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Reciprocal relationships between behaviour and parasites suggest that negative feedback may drive flexibility in male reproductive behaviour

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Parasites are ubiquitous components of the environment that contribute to behavioural and life-history variation among hosts. Although it is well known that host behaviour can affect parasite infection risk and that parasites can alter host behaviour, the potential for dynamic feedback between these processes is poorly characterized. Using Grant's gazelle (*Nanger granti*) as a model, we tested for reciprocal effects of behaviour on parasites and parasites on behaviour to understand whether behaviour–parasite feedback could play a role in maintaining variation in male reproductive behaviour. Adult male gazelles either defend territories to attract mates or reside in bachelor groups. Territoriality is highly variable both within- and between-individuals, suggesting that territory maintenance is costly. Using a combination of longitudinal and experimental studies, we found that individual males transition frequently between territorial and bachelor reproductive status, and that elevated parasite burdens are a cost of territoriality. Moreover, among territorial males, parasites suppress aspects of behaviour related to territory maintenance and defence. These results suggest that territorial behaviour promotes the accumulation of parasites in males, and these parasites dampen the very behaviours required for territory maintenance. Our findings suggest that reciprocal feedback between host behaviour and parasitism could be a mechanism maintaining variation in male reproductive behaviour in the system.

1. Introduction

Animal behaviour has profound effects on the transmission of parasites and pathogens, likewise parasite infection commonly affects animal behaviour [1–4]. Although studied largely independently, these two processes can occur in concert generating positive or negative feedback that drives significant variation in host behaviour at within- and between-population scales (e.g. [5]). For example, certain aspects of host behaviour might enhance parasite infection risk, and in turn, the effects of infection on the host might strengthen (positive feedback) or dampen (negative feedback) relevant behaviours. At present, aspects of animal behaviour most commonly influenced by behaviour–parasite feedbacks are unknown, yet given the ubiquity of parasitism this phenomenon may be central to our understanding of the maintenance of high levels of behavioural variation in the wild.

One aspect of behaviour where parasites may play a key role in shaping variation is male reproductive behaviour. Data from a number of species show that variation in reproduction is often correlated with differences in parasite infection [6–10]. Moreover, parasites feature prominently in several key hypotheses explaining the maintenance of variability in male secondary sexual traits [11,12]. So far, recurring correlations between parasite infection and male reproductive behaviour provide evidence that investment in reproduction and parasitism are linked in some way. Territorial male alpine chamois (*Rupicapra*

rupicapra), for example, have significantly higher bronchopulmonary nematode burdens than non-territorial males during the rutting season [10]; while dominant male chimpanzees harbour a more diverse intestinal helminth community than low ranking individuals [13]. Indeed, a recent meta-analysis found that across multiple vertebrate taxa, dominant males show consistently higher rates of parasitism [14]. However, based on current evidence, it is difficult to tease apart whether correlations between parasites and male behaviour are a consequence of increases in infection risk that accompany the expression of certain reproductive behaviours (e.g. [10]); direct or indirect effects of parasites on reproductive behaviour (e.g. [8,15]); or dynamic feedback between these two processes. The potential for feedback between both processes has rarely been investigated, but in the context of male reproductive behaviour, negative feedback between the effects of behaviour on infection and parasites on behaviour could play a crucial role in maintaining flexibility in behaviour over time. Specifically, if a male reproductive behaviour enhances parasitism but parasites simultaneously suppress the behaviour, then bidirectional host–parasite interactions may play a role in shaping when and why males adopt different reproductive strategies.

Here, we used longitudinal and experimental studies of the African antelope, Grant's gazelle (*Nanger granti*), to investigate the possible role of behaviour–parasite feedback in maintaining variation in male reproductive behaviour. Male Grant's gazelles either defend territories or join roving bachelor herds as adults. Territorial males defend discrete resource patches where females congregate, whereas bachelor groups reside outside of the territorial network [16]. All males become bachelors as sub-adults, and young bachelors naturally transition into territorial males once they reach adulthood [16,17]. However, age alone cannot explain bachelorhood since bachelor herds contain both sub-adult and adult males, and many adult males who hold territories transition back to bachelor status. Thus, males may frequently make the switch between reproductive (territorial) and non-reproductive (bachelor) status during adulthood. Our previous work suggests that territorial status in gazelles is associated with physiological changes that might enhance parasite infection risk. For example, higher testosterone predicts future territoriality on the one hand, but is associated with lower immune function on the other [18]. Territorial status is also correlated with higher parasite burdens [19]. To determine whether feedback between behaviour and parasite infection can help explain variation in male reproductive behaviour, we examined: (i) the degree of flexibility in male reproductive behaviour, (ii) if reproductive behaviour can explain variation in parasitism, and (iii) if aspects of territoriality are suppressed by infection. We predicted that territorial status would be associated with elevated parasite infection risk, and that parasites would in turn suppress territorial behaviours providing the essential ingredients for a negative behaviour–parasite feedback loop which maintains flexibility in male reproductive behaviour.

2. Material and methods

(a) Longitudinal study

Male Grant's gazelles were captured at the Mpala Research Center (MRC), Kenya (0°17′ N, 37°52′ E) in January–February ($n = 4$) and August ($n = 17$) 2009. Animals were captured using drive nets on the ground (January–Feburary) or a hand-held net gun fired from a helicopter (August), fitted with unique colour ear tags, and then released after sample collection and morphological measurements [18]. Individuals were anaesthetized to facilitate age estimation via tooth wear. Tooth wear was measured by making an impression of the upper molar using dental putty (Provil Novo, Heraus Kulzer), and discerning wear patterns from the tooth moulds. Age was determined using tooth wear criteria described in [17]. Captures were biased towards sub-adult and adult males so all males in the sample were at least 2 years old. Sub-adult males get excluded from female groups beginning around age 2 [16], and one focal male was in this age range and initially observed in a female group, so data collection did not begin for this individual until his transition to a bachelor herd.

To assess variation in male parasite infection with natural variation in reproductive status, individually identifiable males were tracked after capture to monitor reproductive status and parasite infection. Since territoriality and breeding occur year round at the study site [18], males were monitored continuously from the month after capture (starting in either March or September 2009) through to June 2011, or until the subject was lost from the study due to death or emigration from the study site. At each sighting, male status was recorded as territorial (T), bachelor (B), or unknown (U). Territorial status was assigned based on an assessment of male behaviour, spatial location, and group composition [18]. In cases where these factors could not be reliably evaluated, male status was classified as unknown. Concurrent with reproductive status assessments, faecal samples were collected for parasitological analysis. Samples were collected within 30 min of observing a known male defecate and stored on ice prior to transport to the laboratory for processing. All samples were collected between the hours of 06.30 and 18.30, and attempts were made to collect at least one sample per male per month. Parasitological analyses focused on strongyle nematodes (Nematoda: Strongylida) which occur at extremely high prevalence (approx. 100%) in Grant's gazelles at the study site [19,20]. Strongyle egg output in faeces was quantified using a modification of the McMaster faecal egg counting technique [20]. Faecal egg counts reflect a combination of the number, size, and fecundity of the worm population within a host [21], and are used here as a proxy for the intensity of a host's worm infection. All egg counts were performed on the day of sample collection. Overall, 354 faecal samples with matching reproductive status information were collected from 21 males (average no. samples/male = 16; range: 1–54); 127 samples were from bachelor males and 227 were from territorial males.

(b) Experimental study

A second cohort of males were captured in June 2011 and a subset were treated with an anthelmintic drug to experimentally test for differences in parasite infection risk by reproductive status and to evaluate the effects of parasites on behaviour. Over a 5-day period, 24 males were captured by helicopter and half were given a subcutaneous injection of moxidectin (1 ml/20 kg of Cydectin Long Acting Injection for Sheep, Virbac Animal Health), a drug which provides protection against a broad range of gastrointestinal nematodes for up to 120 days in sheep [22]. Individuals were randomly assigned to the treatment or control group based on the sequence of capture, and prior to treatment faecal samples were collected to determine pre-treatment parasite burdens.

A comparison of treated males of different status was used to test for variation in parasite re-accumulation by reproductive status. The reproductive status and parasite loads of nine treated males (five territorial and four bachelor) were monitored from July 2011 through to November 2012, or until the subject was lost from the study, as described above. None of the nine focal males switched status during this experiment, so the data represent parasite re-accumulation for males who maintained a consistent

reproductive status. Over the 18-month re-accumulation study period, an average of 12 faecal samples were collected per month (range: 8–16), for a total of 206 samples used for analysis (average no. samples/male = 22; range: 3–44). Thirty-four samples were from bachelor males and 172 samples were from territorial males.

The effect of parasites on the behaviour of territorial males was assessed by comparing the behaviour of territorial males who did and did not receive treatment. To do this, the behaviour of nine territorial males was monitored before and after the expected approximately 120 day drug efficacy period, from July 2011 to October 2011 (less than or equal to 120 days post-treatment (dpt)) and from November 2011 to February 2012 (more than 120 dpt). Behavioural data collection focused on agonistic and dominance activities associated with territory defence and maintenance, including chasing, fighting, or sparring, vegetation horning, threat displays, scent-marking, and linked urination-defecation displays [16]. Data were collected using focal sampling [23], and for each observation the behaviour of a single male was continuously recorded for up to 35 min using binoculars and a hand-held digital voice recorder. The date, start time, weather (clear, overcast, or rainy), wind conditions (low or high), the type (male only, male plus females, male plus females, and bachelors), and size of the group containing the focal male was recorded for each observation. To account for possible effects of time of day on behaviour, observation periods 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). A single observer performed 198 observations (less than or equal to 120 dpt = 109; more than 120 dpt = 89) ranging in duration from 10 to 33 min (average = 20.8 min). Two subjects were killed by predators during the first 120 days of the observation period, so the dataset includes five treated and four control males during the less than or equal to 120 dpt 'drug efficacy' period, but only four treated and three control males during the more than 120 dpt 'non-efficacy' period. The average number of focal observations per male for each efficacy period was 12 (range: less than or equal to 120 dpt = 7–17; more than 120 dpt = 6–15). Male reproductive status (bachelor versus territorial) was monitored for an additional 18 months (from March 2012 to July 2013) to quantify the effects of treatment on the duration of territoriality.

(c) Statistical analyses

Since we tracked male behaviour over time in our longitudinal study, first we investigated whether age and the duration of time over which an individual was observed were potential confounding factors explaining variability in male behaviour. To do this, we used a logistic regression to test for effects of age at initial capture and observation duration on the likelihood that a male switched tactics during the study period.

Next, we tested for an effect of reproductive status (territorial versus bachelor) on parasite infection intensity using paired longitudinal data on male status and parasite infection. Since individual males were sampled repeatedly over time, we used a mixed effects model to account for between-subject variation (random intercept) and between-subject variation by status (random slope). Because the parasite egg count data were highly overdispersed relative to a Poisson model, we used a generalized linear mixed model (GLMM) with a negative binomial error structure. A male's worm egg count at each observation was used as the response variable in the model. Reproductive status, current age, and year were included as fixed effects.

For our experimental cohort, first we evaluated whether the initial assignment of animals to anthelmintic treatment groups was random with respect to age and worm infection status. We used Wilcoxon rank sum tests for these analyses to address the non-normal distribution of the parasite and age data. Next, we used a negative binomial GLMM to test whether treatment reduced egg shedding during the expected 120 day period of drug efficacy, and whether this effect wore off after 120 days. The response variable for this model was a male's worm egg count at each observation, and the fixed effects were treatment, efficacy period (less than or equal to 120 dpt or more than 120 dpt), and a treatment × efficacy period interaction. Animal ID was included as a random effect to account for repeated sampling of individuals.

After establishing that the drug worked and then wore off, we then tested whether re-accumulation of parasites by individual males was predicted by reproductive status. To do this, we calculated the difference between a male's worm egg count at each observation and his original worm egg count at capture (i.e. prior to treatment) as an index of parasite re-accumulation. This index, which had normally distributed errors, was used as the dependent variable in a linear mixed model (LMM) to test for an effect of reproductive status, the time since treatment (in days), and the interaction between status and time on parasite re-accumulation. Current age was also included as a fixed effect, as was worm egg count at capture to account for any effect of initial parasite load on the re-accumulation process. Animal ID was included as a random effect to account for repeated sampling. All LMMs and GLMMs described above were implemented in R v. 3.0.3 [24] with the packages *lme4* [25] and *lmerTest*. For the GLMMs, models were also run in two additional R packages with qualitatively similar results (electronic supplementary material, tables S1 and S2). Model validity was assessed by visual inspection of residuals as described by Zuur *et al.* [26].

Finally, we used data from treated and control territorial males to test the effect of parasite treatment on male behaviours associated with territorial maintenance and defence. To do this, we converted all of the behavioural recordings to time budgets using JWatcher v1.0 [27] to quantify the proportion of time males spent engaged in territorial behaviours during each focal observation. We used this information to calculate the average amount of time a male devoted to territoriality during the two drug efficacy periods: less than or equal to 120 dpt and more than 120 dpt. This analysis was restricted to behavioural observations involving a territorial male associated with females, which accounted for over 90% of the total observations. Individual male averages were then used to compare behavioural time investment between treated and control males. We used averages over time to improve our ability to detect a treatment effect on behaviour since territorial behaviours are rare to observe, averaging only 1.8% (range: 0–24%) of all activities recorded during a typical focal observation. Because behaviour data were non-normally distributed, we used non-parametric permutation tests to test two hypotheses: that the mean proportion of time treated and control males spent engaged in territorial behaviours differed (i) during the 120 drug efficacy period (less than or equal to 120 dpt), (ii) but not afterwards (more than 120 dpt). Permutation tests use all possible combinations of the available data points to create a permutation distribution against which a test statistic (in this case, the difference between means for treated versus control males) can be compared. We used a bootstrap procedure, implemented in the *simpleboot* package in R to calculate 95% confidence intervals for each test statistic. In addition to the efficacy period analysis, we also examined how investment in territorial behaviour changed with time since treatment for treated and control males on a finer timescale by plotting the difference between the average time spent in territorial activity from one to eight months post-treatment. We excluded month 6 from the plot because only two focal observations were collected from control males during this month. Lastly, we estimated the total duration of territoriality for each territorial male starting from the first observation of territoriality to the last (or until the end of the study), and then compared territorial duration for treated and control males also using permutation tests.

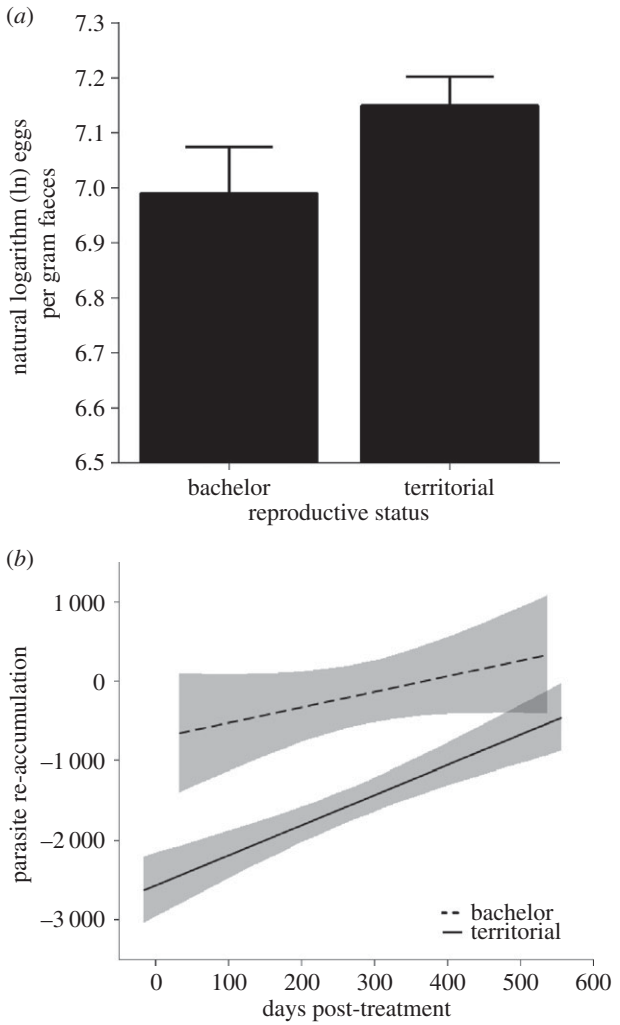

Figure 1. (*a*) Average nematode egg shedding in males during bachelor versus territorial reproductive phases. (*b*) Parasite re-accumulation curves for anthelmintic-treated bachelor (dashed lines) and territorial (solid lines) males. The index of parasite re-accumulation was calculated as the difference between a male's worm egg count at each observation and his original worm egg count prior to treatment.

3. Results

(a) Territorial males maintain higher parasite burdens than bachelors

Of 25 adult males monitored for 21–30 months during the longitudinal study, approximately half ($n = 12$) transitioned between bachelor (B) and territorial (T) status or vice versa; seven stayed exclusively bachelors; and six were exclusively territorial. Age could not explain the likelihood of switching between reproductive states, but switches were more likely among males tracked for longer periods implying that males tend to switch status over time (logistic regression, $n = 21$: age $\chi^2 = 0.135$, $p = 0.713$; average no. months of observation for males with versus without switches: 15 versus 4.9, $\chi^2 = 10.3$, $p = 0.0013$). We tested whether parasite infection varied by status by tracking individual male behaviour and parasite burdens simultaneously. Male worm burdens were significantly higher during territorial phases compared with bachelor phases (figure 1*a*), and age could not account for this difference (GLMM: $n = 354$ observations, 21 males; reproductive status: β estimate $\pm$ standard error (s.e.) (territorial) = 0.340 ± 0.150, $p = 0.0239$; age: β estimate $\pm$ s.e. = 0.069 ± 0.131, $p = 0.598$; year: β estimate $\pm$ s.e. (2010) = -0.757 ± 0.091, $p < 0.0001$, β estimate $\pm$ s.e. (2011) = -0.472 ± 0.140, $p = 0.0007$). The model predicted a 40% ($e^{0.34}$) average increase in worm egg shedding for territorial versus bachelor males; and 19 of 21 individual males were estimated to shed more eggs as territory holders with numbers of eggs increasing by 20–98% (electronic supplementary material, table S3).

Table 1. Effect of territorial status, time since treatment, and their interaction on parasite re-accumulation after anthelmintic treatment ($n =$ 206 observations, nine males). LMM with Animal ID included as a random effect. Significant predictors are shown in bold.

	β estimate $\pm$ s.e.	*t*-value	*p*-value
status: territorial	-1327 ± 539	-2.459	**0.032**
time lag	1.16 ± 1.11	1.041	0.301
status: territorial × time lag	2.46 ± 0.99	2.47	**0.014**
initial egg count	-1223 ± 142	-8.582	**0.001**
age	6.31 ± 11.6	0.544	0.606

(b) Territorial males re-accumulate parasites at a faster rate than bachelors after anthelmintic treatment

In support of the longitudinal study, we found that for a second cohort of males whose worm infections were cleared with an anthelmintic drug, reproductive status was a significant predictor of parasite re-infection rate. At capture, males assigned to the treatment and control groups did not differ in age (Wilcoxon rank sum test, $W = 50.5$, $p = 0.824$). In terms of parasite infection, all males were shedding worm eggs at capture and there was no difference in faecal egg counts by treatment group (untransformed mean $\pm$ s.e., control ($n = 12$): 770 ± 322, treated ($n = 12$): $1\,462 \pm 322$; $W = 56$, $p = 0.370$). After treatment, treated males were shedding fewer eggs than untreated males during the approximately 120-day period of expected drug efficacy, but not afterwards as indicated by a significant treatment by drug efficacy period interaction (GLMM: $n = 186$ observations, 19 males; treatment: β estimate $\pm$ s.e. (treated) = -0.515 ± 0.428, $p = 0.229$; drug efficacy period: β estimate $\pm$ s.e. (less than 120 dpt) = -0.0019 ± 0.355, $p = 0.996$; interaction: β estimate $\pm$ s.e. (treated : less than 120 dpt) = -1.06 ± 0.473, $p = 0.025$). In a statistical model examining the effect of reproductive status on parasite re-accumulation after treatment, the interaction between reproductive status and time since treatment emerged as a significant predictor of the re-accumulation rate (table 1), with territorial males showing a steeper re-accumulation curve than bachelor males (figure 1*b*).

(c) Parasites suppress territorial behaviour

Given evidence that territorial males accumulate parasites faster, we explored whether high parasite burdens in these males affected territorial behaviour. To do this, we tested for an effect of anthelmintic treatment on agonistic behaviours associated with territory maintenance and defence. We found that treated males spent significantly more time engaged in territorial defence behaviours when compared with untreated control males (Permutation test: less than

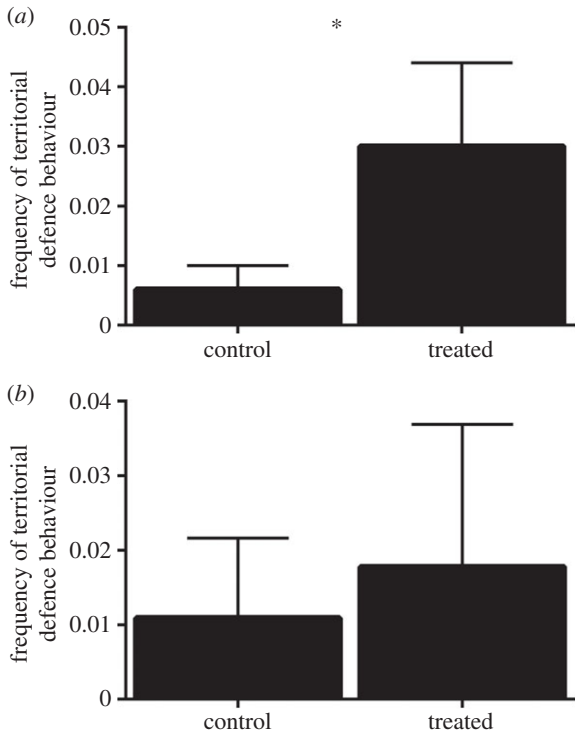

Figure 2. Frequency of territorial defence behaviours in control and anthelminthic-treated territorial males: (*a*) within 120 days of treatment and (*b*) 120 or more days after treatment.

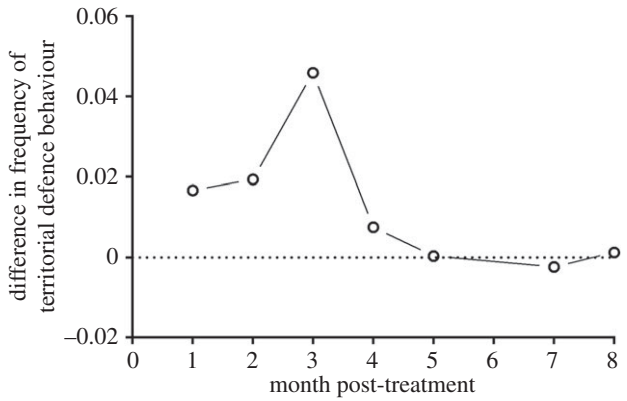

Figure 3. Mean monthly difference in the frequency of territorial defence behaviours between anthelminthic-treated and control territorial males at one to eight months post-treatment.

or equal to 120 dpt, mean difference (control, $n = 4$; treated, $n = 5$) = 0.024; 95% CI = 0.011–0.034; $p = 0.023$; figure 2*a*). However, this difference disappeared after the effects of the anthelminthic drug wore off suggesting that the loss of parasites was directly linked to the change in behaviour (more than 120 dpt, mean difference (control, $n = 3$; treated, $n = 4$) = 0.006; 95% CI −0.008–0.030; $p = 0.742$; figure 2*b*). The results from these drug efficacy analyses were further corroborated by a finer-scale visualization of the difference in territorial defence behaviours between treatment groups. The asymmetry in time invested by treated versus untreated males in defence behaviours peaked at three months (approx. 90 days) post-treatment and then declined to zero by five months (approx. 150 days) post-treatment (figure 3).

Finally, the observed increase in agonism during the drug efficacy period could have improved the ability of treated males to defend their territories extending the duration of territoriality and delaying switching to bachelor status. Of nine males monitored for territorial duration over the period of June 2011 to July 2013, five switched tactics, one remained territorial, and three died. Treated males were territorial for 556 days on average compared to 465 days for control males, however, this difference was not significant (mean difference (control, $n = 4$; treated, $n = 5$) = 90.9; 95% CI = −224.7–417.5, $p = 0.626$).

4. Discussion

Our results suggest that adult male Grant's gazelles commonly switch between territorial and bachelor reproductive status, and parasites may exert a strong negative effect on behaviours associated with maintaining territoriality. First, we found that switching between territorial and bachelor status occurred frequently and was independent of age. Second, territorial males maintained consistently higher worm burdens than bachelor males on average, and a majority of individual males had higher worm burdens when they were territorial versus not. Third, after experimental clearance of parasite infections, territorial males re-accumulated their parasites faster than bachelors did, suggesting a causal link between reproductive status and parasite accumulation. Finally, in addition to the effect of male behaviour on parasite infection, we found that elevated worm burdens suppressed territorial defence behaviours in territorial males. Because these defence behaviours, which include chases, fights, and aggressive displays, are associated with territory maintenance [16], worm infection intensity may directly affect a male's ability to maintain a territory. Taken together, these results suggest that territorial behaviour promotes the accumulation of parasites in males, and these parasites dampen the very behaviours required for territory maintenance. We suggest that this may result in a negative feedback loop that helps maintain natural variation in male reproductive behaviour.

Connections between male reproductive behaviour and parasite infection are fairly well-described and potential mechanisms underlying these links are also well documented. For example, in male vertebrates, the androgen testosterone plays an important role in determining reproductive behaviour [28], but can also suppress the immune system under some circumstances [29–31]. As such, correlations between secondary sexual trait development or dominant reproductive status and increases in parasite infection may often arise as a consequence of the immunosuppressive effects of testosterone [13,32,33]. Differences in parasite exposure rates of males with different reproductive behaviours also alter the relative risks of infection; and in many cases, changes in male behaviour that account for differences in parasite exposure are also influenced by testosterone [34,35]. For example, changes in movement patterns in high testosterone males could affect levels of exposure to parasites. In support of findings from other species, our previous work on Grant's gazelles has shown that testosterone is associated with male reproductive behaviour and may be linked to parasite infection via effects on both host immunity and parasite exposure [18]. So in our study system, like many others, testosterone emerges as an important proximate mechanism connecting reproductive behaviour to changes in parasitism. It is important to note that because males in our observational study were difficult to locate and sample immediately before and after switches

in reproductive status, a lack of parasite data during the time period surrounding switching events precluded us from testing for an increase or decrease in parasite burdens immediately following switches in status. However, our experiment clearly connected territorial status with faster parasite re-accumulation. There are few plausible explanations for this elevated infection risk in territorial males other than higher parasite exposure and susceptibility arising from differences in behaviour and physiology. This process may represent the first step in a dynamic feedback loop.

For behaviour–parasite feedback to occur parasites must also affect male reproductive behaviour. While there is evidence of such effects, they are rarely documented contemporaneously with the effects of behaviour on infection. Nevertheless, there is intriguing data suggesting that the co-occurrence of the two phenomena may be fairly common. For instance, in guppies (*Poecilia reticulata*), Kolluru *et al.* [8] showed that males parasitized by the monogenean parasite *Gyrodactylus turnbulli* altered their mating behaviour by spending less time courting females and making more attempts to steal females from other males. In a different study, Richards *et al.* [36] showed that male courtship behaviour is linked to the transmission of *G. turnbulli*, suggesting that both steps of a potential feedback loop may exist for the guppy–*Gyrodactylus* interaction. In another example, Mougeot *et al.* [15] showed that manipulation of the nematode parasite *Trichostrongylus tenuis*, significantly affected territorial behaviour in male red grouse (*Lagopus lagopus scoticus*). Specifically, territorial call rates were higher among males who had their parasites experimentally cleared when compared with those who were challenged with parasites. Treated males also tended to win more territorial interactions than challenged males. Since high testosterone levels, which are associated with increased aggression and territorial behaviour in red grouse, also increase parasite loads [32,37,38], dynamical interactions between parasites and male territorial behaviour seem highly likely in this system [15].

In Grant's gazelles, in addition to linking reproductive behaviour to parasite infection, we also found evidence that parasites affect reproductive behaviour. Specifically, we showed that parasite clearance increased territorial male investment in behaviours associated with territory maintenance and defence. Although we did not show that an increase in parasites (e.g. via parasite challenge) dampened behaviour, the positive effects of parasite clearance on male behaviour, coupled with a decay in the effect when the drug treatment wore off, suggest that parasites impose costs on territorial males that alter their reproductive behaviours. These costs might arise for at least two reasons. First, parasites may reduce male body condition or energetic reserves, negatively affecting the amount of time and energy that parasitized males can invest in territory defence. This possibility is supported by studies showing that gastrointestinal nematode infections can cause significant declines in the body condition of free-ranging ungulates [39–44]. Second, parasites may have cognitive effects on their hosts that alter certain aspects of behaviour. Behaviours associated with territoriality generally require cognitive attributes related to acquiring, storing, and processing spatial information [45]. Interestingly, nematode infections have been shown to impair cognitive functions such as spatial learning and information processing in laboratory rodents and humans [46,47]. Although there is no evidence for such effects in wild or domestic ungulates, one possibility is that high worm infections induced neurological changes in infected territorial male gazelles that made them less capable of carrying out territorial defence tasks that involve spatial memory.

An important consequence of parasite-induced suppression of territorial defence behaviour could be a reduction in the duration of territoriality in highly parasitized territorial males. Since we found that territorial status incurs a cost in terms of higher parasite burdens, an effect of parasites on territory defence behaviour—that influences status switching—would complete the negative feedback loop between reproductive behaviour and parasitism helping to account for the flexibility in male behaviour that we observed. However, we did not detect a significant effect of parasite removal on status switching, so we cannot yet explicitly link parasite infection to changes in male reproductive status. It is possible that despite reduced investment in territorial defence, highly parasitized territorial males may be of sufficient quality to retain their territories and other factors may drive switches in reproductive status. For instance, the availability of oestrous females could underlie patterns of status switching; however, consistency in numbers of territorial males at our study site over time, few vacancies in historically occupied territories, and consistency in levels of mating activity all suggest that resources (i.e. territories) are more limiting than oestrous females, setting the stage for intense competition between males for these resources. Our observation that treated territorial males retained their territories for approximately 90 days longer than control males lends preliminary support to the hypothesis that parasitism may influence switching in reproductive status via effects on territorial defence behaviour. However, given the small sample size for this analysis and the waning effects of the anthelmintic treatment over time, rigorously evaluating the impact of parasitism on territorial duration in this system is an important area for future work.

More generally, links between male reproductive behaviour and parasite infection are common across multiple taxa. Using Grant's gazelle as a model, we showed that higher rates of parasitic nematode infection are not only a consequence of territorial behaviour in male gazelles, but that these parasites also appear to simultaneously suppress territorial defence behaviours. Our results reveal a possible role for parasites in catalysing switches in male reproductive status in this system, pointing to a potentially general mechanism that might contribute to the maintenance of variation in male behaviour in nature.

Ethics. The Kenya Ministry of Science, Education and Technology and the Kenya Wildlife Service gave permission to conduct this research in Kenya. Animal protocols used in this study were approved by the University of Montana (no. 023-09VEDBS-051509) and the University of Georgia (no. A2010 10-188) Animal Care and Use Committees.

Data accessibility. Data are available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.ct517.

Authors' contributions. V.O.E. conceived and designed the study, collected data, performed data analysis, and drafted the manuscript. M.H.S. collected data. Both authors approved the final submission.

Competing interests. We have no competing interests.

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