority of the study site. Since 2017, we have been routinely catching mousebirds in the reserve as part of an ongoing long-term project about their reproductive and social behaviour.

Catching and sampling methods

Between 2017 and 2023, we used walk-in traps to catch and sample 348 speckled mousebirds (229 first-time catches and 119 re-catches of previously caught birds) within a ca. 5km^2 area of Mbuluzi Game Reserve. Most birds (84%) were caught in July and August during the non-breeding season, with the remainder (16%) being captured from September to November during the breeding season.

Every day for at least four days before catching, suitable sites were baited with fresh fruit (varying combinations of pineapple, orange, banana and papaya) to attract mousebirds to the site and

train them to return each day. Before sunrise on the day of catching, we placed a 50x50cm wire cage at the same location. Each cage was baited with the same sorts of fruit as above and was fitted with two funnel entrances that allowed mousebirds to enter, but not to leave. Observations in the field have shown that once in the cage, mousebirds typically start eating the fruit and do not attempt to escape or show any visible signs of stress until approached by a human observer (*pers. obs.*). In order to reduce disturbance, we therefore checked the cages from a safe distance once every hour and used motion-triggered cameras (Wilsus Tradenda 4G Wireless) that allow remote-viewing of footage to determine when mousebirds had entered the cage. If other mousebirds were seen in the vicinity, we did not approach the cage until they had either entered it or left the area.

Once all mousebirds had entered the cage, we removed each individual, placing it in a separate cloth bag for processing. Each bird was fitted with a unique combination of three coloured plastic leg rings and a uniquely-coded metal ring provided by SAFRING for individual identification. We recorded the identities of all birds that were caught together as a single group and considered the number of individuals caught together, plus any that were observed arriving together with the caught group but that did not enter the cage, to be the social group size. Although we cannot be certain that birds caught together truly constituted a single social group that consistently interacted with each other for longer periods, preliminary tracking data from radio-tagged mousebirds in our population shows that individuals who are caught together have highly overlapping ranges for several months after capture (unpublished data in prep.), and observations of birds arriving at feeding stations strongly suggests that birds caught together at least moved into the area as a cohesive group. We caught a total of 82 separate groups caught across the study period. Since birds from multiple groups were often being processed simultaneously, observers were often blind to the group size while collecting data on ectoparasite load and morphology (though we cannot rule out the possibility of some limited bias). Age class was determined based on the colour of the eye ring, which changes over time in this species (Bebbington et al. in prep). Three of the individuals caught during the study period were juveniles (brown eye ring) and were excluded from all analyses. A small blood sample (ca. 150µL) was drawn from the brachial vein into 2-3 heparinised capillary tubes, which were immediately stored vertically on ice and

subsequently transported to the field laboratory. We then used callipers and a 100g spring-scale Pesola to record each bird's tarsus length and body mass (to 0.01mm and 0.1g). We determined ectoparasite load by semi-quantitatively scoring two ectoparasite types: feather mites and chewing lice. We searched for feather mites on the underside of the primary and secondary flight feathers of one wing (feather mite numbers on each wing are highly similar (Behnke et al. 1999)) and scored the observed abundance as either "none", "rare" (<30 mites) or "abundant" (>30 mites), following Behnke et al. (1999). Although we were unable to distinguish between live mites and skin casts following this method (Proctor and Owens 2000), studies elsewhere suggest that this measure is highly correlated with more accurate quantifications such as 'dust ruffling' (e.g. Dowling et al. 2001). Since the proportion of observed mites that were in fact skin casts is likely to remain constant, the potential inclusion of skin casts in our estimates is also unlikely to bias our conclusions relating to group size. We also recorded the number of chewing lice observed opportunistically across the entire body during the bleeding and measuring process. We did not identify the species of either ectoparasite, but previous studies in mousebirds have identified feather mites of the species *Megninia contora, M. grandispina* and *Pterolichus proctophyllus* (Ledger 1968). Chewing lice were highly likely to be *Colimenopon urocolius* (Takano et al. 2019). Since chewing lice were observed only rarely (<10% of catches, with usually just one louse per individual (range 0-6)), each individual was then given a total ectoparasite score between 0 and 2: "0" indicates no ectoparasites; "1" indicates mites were rare and lice were absent or mites were absent but at least 1 louse was present; "2" indicates mites were abundant (regardless of louse count) or mites were rare but at least 1 louse was present. After processing, the entire group was released together at their original catch site.

Biomarkers of health status

We calculated three biomarkers of health status: one morphological and two hematological. Using the tarsus and mass values, we calculated the scaled mass index (SMI) of each bird as a measure of its general body condition (following Green and Peig (2009). Three individuals who were suspected to be carrying an egg at the time of capture were excluded from this analysis. For hematological analysis,

blood samples were separated by centrifugation within approximately 4.5 hours of collection (mean ± SE = 254 ± 8 minutes) at 8,000RPM for 8 minutes. For each centrifuged hematocrit tube, we used calipers to measure (to the nearest 0.01mm) the length of the full sample, the red blood cell fraction, and the buffy coat (layer of platelets and white blood cells in between the plasma and red blood cell components; made visible using a magnifying glass). Values were summed across all capillaries containing blood from the same sample; hematocrit and buffy coat were then calculated as proportional values of red and white blood cells, respectively, of the total sample volume. Due to time constraints during catching and occasional limitations on blood processing, not all health status measures were available for all individuals; sample sizes per analysis are shown in the results. Hematological measures were conducted blind to group size.

Statistical methods

All analyses were performed in R (version 4.2.3; R Core Team 2023). We constructed full models containing all variables of potential interest using "lme4" (Bates et al. 2015), "glmmTMB" (Brooks et al. 2017) and "ordinal" (Christensen 2023) packages for Gaussian, proportional and ordinal response variables, respectively. Models and their residuals were then assessed for collinearity, dispersion and overall fit using the "performance" (Lüdecke et al. 2021) and "DHARMa" (Hartig and Hartig 2017) packages; no issues in model assumptions were detected.

First, we tested whether ectoparasite load was associated with group size. We constructed a cumulative link mix model (package "ordinal"; Christensen 2023) with ectoparasite score as the ordinal response variable, including both linear and quadratic effects of group size as predictors. We also included season of capture to test for seasonal differences in ectoparasite load. Since group size may affect ectoparasite load differently during the non-breeding season (July-August) and the breeding season (September-November), we also tested the interaction between season and both the linear and quadratic group size predictors. We included a random intercept for year to account for temporal variation in sampling and parasite loads, along with random intercepts for individual and group identity

to control for repeat sampling of individuals and of individuals in the same group, respectively. We tested for model convergence and fit using functions within the "ordinal" package.

Next, we tested whether biomarkers of health status were associated with ectoparasite load and whether this relationship varied with group size. (i) To test for effects on body condition, we constructed a general linear model in package "lme4" (Bates et al. 2015) with scaled mass index (SMI) as the Gaussian response variable. We included ectoparasite load and both linear and quadratic effects of group size as predictors, along with time of capture (minutes since sunrise) and season. We tested for interactions between ectoparasite load and both the linear and quadratic group size predictors, and we included individual and group identity as random intercepts. We did not include year as a random intercept, as it explained very little variation in SMI and caused model convergence issues. (ii) To test for effects of ectoparasite load on the two hematological markers of health, we constructed two beta regression models in the package "glmmTMB" (Brooks et al. 2017) with the proportional volume of buffy coat and red blood cells (HCT) as the response variables. In both models, we included as predictors the linear and quadratic terms for group size, ectoparasite load, season and the time in minutes between bleeding and centrifugation. Again, we tested for interactions between ectoparasite load and both the linear and quadratic group size predictors, and we included random intercepts for individual and group identities.

Final models were produced by removing any non-significant interactions and quadratic terms. Such non-significant terms were reintroduced one at a time into the final model to obtain parameter values. Since we had few predictors and all were of biological interest to us, we retained all other fixed effects regardless of significance. If a significant interaction term or quadratic term was present, we assessed its robustness by comparing models with and without the interaction or quadratic term using likelihood ratio tests.

All data generated or analysed during this study will be uploaded to a digital repository and a link will be included in the published article.

Results

Group size effects on ectoparasite load

We evaluated the relationship between group size and ectoparasite load across 345 samples from 229 individuals in our dataset. Group size had a non-linear effect on ectoparasite load, with individuals in medium-sized groups showing the highest ectoparasite load (Table 1; Fig. 1). The greatest infestation levels occurred in group sizes of 7 and decreased in groups above and below this size (Fig.1). Model comparison showed that the model containing the quadratic group size term was a significantly better fit than a model containing only the linear group size term (likelihood ratio test: $\chi^2 = 5.07$, $p = 0.02$). There was no effect of season on ectoparasite load and also no interaction between group size and season (Table 1).

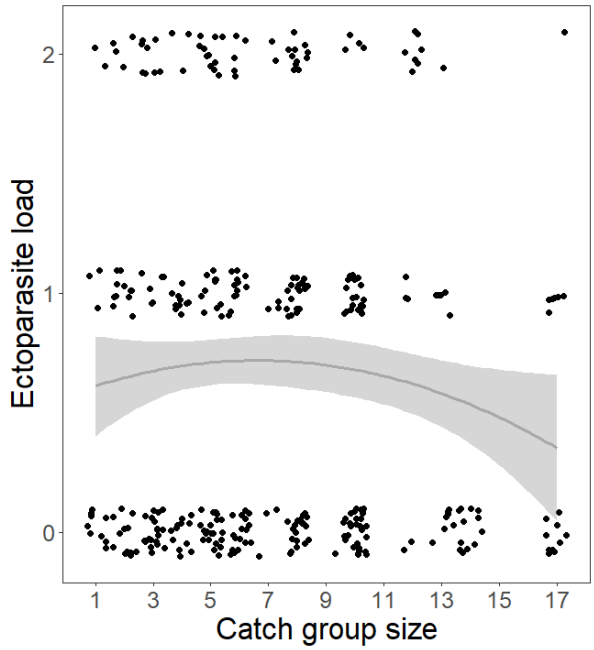

Figure 1. The quadratic association between group size and ectoparasite load in speckled mousebirds. Dots represent raw data points (jittered to aid visualisation), line and shading represent predicted quadratic relationship and 95% confidence interval, respectively. *N* = 345 measurements from 229 individuals.

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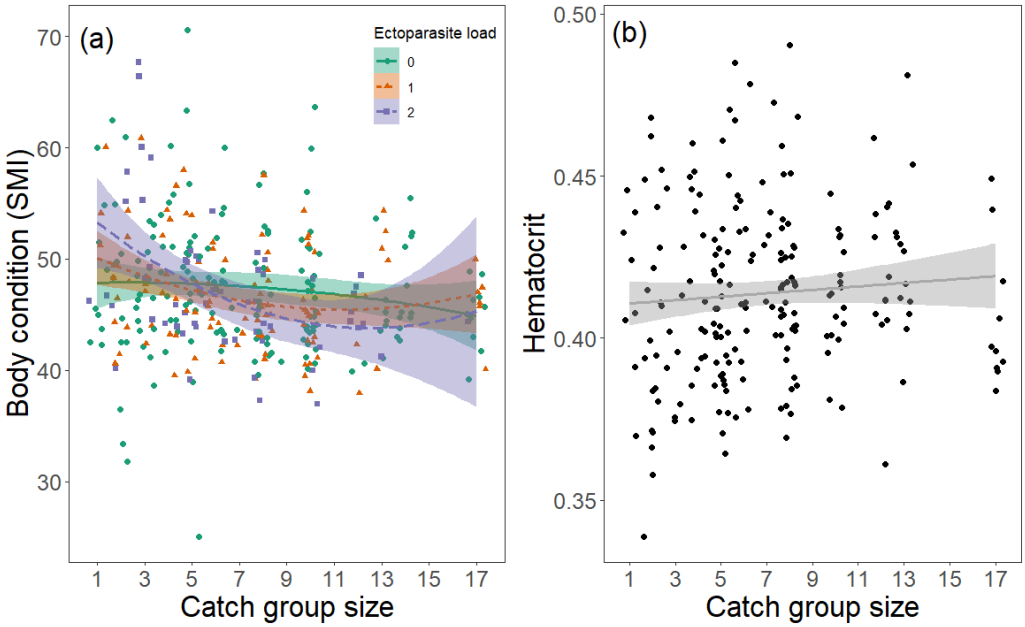
Table 1. Model parameters for the influence of group size and season on ectoparasite load in speckled mousebirds. *N* = 345 measurements from 229 individuals, significant predictors are highlighted in bold font.

Predictor	Estimate ± SE	Z value	P value
Group size	**2.63 ± 1.18**	**2.24**	**0.02**
Group size^2	**-2.81 ± 1.19**	**-2.35**	**0.02**
Season (non-breeding)	0.33 ± 0.97	0.34	0.73
Group size x season	0.41 ± 1.51	0.27	0.79
Group size^2 x season	1.63 ± 2.38	0.69	0.49
Random effects	*Variance ± SD*		
Individual identity	0.19 ± 0.44		
Group identity	0.29 ± 0.53		
Year of capture	7.00 ± 2.65		

Group size effects on biomarkers of health status

Body condition (SMI) values were available for 228 individuals across a total of 342 catches. Individuals caught in the non-breeding season had lower body condition and there was a significant interaction between quadratic group size and ectoparasite load (Table 2). Among infested individuals and particularly those with high ectoparasite loads, body condition was lowest in medium-sized groups. Body condition of infected individuals was worst in groups of 11-12 and in groups above and below this size the birds were in better condition (Fig. 2a). However, body condition varied little with group size among individuals with no ectoparasite infestation (Fig. 2a). The full model containing both interaction terms was a significantly better fit than the model containing no interactions (likelihood ratio test: $\chi2 = 10.86$, $p < 0.01$), the model with only the interaction between linear group size and ectoparasite load (likelihood ratio test: $\chi2 = 7.24$, $p < 0.01$) and the model with only the interaction between quadratic group size and ectoparasite load (likelihood ratio test: $\chi2 = 10.24$, $p < 0.01$). Time of capture had no effect on body condition (Table 2).



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321 **Figure 2.** Relationship between group size and (a) body condition (scaled mass index) of individuals
322 with different ectoparasite loads (*N* = 174, 109 and 59 individuals with scores of 0, 1 and 2,
323 respectively), and (b) hematocrit (*N* = 210) in speckled mousebirds. Lines and shaded areas represent
324 predicted relationship and 95% confidence intervals, respectively.

325

326 Buffy coat values were available for 205 blood samples from178 different individuals.
327 Individuals caught in the breeding season had larger buffy coats, but we found no effect of either
328 linear or quadratic group size, ectoparasite load, or the interactions between them (Table 2). There
329 was also no effect of time until centrifugation on the size of the buffy coat (Table 2).

330 Across the 210 blood samples from 181 individuals where HCT was measured, those caught in
331 larger groups had a higher hematocrit (Fig. 2b, Table 2) – this effect was linear with no evidence for a
332 quadratic relationship (Table 2). Ectoparasite load was not associated with HCT, and there was no
333 interaction between either linear or quadratic group size and ectoparasite load on HCT values. HCT
334 values were also higher during the breeding season and in samples where the time between sampling
335 and centrifugation was longer (Table 2).

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338 **Table 2.** Model parameters for predictors of body condition (scaled body mass), buffy coat and
339 hematocrit in speckled mousebirds. Significant predictors are indicated in bold font.

Response	**Predictor**	**Estimate ± SE**	***t* or *z* value**	**P value**
Scaled	Group size	-3.25 ± 2.54	-1.28	0.21
body mass	Group size^2	1.71 ± 2.72	0.63	0.53
N = 242	Ectoparasite load	0.38 ± 0.39	0.98	0.33
	Season (non-breeding)	**-2.90 ± 0.95**	**-3.04**	**<0.01**
	Time of capture	0.63 ± 0.63	1.00	0.32
	Group size x ectoparasite load	**-8.63 ± 2.75**	**-3.13**	**<0.01**
	Group size^2 x ectoparasite load	**7.29 ± 2.77**	**2.63**	**<0.01**
	Random effects	*Variance ± SD*		
	Individual identity	15.15 ± 3.89		
	Group identity	1.95 ± 1.40		
Buffy coat	Group size	0.13 ± 0.13	0.93	0.35
N = 205	Group size^2	-0.48 ± 0.44	-1.07	0.28
	Ectoparasite load	-0.11 ± 0.07	-1.66	0.10
	Season (non-breeding)	**-0.33 ± 0.15**	**-2.21**	**0.03**
	Time until centrifugation	-0.16 ± 0.11	-1.40	0.16
	Group size x ectoparasite load	0.93 ± 0.56	1.66	0.10
	Group size^2 x ectoparasite load	-0.97 ± 0.58	-1.66	0.10
	Random effects	*Variance ± SD*		
	Individual identity	0.03 ± 0.18		
	Group identity	0.05 ± 0.22		
Hematocrit	**Group size**	**0.05 ± 0.02**	**2.24**	**0.02**
N = 210)	Group size^2	9.58 ± 7.40	-1.30	0.20
	Ectoparasite load	<-0.01 ± <0.01	-0.10	0.92
	Season (non-breeding)	**0.09 ± 0.02**	**-3.70**	**<0.01**

Time until centrifugation	**0.03 ± 0.01**	**2.05**	**0.04**
Group size x ectoparasite load	-0.11 ± 0.07	-1.49	0.14
Group size^2 x ectoparasite load	0.11 ± 0.08	1.44	0.15
Random effects	*Variance* ± *SD*		
Individual identity	<0.01 ± 0.07		
Group identity	<0.01 ± 0.05		

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341 **Discussion**

342 In this study, we report a non-linear effect of group size on ectoparasite load: speckled mousebirds
343 caught in medium-sized groups had the highest ectoparasite loads. This relationship did not differ
344 between the non-breeding and breeding seasons, despite mousebirds having very different social
345 behaviour during these two periods. In addition, infested individuals in medium-to-large groups seemed
346 to suffer most in terms of body condition. Taken together, these results add to the growing consensus
347 in the field that the relationship between parasites and group size is affected by many different factors
348 and should be studied in greater detail if we are to fully understand how sociality evolves.

349 Although associations between social group size and various parasite-related parameters (i.e.,
350 transmission, exposure and load) have been studied since the 1970s (e.g. Freeway 1976), most studies
351 have so far reported on linear relationships or differences between social and nonsocial species or
352 groups (e.g. Brown et al. 2001; Ezenwa 2004; Rifkin et al. 2012; Lutterman et al. 2013; Lynsdale et al.
353 2021). However, if social species are under selection to adapt to increased parasite exposure (Cremer
354 2019), individuals in larger groups may be able to mitigate the costs of increased parasite exposure. The
355 predicted non-linear relationship between group size and parasite load has been suggested, but not
356 formally tested, in prairie dogs *Cynomys* spp. (Hoogland 1979), as well as in mousebirds as we
357 demonstrate here. While more research is needed and we can only speculate on this matter, we propose
358 that the costs (i.e., increased parasite transmission) and benefits (e.g., allopreening) associated with
359 group living lead to non-linear relationships between group size and parasite loads, including the one
360 we report here. This is in line with our second hypothesis (*H2: high risk-low load*): individuals living
361 in pairs or small groups may have low ectoparasite loads because they are simply at limited risk of

362 infestation (low within group transmission). Those in the largest groups experience more transmission
363 possibilities, but these individuals also seem to benefit most from social immunity in the form of
364 allopreening and potentially other social traits that reduce parasite load (Cremer 2007; Bonoan et al.
365 2020). Individuals in medium group sizes have both relatively frequent social contact and relatively
366 limited social immunity, leaving them most prone to parasite infestation. To fully test this hypothesis,
367 three further pieces of information are needed. Firstly, the above assumes that larger groups have higher
368 parasite transmission risk because the chance that at least one group member comes into contact with
369 parasites (which can then be transmitted with the group) increases with group size. However, if
370 individuals in smaller groups have contact with extra-group individuals at equal or greater frequency
371 than individuals in larger groups, this assumption would not hold. Detailed quantification of social
372 networks could shed some light on this first assumption. Related to this, our estimate of group size also
373 relies on the assumption that individuals who arrived at and were caught together at a feeding station
374 were part of a social group, which requires further investigation to confirm. Even if catch group size is
375 not entirely representative of the social groups in which mousebirds exist outside of the context of
376 foraging, our estimate of group size still likely describes at least a proportion of the variation in social
377 contact; mousebirds spend a great deal of time foraging and their propensity to share resource patches
378 with others is likely to affect their infection risk, regardless of other social structures that are in place at
379 other times of the day or season. Second, further work is needed to determine how allogrooming and
380 other forms of social immunity vary with group size and according to intragroup relationships. Lastly,
381 relationships between group size and different types of parasites (e.g., microparasites, parasites with
382 different transmission routes including via vectors, etc.) should be evaluated to better understand the
383 generality of this relationship and to make inferences about potential mechanisms underlying variation
384 in parasite infestation. Nonetheless, our finding that sociality is associated with ectoparasite load in a
385 non-linear manner may have important consequences for understanding the role of social immunity in
386 shaping animal societies more broadly (van Meyel et al. 2018).

387 In many social species, including the speckled mousebird, there is seasonal variation in the
388 extent of sociality and the size and structure of groups (Decoux 1982; Papageorgiou and Farine 2021;
389 Camerlenghi et al. 2022). We predicted that individuals sampled in the non-breeding season would have

higher ectoparasite load due to the high frequency of communal roosting behaviour that occurs, both day and night, during that cooler part of the year (Bartholomew and Trost 1970). However, ectoparasite load did not differ with season. There was also no evidence that the effect of group size on ectoparasite load varied between the seasons. The fact that individuals in larger groups had similar parasite loads in the non-breeding season (when communal roosting is common) and the breeding season (when this behaviour is rare), suggests that physical contact between individuals in a communal roost is not riskier (in terms of parasite transmission) than other facets of group living. For example, mousebird behaviour in the breeding season may presents similar ectoparasite transmission risks to that in the nonbreeding season. Although groups in the warmer season spend much less time in communal roosts, they interact frequently at the nest, especially given that communal and cooperative breeding are both common in this species (Decoux 1982). Moreover, multiple individuals have been observed to even sleep together on the nest at night (Decoux 1982; *pers. obs.*), which is itself also a form of communal roosting, albeit with fewer individuals. Given that the nest environment is well known for harbouring a wealth of ectoparasites (Rendell and Verbeek 1996; Hund et al. 2015), perhaps speckled mousebird groups effectively experience comparable parasite transmission during both the breeding season and the non-breeding (i.e., communal roosting) period. Testing whether ectoparasite abundance in the nest is also related to social group size and whether adaptations exist to reduce transmission in reproductive contexts, represent exciting avenues for further research.

Individuals in medium-sized groups also suffered the greatest physiological costs of infection: body condition of infected individuals was lowest in groups of around 11. Interestingly, body condition appeared to converge in the large group sizes such that infection status no longer influenced body condition (Fig. 2a). The impact of ectoparasites on condition in these largest groups might be compounded by other individual-level costs of group living such as chronic stress, food competition, or physical conflict (e.g., Creel 2001; Selva et al. 2011). In Natal mole rats (*Cryptomys hottentotus natalensis*), the energetic benefits of living in larger groups appear to allow individuals to divert energetic resources towards anti-parasite defences (Lutterman et al. 2013); the fact that infected mousebirds in larger groups were in slightly better condition than those in medium-sized groups offers some support for a similar process in this species and for our third hypothesis (*H3: high risk-low*

418 *impact*). Whether individuals in larger groups are better- or worse-equipped to cope with parasites
419 probably depends on how a host organism benefits from sociality, and these benefits are can vary greatly
420 within and among species (Shen et al. 2017; Guindre-Parker and Rubenstein 2020).

421 We found no evidence of a relationship between ectoparasite load and either of our
422 hematological health markers (i.e., hematocrit and buffy coat). Both were instead related to season:
423 buffy coat was higher, and hemaotcrit lower, in the breeding season. Buffy coat, a measure of white
424 blood cell abundance (Wardlaw and Levine 1983), typically increases in response to infection
425 (Gustaffson et al. 1994; Chagas et al. 2020), which provides tentative support for observations
426 elsewhere that birds are exposed to more parasites more generally (i.e. beyond ectoparasites) during the
427 warmer months of the year (Martin II et al. 2007; Salam et al. 2009). In line with the seasonal patterns
428 in buffy coat size, hematocrit, which is often used as a measure of overall physiological condition
429 (reviewed in Johnstone et al. 2017), was lower in the breeding season. Taken together, our
430 hematological indicators therefore broadly indicate that mousebird health varies with season, as has
431 been suggested elsewhere for other species (reviewed in Fair et al. 2007 and Johnstone et al. 2017).
432 Interestingly, hematocrit was also positively correlated with group size, which might suggest that
433 individuals in larger groups may have better overall condition. Given that communal roosting is known
434 to reduce energy expenditure in mousebirds (McKechnie et al. 2006), individuals in larger groups might
435 be able to allocate more resources towards self-maintenance. Alternatively, perhaps the higher
436 hematocrit found in individuals from larger groups reflects a difference in the extent to which such
437 individuals are infected with other, un-measured parasites. At least with respect to blood parasites, there
438 is evidence for both positive (Booth and Elliot 2002; Christe et al. 2002) and negative (Dawson and
439 Bortolotti 1997) relationships between infection and hematocrit. Further work quantifying a broader
440 panel of parasites is needed to test whether the link between hematocrit and group size is truly a
441 consequence of variation in infection status. In any case, hematocrit values across all group sizes in this
442 study were within the range considered to be 'normal' (35-55%: Cambell 1994; Scoville and Dogerty
443 2017); firm conclusions about the link between seasonality, group size and physiological condition
444 would require further investigation using other biomarkers of health.

The fact that neither hematological measure was related to ectoparasite load in the current study might have several possible explanations. Both buffy coat and hematocrit have been linked to ectoparasite loads in other avian species (e.g. Simon et al. 2005; Heylen and Matthysen 2008; Heylen et al. 2020), but many other studies fail to report such relationships (e.g. O'Brien et al. 2001; Carleton 2008). One possibility is that the ectoparasites that we quantified do not impose severe enough physiological damage to induce hematological changes (Proctor & Owens 2000); alternatively, relatively small effects of measured ectoparasites on hematocrit and buffy coat is masked by stronger influences by other parasites not correlated with mite and lice loads. In the case that the parasites quantified in this study are largely commensal, as has been argued elsewhere (Proctor & Owens 2000, Brown et al. 2006), this does not preclude their use as indicators for the potential for parasite transmission between group members in different social settings. Exploring relationships between social group size and physiological health indicators in relation to other kinds of parasites could provide more insights into whether social immunity and social behaviour can mediate host-parasite interactions in animal societies.

Parasites exert a strong selective pressure on animals, shaping the evolution of life history and behaviour across a range of taxa (Sarabian et al. 2018). Here, we demonstrate that the association between parasite load and group size can be non-linear, and we speculate that defences rooted in social immunity, e.g., allogrooming, might mediate this relationship. To increase our understanding of how host-parasite interactions have shaped the evolution of animal sociality, further work is needed to elucidate (i) the relationships between group size and the transmission and load of diverse pathogens and parasites and (ii) the mechanisms of social immunity that operate in diverse host species and animal societies.

Ethics statement

Disclosure of potential conflicts of interest: the authors declare no conflicts of interest.

Research involving Human Participants and/or Animals: All capture and handling techniques used in this study follow the recommendations of the South African Bird Ringing Unit (SAFRING). Ethical permission for this work was granted by Big Game Parks and Mbuluzi Game Reserve.

Data availability statement

The datasets generated during and/or analysed during the current study are available in the Dryad repository:

https://datadryad.org/stash/share/MF99FLad2HagxA5a0omeRSoeSRVPQr53h_ibkzeV8gM

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