PROCEEDINGS B

rspb.royalsocietypublishing.org

Research

Cite this article: Ezenwa VO, Worsley-Tonks KEL. 2018 Social living simultaneously increases infection risk and decreases the cost of infection. *Proc. R. Soc. B* **285**: 20182142. http://dx.doi.org/10.1098/rspb.2018.2142

Received: 22 September 2018
Accepted: 5 November 2018

Subject Category:
Behaviour

Subject Areas:
behaviour, health and disease and epidemiology

Keywords:
social living, group size, parasites, gastrointestinal nematode, anorexia

Author for correspondence:
Vanessa O. Ezenwa
e-mail: vezenwa@uga.edu

Electronic supplementary material is available online at https://dx.doi.org/10.6084/m9.figshare.c.4297907.

THE ROYAL SOCIETY PUBLISHING

Social living simultaneously increases infection risk and decreases the cost of infection

Vanessa O. Ezenwa[1,2] and Katherine E. L. Worsley-Tonks[1,3]

[1]Odum School of Ecology, and [2]Department of Infectious Diseases, College of Veterinary Medicine, University of Georgia, Athens, GA, USA
[3]Department of Veterinary Population Medicine, University of Minnesota, St Paul, MN, USA

VOE, 0000-0002-8078-1913

Elevated parasite infection risk is considered to be a near-universal cost of social living. However, living in groups may also provide benefits that reduce the negative impacts of infection. These potential 'tolerance' benefits of living socially are theoretically possible, but have rarely been described. In this study, we used an anthelmintic treatment experiment in wild Grant's gazelles (*Nanger granti*), who are commonly infected with gastrointestinal nematodes (GIN), to show that social living confers both costs and benefits related to GIN parasitism. We show that although larger group size increases GIN infection risk, a key cost of GIN infection—the suppression of food intake—is simultaneously moderated by living in larger groups. Our findings help illuminate the complex role parasites play in the evolution of host social behaviour.

1. Introduction

Social living comes with both costs and benefits [1]. One well-documented cost of living in social groups is the increased transmission of parasites spread by close contact [1,2]. However, emerging evidence suggests that being social also provides benefits that can ameliorate the fitness costs of infection [3,4]. One way in which such benefits can accrue is if social living minimizes the negative effects of infection, conferring tolerance [4]. What is most intriguing about these potential socially mediated tolerance benefits is that because disease tolerance acts by reducing the damage inflicted by parasites rather than by affecting parasite numbers [5], social animals may simultaneously have higher parasite burdens than non-social animals, yet experience lower fitness costs of infection. This idea challenges our current understanding of the costs and benefits of social living in the context of parasitism.

Gastrointestinal nematodes (GIN) are among the most common parasites of vertebrates. Group size is a broadly important risk factor for GIN infection [6,7], and higher GIN infection has a number of ramifications for host fitness [8–10]. One well-described negative effect of GIN, with important fitness consequences, is the depression of host food intake (i.e. anorexia) [11]. Interestingly, group size is also linked to food intake. In birds and mammals, for example, associations between group size and individual feeding rate are frequently reported, and an increase in feeding rate is a common benefit of larger group size [12]. Given this, socially mediated tolerance benefits may be particularly relevant for GIN infection. Group size may elevate GIN infection risk on the one hand, but counteract a major fitness cost of GIN infection on the other. If so, highly social animals may commonly experience reduced costs of GIN infection despite being more parasitized.

In this study, we investigated the costs of group size with respect to GIN infection and asked whether negative effects of GIN are simultaneously ameliorated by living in larger groups. Specifically, we used an anthelmintic treatment experiment in wild Grant's gazelles (*Nanger granti*) to quantify both the

parasite-related costs and benefits of group size. To evaluate the costs, we quantified the effect of group size on GIN infection in anthelmintic-treated gazelles. To evaluate the benefits, we compared associations between group size and feeding rate in anthelmintic-treated and -untreated animals to understand how group size modifies the impact of GIN parasitism on feeding behaviour in the presence versus the absence of infection. We have previously shown that anthelmintic-treated gazelles spend significantly more time feeding than do untreated, parasitized, animals [13], indicating that gazelles, like many domesticated ruminants [14], face a food intake cost of GIN parasitism that can be ameliorated by parasite treatment.

2. Material and methods

(a) Study animals and anthelmintic treatment

From 20 to 24 June 2011, we captured wild Grant's gazelles (*Nanger granti*) at the Mpala Research Centre (MRC), Kenya (0°17′ N, 37°52′ E). Gazelles were located by helicopter and captured using a handheld net gun fired from the aircraft. All animals were ear-tagged and weighed, and information on individual morphometrics was collected for age estimation. To perturb gazelle GIN infections, individuals were randomly assigned to an anthelmintic treatment group (treated versus control) based on the temporal sequence of capture. Prior to group assignment, faecal samples were collected from all individuals for parasitological analysis. Treated individuals received a subcutaneous injection of moxidectin (1 ml/20 kg of Cydectin Long-Acting Injection for Sheep, Virbac Animal Health). This drug provides protection against a broad range of nematodes for approximately 120 days in sheep [15]. Control animals received saline injections. Animal captures were performed under the authority of the Kenya Wildlife Service and approved by the Kenya National Council for Science and Technology. Animal protocols were approved by the Institutional Animal Care and Use Committee of the University of Georgia (protocol number A2010 10-188) and conformed to the Association for the Study of Animal Behaviour (ASAB) and the Animal Behavior Society (ABS) guidelines for the treatment and use of animals in behavioural research (http://www.sciencedirect.com/science/article/pii/S0003347211004805).

(b) Group size and GIN infection

We monitored group sizes and GIN infection rates of nine anthelmintic-treated females to evaluate the effect of group size on parasite reinfection. Treatment significantly reduced GIN burdens in treated females (as compared to controls) for approximately 120 days [13], and we monitored individuals for approximately 500 days following treatment, from 4 July 2011 to 12 November 2012. We used regularly occurring road transects distributed throughout the day (06.30–18.30 h) to locate animal groups. When a group was located, the identity of all ear-tagged individuals, the size of the group, and its composition in terms of sex and age structure were recorded. A group was considered to be any set of individuals engaged in coordinated activity that were spatially distinct from other groups at the time of observation [16].

During the group size transects, we also collected faecal samples from individually identifiable (i.e. ear-tagged) individuals who were seen defecating, which allowed us to directly pair group size observations with parasite counts. Since female gazelle have a relatively fluid social structure in which individuals can move between groups [16], our study design allowed us to capture potential variability in a single individual's group size over time. However, individual group size was significantly repeatable in our dataset ($R = 0.311 \pm 0.115$, CI: 0.079–0.533, $p = 0.001$; estimated using the linear mixed model (LMM) method in the *rptR* package in R [17]), suggesting there is some degree of consistency in individual group size that could translate into differential infection risk. Faecal samples were collected within 10 min of observing a defecation event, and the individual identity, time of day, and location of the collection were recorded for all samples. Following collection, samples were kept on ice in the field until being transported to the laboratory for processing. We quantified parasite infection status by measuring faecal egg output of the major GIN taxa infecting gazelle (strongyle nematodes). This was done using a modification of the McMaster faecal egg counting technique [18]. All samples were processed on the day of collection, and across all nine study individuals, we collected a total of 175 faecal samples (mean per female = 19, range = 7–28) that were paired with group size data.

(c) Feeding behaviour

To investigate the impact of GIN parasitism on feeding behaviour and test whether this relationship was affected by group size, we quantified the feeding behaviour of nine treated and 10 control females between 26 July 2011 and 30 April 2012 using focal animal sampling [19]. Behavioural observations were recorded from a distance of 100–200 m using binoculars and a handheld digital voice recorder. To begin a focal observation, a single individually identifiable individual was randomly selected within a group and followed for up to 30 min. The recording was paused if the focal individual went out of sight, and if the individual was out of sight for more than approximately 10 min the observation was terminated. A single observer performed all focal observations, which ranged in duration from 15 to 28 min. Behaviours were classified into five categories: feeding, vigilance, resting, moving, and other activities. Feeding was defined as grazing or browsing at any height or actively searching for food. For grazing herbivores, total daily feeding time is thought to scale with total daily food intake, with total daily feeding time being the product of three components: time spent feeding, rate of biting, and size/composition of bites [20]. We used the first of these three components (time spent feeding) as a proxy of individual intake rate. Focal observations were distributed across four time periods: early morning (06.00–08.59), late morning (09.00–11.59), early afternoon (12.00–14.59), and late afternoon (15.00–17.59), to account for potential effects of time of day on gazelle activity. All observations were terminated at 18.00 h. For each observation, we recorded the date, start time, weather (clear, overcast, or rainy), wind conditions (low or high), and the size and type of group containing the focal female.

(d) Statistical analyses

To examine the effects of group size on GIN infection status and quantitative parasite egg output in anthelmintic-treated individuals following treatment, we used a zero-inflated negative binomial mixed model which accounted for excess zeros and overdispersion in the parasite data as well as repeated sampling of the same individuals. A zero-inflated model treats excess zeros independently from count data, thus our parasite response variable was modelled in two parts, as a binary process (zero-inflated model) and as a count process (negative binomial model). Animal ID was included as a random effect in the model, and group size and time since anthelmintic treatment (in days) were included as fixed effects. The model was implemented in R version 3.4.4 using the *glmmTMB* package [21]. Since the probability of being infected was expected to increase over time as treatment

efficacy waned, we included time since treatment in the model to account for this potential source of temporal autocorrelation. We also tested for evidence of temporal autocorrelation in model residuals using a Durbin–Watson test applied to scaled residuals and implemented in the R package *DHARMa* [22]. There was no evidence of either positive or negative autocorrelation in model residuals (DW = 2.03, $p = 0.825$).

To assess the effect of group size on feeding rate we used linear mixed effects models. Separate models were run for control and treated individuals. Animal ID was included as a random effect to account for repeated sampling and group size, time of day, season (wet versus dry), and focal observation duration were included as fixed effects. We used the behavioural analysis software JWatcher [23] to convert voice recordings into time budgets summarizing the proportion of time spent feeding by a focal individual during each observation period, and this was used as the response variable in both models. Prior to analysis, we normalized distributions of the feeding rate data using arcsine square root transformations. Seasonality was assigned to each focal observation based on the month in which the observation was made. Monthly rainfall records from the study site were used to classify each observation month as either wet or dry. Wet months (June–November 2011, April 2012) averaged 113.2 mm of rainfall and dry months (December 2011–March 2012) averaged 12.4 mm. Models were run in R using the packages *lme4* and *lmerTest* [24].

3. Results

(a) Group size predicts GIN infection risk

Living in larger social groups was associated with a higher risk of GIN infection. Controlling for time since anthelmintic treatment, we found that the probability of an individual remaining parasite free in the post-treatment period declined sharply with group size (zero-inflated mixed model: $n = 9$ individuals, 175 observations, estimate ± s.e. = −0.332 ± 0.154, $p = 0.032$; figure 1; electronic supplementary material, table S1), such that being in a larger group was associated with a 39% higher chance of acquiring parasites. However, group size was not significantly correlated with parasite egg count (negative binomial mixed model: $n = 9$ individuals, 175 observations, estimate ± s.e. = −0.021 ± 0.015, $p = 0.164$; electronic supplementary material, table S1), suggesting that while group size affects the risk of GIN acquisition it cannot explain variation in parasite egg shedding rates.

(b) Feeding increases with group size in the presence of infection

Group size was also associated with feeding behaviour. In control animals, group size was significantly and positively correlated with feeding rate (mean group size with [range]: 7 [2–21]; [LMM]: $n = 10$ individuals and 248 observations, estimate ± s.e. = 0.015 ± 0.007, $p = 0.033$; figure 2*a*; electronic supplementary material, table S2). When two outliers were removed from the analysis, there was still a strong positive trend ($n = 10$ individuals and 246 observations, estimate ± s.e. = 0.014 ± 0.008, $p = 0.0605$; see electronic supplementary material, table S3 for results based on excluding different combinations of the two outliers). By contrast, the positive association between group size and feeding rate disappeared in anthelmintic-treated animals (mean group size with [range]: 9 [2–23]; LMM: $n = 9$ individuals and 226 observations, estimate ± s.e. = 0.007 ± 0.007, $p = 0.313$; figure 2*b*; electronic supplementary material, table S2). Interestingly, among treated gazelles, feeding rates in the upper (greater than or equal to 11) and lower (less than or equal to 7) group size quartiles were similar, averaging 37% and 34%, respectively; whereas among control gazelles, the average feeding rate was 30% in the upper group size quartile (greater than or equal to 9) and only 25% in the lower (less than or equal to 5) quartile. Thus, while the relaxation of anorexia due to parasite clearance allowed treated individuals to feed at a relatively high rate irrespective of group size, control individuals only achieved comparably high levels of feeding in larger groups.

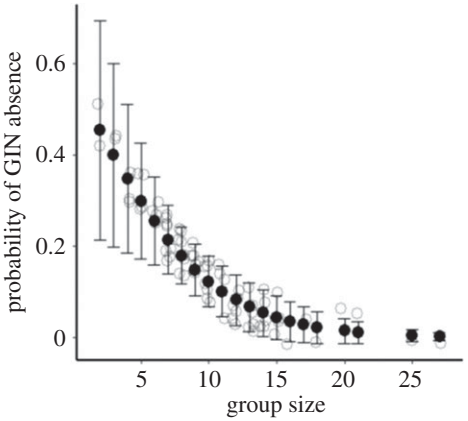

Figure 1. Following treatment with an anthelmintic drug, individuals in smaller groups were significantly more likely to remain parasite free over time, whereas those in larger groups were more likely to re-acquire parasites (open circles indicate model predicted values from the zero-inflated component of a zero-inflated negative binomial mixed model run on 175 observations of nine treated individuals; filled circles indicate mean predicted values by group size with standard errors).

4. Discussion

Our results show that social living increases gastrointestinal nematode (GIN) infection risk in wild gazelles, but simultaneously relaxes anorexia, a key cost of GIN infection. By tracking parasite reinfection rates in anthelmintic-treated individuals over time, we found that individuals in larger groups were significantly more likely to re-acquire parasites. However, group size was also positively associated with feeding rate, and GIN-infected (control) individuals in the largest groups fed at rates that were higher than individuals in the smallest groups. Our previous work has shown that, on average, treated individuals feed at a higher rate than do controls [13]. Interestingly, here we show that parasite clearance allowed treated individuals to feed at a relatively consistent rate irrespective of group size. Importantly, the fact that control individuals achieved feeding rates comparable to that of treated individuals only when in larger groups, suggests that large group size plays a role similar to anthelmintic treatment in counteracting GIN-associated anorexia. Taken together, these results suggest that social living moderates a key fitness cost of GIN parasitism, potentially offsetting the costs of higher transmission.

There are several potential explanations for the moderating effect of group size on GIN-associated anorexia. First, this effect may be explained by changes in time allocation by hosts. There is ample evidence that group size influences time allocation decisions in social animals, with larger

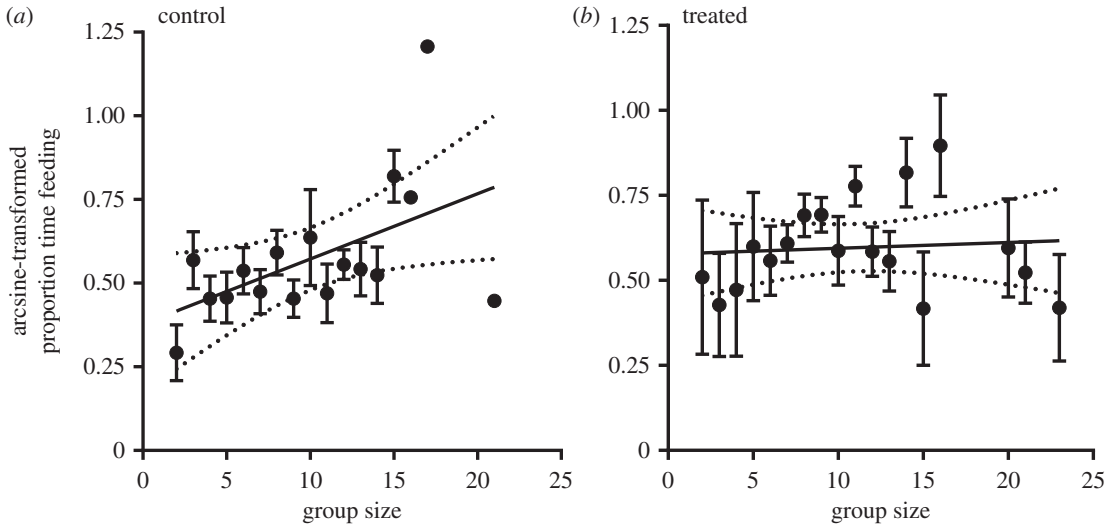

Figure 2. (*a*) The proportion of time control (untreated) individuals spent feeding increased with group size, while (*b*) feeding rate did not vary significantly with group size in treated individuals. Points represent mean arcsine-transformed feeding rates by group size with standard error; regression lines depict the relationship between group size and feeding with 95% confidence intervals.

group size often allowing for the re-allocation of time toward feeding and away from vigilance [25]. Therefore, it is possible that parasitized gazelles in larger groups may simply allocate more time to feeding, which allows them to overcome parasite-associated anorexia. This explanation is supported by a recent study on predation risk and group size in African ungulate communities which showed that vigilance imposes a significant foraging cost on Grant's gazelles and that dilution of predation risk via grouping generally reduces the need for individual vigilance in African ungulates [26]. However, if trade-offs between feeding and vigilance account for the pattern we observed, an important unanswered question is how behavioural time allocation decisions translate into the physiological signals required to suppress anorexia. A second explanation is that the group size effect emerges from interactions between social behaviour, the immune and endocrine systems. Parasite-associated anorexia is thought to be triggered by immune and endocrine responses to infection that influence appetite [27]. Since many of these responses (e.g. inflammation [28], stress [29]) also covary with social behaviour, a number of plausible hypotheses emerge for how group size might indirectly affect GIN-associated anorexia.

It is important to note that because we used feeding rate as a proxy for intake rate, we inferred a moderating effect of group size on GIN-associated anorexia based on changes in feeding patterns. This assumption is supported by studies of domestic herbivores (e.g. sheep [30–31] and goats [32]) which show that larger group size increases both foraging time and intake rate, in tandem. Nevertheless, an alternative explanation for our findings could be that the increase in feeding rate with larger group size we observed in parasitized animals reflects declining intake rates due to food competition. If so, larger group size could exacerbate, rather than moderate, the costs of GIN infection by imposing additional intake losses. Based on the current understanding of the relationship between group size and food competition in grazing herbivores, this interpretation is unlikely. For example, intake rates increase with numbers of competitors in domestic goats, suggesting that the perception of exploitative competition can actually promote higher food intake [32]; whereas in free-ranging bison and elk, interference competition accounts for negligible losses of foraging time, and time lost due to interference is not associated with group size [33]. Together, these studies suggest that competition in groups does not negatively impact net food intake in some grazing ungulates, likely because individuals behaviourally compensate for the presence of competitors. In fact, these findings raise the intriguing possibility that competition itself might serve as a mechanism that facilitates the suppression of GIN-induced anorexia in larger groups by stimulating an increase in feeding.

Although our current study does not allow us to speculate in detail on specific mechanisms underlying the effects we observed, it does shed new light on infection-related tolerance benefits that may be associated with social living. While it is well known that many social insects benefit from mechanisms that counteract the enhanced risks of infection that accompany social living, so far only mechanisms that reduce overall parasite burdens (e.g. avoidance and resistance mechanisms) have been described [34]. Recently, a study on Yellowstone wolves found that mange-infected individuals were better able to survive infection if they lived in larger groups [35], a result which is highly suggestive of socially mediated tolerance benefits. However, in the wolf-mange system, group size was not a predictor of infection risk [35]. Here, we show that more social animals are simultaneously more parasitized and better protected from the costs of infection. For parasites like GIN, where host infection probability may be routinely high and infections can be chronic, mechanisms that reduce the fitness impacts of infection may be under strong selection. If social living is such a mechanism, then under some conditions, parasitism may select for larger group size despite the higher risk of infection. Investigating the specific conditions under which this outcome is likely will help advance our understanding of the role parasites play in the evolution of sociality.

Ethics. The Kenya National Council for Science and Technology and the Kenya Wildlife Service granted permission to conduct this research in Kenya. Animal protocols were approved by the Institutional Animal Care and Use Committee of the University of Georgia (protocol number A2010 10-188) and conformed to the ASAB/ABS guidelines for the treatment and use of animals in

behavioural research (http://www.sciencedirect.com/science/article/pii/S0003347211004805).

Data accessibility. Data presented in this paper are available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.80f293g [36].

Authors' contributions. V.O.E. designed the study. V.O.E. and K.E.L.W. collected and analysed the data. V.O.E. wrote the paper and both authors approved the final manuscript.

Competing interests. We declare we have no competing interests.

Funding. This work was supported by a United States National Science Foundation CAREER Award to V.O.E. (IOS-1101836).

Acknowledgements. Animal captures were conducted by Frontier Helicopters, NZ and the Kenya Wildlife Service Game Capture Unit. We thank J. Ewoi and M. Snider for assistance in the field, and the Mpala Research Center for logistical support. L. Briard and R. Holdo provided helpful feedback on the manuscript and statistical approach, respectively.

References

1. Alexander RD. 1974 The evolution of social behavior. *Annu. Rev. Ecol. Syst.* **5**, 325–383. (doi:10.1146/annurev.es.05.110174.001545)
2. Altizer S *et al.* 2003 Social organization and parasite risk in mammals: integrating theory and empirical studies. *Annu. Rev. Ecol. Evol. Syst.* **34**, 517–547. (doi:10.1146/annurev.ecolsys.34.030102.151725)
3. Kappeler PM, Cremer S, Nunn CL. 2015 Sociality and health: impacts of sociality on disease susceptibility and transmission in animal and human societies. *Phil. Trans. R. Soc. B* **370**, 20140116. (doi:10.1098/rstb.2014.0116)
4. Ezenwa VO, Ghai RR, Mckay AF, Williams AE. 2016 Group living and pathogen infection revisited. *Curr. Opin. Behav. Sci.* **12**, 66–72. (doi:10.1016/j.cobeha.2016.09.006)
5. Medzhitov R, Schneider DS, Soares MP. 2012 Disease tolerance as a defense strategy. *Science* **335**, 936–941. (doi:10.1126/science.1214935)
6. Rifkin JL, Nunn CL, Garamszegi LZ. 2012 Do animals living in larger groups experience greater parasitism? A meta-analysis. *Am. Nat.* **180**, 70–82. (doi:10.1086/666081)
7. Patterson JEH, Ruckstuhl KE. 2013 Parasite infection and host group size: a meta-analytical review. *Parasitology* **140**, 803–813. (doi:10.1017/S0031182012002259)
8. Gulland FMD. 1992 The role of nematode parasites in Soay sheep (Ovis-aries l) mortality during a population crash. *Parasitology* **105**, 493–503. (doi:10.1017/S0031182000074679)
9. Stien A, Irvine RJ, Ropstad E, Halvorsen O, Langvatn R, Albon SD. 2002 The impact of gastrointestinal nematodes on wild reindeer: experimental and cross-sectional studies. *J. Anim. Ecol.* **71**, 937–945. (doi:10.1046/j.1365-2656.2002.00659.x)
10. Budischak SA, O'Neal D, Jolles AE, Ezenwa VO. 2018 Differential host responses to parasitism shape divergent fitness costs of infection. *Funct. Ecol.* **32**, 324–333. (doi:10.1111/1365-2435.12951)
11. Walkden-Brown SW, Kahn LP. 2002 Nutritional modulation of resistance and resilience to gastrointestinal nematode infection-a review. *Asian-Australasian J. Anim. Sci.* **15**, 912–924. (doi:10.5713/ajas.2002.912)
12. Beauchamp G. 1998 The effect of group size on mean food intake rate in birds. *Biol. Rev.* **73**, 449–472. (doi:10.1111/j.1469-185X.1998.tb00179.x)
13. Worsley-Tonks KE, Ezenwa VO. 2015 Anthelmintic treatment affects behavioural time allocation in a free-ranging ungulate. *Anim. Behav.* **108**, 47–54. (doi:10.1016/j.anbehav.2015.07.018)
14. Gunn A, Irvine RJ. 2003 Subclinical parasitism and ruminant foraging strategies: a review. *Wildl. Soc. Bull.*, **31**, 117–126.
15. Papadopoulos E *et al.* 2009 Persistent efficacy of long-acting moxidectin for control of trichostrongylid infections of sheep. *Small Ruminant Res.* **81**, 171–173. (doi:10.1016/j.smallrumres.2008.11.004)
16. Williams AE, Worsley-Tonks KE, Ezenwa VO. 2017 Drivers and consequences of variation in individual social connectivity. *Anim. Behav.* **133**, 1–9. (doi:10.1016/j.anbehav.2017.08.021)
17. Stoffel MA, Nakagawa S, Schielzeth H. 2017 rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods Ecol. Evol.* **8**, 1639–1644. (doi:10.1111/2041-210X.12797)
18. Ezenwa V. 2003 Habitat overlap and gastrointestinal parasitism in sympatric African bovids. *Parasitology* **126**, 379–388. (doi:10.1017/S0031182002002913)
19. Altmann J. 1974 Observational study of behavior: sampling methods. *Behaviour* **49**, 227–266. (doi:10.1163/156853974X00534)
20. Iason GR, Mantecon AR, Sim DA, Gonzalez J, Foreman E, Bermudez FF, Elston DA. 1999 Can grazing sheep compensate for a daily foraging time constraint? *J. Anim. Ecol.* **68**, 87–93. (doi:10.1046/j.1365-2656.1999.00264.x)
21. Brooks ME *et al.* 2017 glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal* **9**, 378–400.
22. Hartig F. 2018 DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. R package version 0.2.0. See http://florianhartig.github.io/DHARMa/.
23. Blumstein DT, Daniel JC. 2007 *Quantifying behavior the JWatcher Way*. Sunderland, MA: Sinauer Associates.
24. Bates D, Maechler M, Bolker B, Walker S. 2015 Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48. (doi:10.18637/jss.v067.i01)
25. Krause J, Ruxton GD. 2002 *Living in groups*. Oxford, UK: Oxford University Press.
26. Creel S, Schuette P, Christianson D. 2014 Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. *Behav. Ecol.* **25**, 773–784. (doi:10.1093/beheco/aru050)
27. Johnson R. 1998 Immune and endocrine regulation of food intake in sick animals. *Domest Anim. Endocrinol.* **15**, 309–319. (doi:10.1016/S0739-7240(98)00031-9)
28. Snyder-Mackler N *et al.* 2016 Social status alters immune regulation and response to infection in macaques. *Science* **354**, 1041–1045. (doi:10.1126/science.aah3580)
29. Kohn JN, Snyder-Mackler N, Barreiro LB, Johnson ZP, Tung J, Wilson ME. 2016 Dominance rank causally affects personality and glucocorticoid regulation in female rhesus macaques. *Psychoneuroendocrino.* **74**, 179–188. (doi:10.1016/j.psyneuen.2016.09.005)
30. Penning PD, Parsons AJ, Newman JA, Orr RJ, Harvey A. 1993 The effects of group size on grazing time in sheep. *Appl. Anim. Behav. Sci.* **37**, 101–109. (doi:10.1016/0168-1591(93)90103-V)
31. Sevi A, Casamassima D, Muscio A. 1999 Group size effects on grazing behaviour and efficiency in sheep. *J. Range Manag.* **52**, 327–331. (doi:10.2307/4003541)
32. Shrader AM, Kerley GI, Kotler BP, Brown JS. 2006 Social information, social feeding, and competition in group-living goats (*Capra hircus*). *Behav. Ecol.* **18**, 103–107. (doi:10.1093/beheco/arl057)
33. Fortin D, Boyce MS, Merrill EH, Fryxell JM. 2004 Foraging costs of vigilance in large mammalian herbivores. *Oikos* **107**, 172–180. (doi:10.1111/j.0030-1299.2004.12976.x)
34. Cremer S, Pull CD, Furst MA. 2018 Social immunity: emergence and evolution of colony-level disease protection. *Annu. Rev. Entomol.* **63**, 105–123. (doi:10.1146/annurev-ento-020117-043110).
35. Almberg ES, Cross PC, Dobson AP, Smith DW, Metz MC, Stahler DR, Hudson PJ. 2015 Social living mitigates the costs of a chronic illness in a cooperative carnivore. *Ecol. Lett.* **18**, 660–667. (doi:10.1111/ele.12444)
36. Ezenwa VO, Worsley-Tonks KEL. 2018 Data from: Social living simultaneously increases infection risk and decreases the cost of infection. Dryad Digital Repository. (doi:10.5061/dryad.80f293g)