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Anthelmintic treatment affects behavioural time allocation in a free-ranging ungulate

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Social, ecological and environmental factors all influence how much time animals allocate to different behaviours. Here, we investigated whether parasites affect behavioural time allocation in a free-ranging ungulate that must apportion time to multiple competing activities crucial for maintenance, survival and reproduction. We examined how experimental removal of gastrointestinal and pulmonary nematodes influenced the relative amounts of time that female Grant's gazelle, *Nanger granti*, allocated to core behaviours including foraging, vigilance, moving and resting. The anthelmintic treatment reduced female parasite load for ~120 days, and during this period, females relieved of their parasitic nematodes adjusted their daily time budgets. At the group level, parasite removal resulted in an increase in foraging time and a decrease in vigilance. This effect was also apparent at the individual level, where treated females allocated more time to foraging at the expense of vigilance. In addition to treatment, group size was a significant predictor of the relative time spent foraging versus vigilant, where females in larger groups allocated more time to foraging at the expense of vigilance. Our results suggest that parasites may induce changes in host behaviour that are of similar magnitude to some of the most commonly studied social drivers of behavioural time allocation.

The amount of time animals can allocate to essential daily activities is limited. Time allocated to one behaviour takes time away from mutually exclusive behaviours that are equally important for survival and reproduction (Dunbar, Korstjens, & Lehmann, 2009; Rauter & Moore, 2004; Sibbald & Hooper, 2004; Stearns, 1992). In most cases, animals' time budgets revolve around resource acquisition; however, time and energy must also be invested in antipredator and reproductive behaviours, and in some cases in forming social relationships (Dunbar et al., 2009). Animals therefore face constraints on how much time they can devote to competing activities and must frequently substitute one behaviour for another. How individuals optimize these time allocation decisions often depends on their physiological status and ecological requirements (Bachman, 1993; Edwards, Best, Blomberg, & Goldizen, 2013; Illius, Duncan, Richard, & Mesochina, 2002).

A variety of intrinsic and extrinsic factors determine the relative amounts of time that individuals allocate to different behaviours. For instance, during lactation, female Mountain goats, *Oreamnos americanus*, allocate more time to foraging at the expense of time spent resting to meet their increased energetic demands (Hamel & Cote, 2008). Other life history and social traits such as age (Gélin, Wilson, Coulson, & Festa-Bianchet, 2013; Ruckstuhl, Festa-Bianchet, & Jorgenson, 2003), sex (Key & Ross, 1999; Prates & Bicca-Marques, 2008) and group size (Creel, Schuette, & Christianson, 2014; Lashley et al., 2014; Michelena, & Deneubourg, 2011) also affect time allocation to competing behaviours. For example, both group size and adult sex ratio influence time allocation to major activities in alpine ibex, *Capra ibex* (Tettamanti & Viblanc, 2014). More generally, group size is recognized as being a major determinant of how much time animals invest in foraging and vigilance (Creel et al., 2014; Fuller, Bearhop, Metcalfe, & Piersma, 2013; Halupka & Osińska-Dzienniak, 2013). When group sizes are large, individuals often invest more time foraging and less time being vigilant, but the strength of this effect depends on other factors such as predator abundance (e.g. Cresswell, 1994), group composition (e.g. Tettamanti & Viblanc, 2014) and individual status (e.g. Powolny, Bretagnolle, Aguilar, & Eraud, 2014). Abiotic factors also play a role. When food is abundant, individuals often increase time invested in resource acquisition and decrease time spent on vigilance (Ruckstuhl et al., 2003) and other activities such as social behaviour (Alberts et al., 2005). In

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contrast, when resources are patchily distributed, individuals often invest more time in movement behaviours and less on feeding and vigilance (Kotler, Gross, & Mitchell, 1994; Tadesse & Kotler, 2014), illustrating the complex ways in which social, ecological and environmental factors shape animal time budgets.

Parasites can have profound effects on animal behaviour, including changing the amounts of time that individuals invest in specific activities. In Australian scincid lizards (*Egernia stokesii*), individuals relieved of nematode infections spend almost five-fold more time basking compared with controls (Fenner & Bull, 2008). Similarly, dairy cattle relieved of nematode infections graze ~50 min longer per day than do controls (Forbes, Huckle, & Gibb, 2004, 2007). Feeding depression, where infected individuals voluntarily reduce forage intake, is actually a common by-product of gastrointestinal nematode infection in domestic ruminants (Coop & Holmes, 1996). These types of direct effects of parasites on host behaviour may influence how much time animals allocate to competing activities. For instance, a recent study on reindeer, *Rangifer tarandus*, found that insect harassment resulted in individuals investing more time grooming at the expense of foraging (Witter, Johnson, Croft, Gunn, & Gillingham, 2012), suggesting that parasites induced a reallocation of time between resource acquisition and parasite defence.

Here, we investigated whether parasitic nematodes can influence behavioural time allocation in Grant's gazelle, *Nanger granti*. Grant's gazelles experience high rates of gastrointestinal and pulmonary nematode infection (Ezenwa, 2004; Ezenwa, Ekernas, & Creel, 2012); and given the strong direct effects that nematodes can have on livestock feeding behaviour (Arneberg, Folstad, & Karter, 1996; Forbes, Huckle, Gibb, Rook, & Nuthall, 2000; Fox, 1997), our goal was to establish whether these parasites influence time allocation in a species that must balance multiple competing activities crucial for maintenance and survival (e.g. foraging, antipredator behaviour, movement). We manipulated female gazelle parasite loads using an anthelmintic drug to examine the effects of parasite removal on major components of the daily activity budget including foraging, vigilance, moving, resting and other behaviours, and to evaluate how parasite removal affected time allocation to different components of individual activity budgets. We tested the hypothesis that parasite treatment would counteract nematode-induced feeding depression in gazelles with repercussions for time allocation. We predicted that treated animals would increase time spent foraging, and that this would be accompanied by simultaneous reductions in one or more other activities, such as vigilance, moving or resting.

METHODS

Study Animals

We studied the behaviour of female Grant's gazelle at the Mpala Research Centre (MRC), Kenya (0°17′N, 37°52′E) from 20 June 2011 to 30 April 2012. Gazelles were captured and eartagged over a 5-day period in June 2011 as part of a long-term study of parasitism and host behaviour (Ezenwa et al., 2012). Animals were located by helicopter and captured using a hand-held net gun fired from the aircraft. All animals were weighed and a single observer (V.O.E.) collected information on individual morphometrics, including horn length (distance between the base and tip of horn on both the right and left sides) to facilitate age estimation. Age was estimated from an equation relating horn length to tooth wear developed for a subset of nine female gazelles from the same population (Ezenwa, n.d.; see also Spinage, 1976). To experimentally assess the effects of nematodes on host behaviour, all captured females 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 ~120 days in sheep (Papadopoulos et al., 2009). Control animals received saline injections.

Average handling time per animal was 17 min and all possible precautions were taken to minimize stress. Throughout the process, animals were monitored by a wildlife veterinarian. Because no drugs were used to subdue captured females, individuals resumed normal behaviour within minutes of release. Captures were performed under the authority of the Kenya Wildlife Service. 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).

Behavioural Observations

We monitored the behaviour of nine treated and nine control females for approximately 9 months, during 26 July–30 November 2011 and 5 January–30 April 2012 using focal animal sampling (Altmann, 1974). Behavioural observations were taken from a vehicle or on foot from a distance of 100–200 m using binoculars and a hand-held digital voice recorder. To begin a focal observation we located a group of females and randomly selected one individual that was in clear view. We paused the recording if the focal individual went out of sight, and if the individual was out of sight for more than ~10 min, the observation was terminated. Observations shorter than 15 min were excluded from the data set. A single observer (K.W.T.) performed 454 focal observations ranging in duration from 15 to 26 min (average = 20.2 min). The average number of observations per female was 25.2 (range 7–35).

We classified behaviours into five categories: (1) foraging, (2) vigilance, (3) resting, (4) moving and (5) other activities. Foraging involved feeding at any height (e.g. grazing or browsing) or actively searching for food. Vigilance was defined as head-up awareness where an animal raised its head above shoulder height and was actively looking around with ears cocked (Brivio, Grignolio, Brambilla, & Apollonio, 2014; Frid, 1997; Geist, 1971; Hunter & Skinner, 1998). To capture aspects of vigilance and foraging that are mutually exclusive, we coded a behaviour as vigilance, not foraging, if an individual interrupted a foraging bout to raise its head and look around, even if it was still handling food (e.g. chewing). Resting was considered as periods when individuals were either standing or lying while idle. Resting periods often corresponded to rumination bouts, but we did not distinguish between resting and rumination. If an individual became vigilant while resting, the period of time during which the animal's head was raised with ears cocked was coded as vigilance not resting. Moving included directional movement either walking or running; other activities included agonistic, reproductive and maintenance behaviours such as grooming and defecating.

To account for potential effects of time of day on gazelle activity, we distributed focal observations across four time periods: early morning (0600–0859 hours), late morning (0900–1159 hours), early afternoon (1200–1459 hours) and late afternoon (1500–1759 hours). All behaviour observations were terminated after 1800 hours. 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. We classified group type according to sex and age composition as follows: females with juveniles (nursery groups), nursery groups in the company of a territorial male, or nursery groups with bachelor males.

Parasitological Analyses

Faecal samples collected prior to the anthelmintic treatment (i.e. during capture in June 2011) and throughout the behavioural observation period (July 2011–April 2012) were used to monitor the effects of treatment on parasite infection. At capture, we collected faecal samples directly from the rectum of all females. In all other instances, we collected samples opportunistically from known individuals within 10 min of observing a defecation event. Faecal samples were collected between ~0630 and 1830 hours, two to three times per month for each female. Animal ID, time of day and location were recorded for all samples collected. After collection, the samples were kept on ice in the field until being transported to the laboratory for processing.

We focused our parasitological analyses on gastrointestinal and pulmonary nematodes, which occur at high prevalence in Grant's gazelles (Ezenwa, 2003, 2004; Ezenwa et al., 2012). We quantified faecal egg output of strongyle nematodes using a modification of the McMaster egg counting technique (Ezenwa, 2003). First-stage lungworm larvae in faeces were measured using a beaker-modified Baermann method (Ezenwa et al., 2012; Forrester & Lankester, 1997). Although factors such as host faecal output rate and differential parasite fecundity can affect egg and larval counts, we used faecal egg and larval counts as a proxy of individual parasite loads based on other ungulate studies showing that faecal egg counts can provide an accurate estimate of adult worm burdens (Budischak, Hoberg, Abrams, Jolles, & Ezenwa, 2015; Cabaret, Gasnier, & Jacquiet, 1998; Grenfell, Wilson, Isham, Boyd, & Dietz, 1995; Irvine et al., 2001; Schultz, Barry, Forbes, & Johnson, 1993). All samples were processed on the day of collection. A total of 270 faecal samples were collected (131 treated, 139 control). The average number of faecal samples collected per female was 14.9 (range 7–21).

Statistical Analysis

To verify that our assignment of individuals to the two treatment groups was random with respect to traits that might affect host behaviour, we tested for differences in gazelle age and body mass prior to treatment using ANOVA. We then evaluated the efficacy of the anthelmintic drug by comparing strongyle nematode and lungworm counts between treated and control females both prior and after treatment. We log transformed the parasite data to meet the assumptions of normality. For the pre-treatment analysis, which used data from faecal samples collected at capture, we tested for differences in parasite counts between the two treatment groups using ANOVA. For the post-treatment analysis, we accounted for repeated observations by using linear mixed models (LMM) with Animal ID included as a random effect. As fixed effects, we included treatment, treatment period and the interaction between these two terms. We divided the study period into two distinct time periods based on the expected duration of the drug treatment (Papadopoulos et al., 2009): a 120-day ‘treatment’ period and a ‘post-treatment’ period during which the effects of the drug wore off (>120 days after treatment). We used the treatment $*$ treatment period interaction in all models to capture changes in anthelmintic drug efficacy through time. We also included a series of covariates in the LMMs, including age, group size and season (wet versus dry). Each observation month was classified as either wet or dry using monthly rainfall records from the study site. Wet months (June–November 2011, April 2012) averaged 113.2 mm of rainfall, while dry months (December 2011–March 2012) averaged 12.4 mm.

Next, we examined the effects of treatment on female time budgets by comparing the time spent by treated and control females in each behaviour category (foraging, resting, moving, vigilance and other behaviours). We used JWatcher (Blumstein & Daniel, 2007) to convert the behavioural voice recordings into time budgets summarizing the proportion of time that each female devoted to each behaviour. We used Wilcoxon signed-ranks tests to evaluate differences in behaviour between treatment groups separately for the treatment and post-treatment periods.

Finally, to determine whether parasite removal had individual-level effects on behavioural time allocation, we used multivariate models to test for effects of treatment on the ratio of time females spent foraging versus engaging in other activities. We based our behaviour ratio analyses around foraging because time allocation to this behaviour has been linked to nematode parasitism in livestock (Coop & Kyriazakis, 1999; Forbes, Huckle, & Gibb, 2007; Kyriazakis, Tolkamp, & Hutchings, 1998), and because we observed an effect of anthelmintic treatment on foraging in our own time budget analysis. We calculated four behaviour ratios as indicators of potential changes in time allocation to competing activities with foraging: (1) foraging:vigilance, (2) foraging:resting, (3) foraging:moving and (4) foraging:other. Ratios were calculated only for observations where individuals performed both behaviours of interest. For each observation, the proportion of time allocated to all behaviours sums to one, therefore the ratios reflect the relative proportion of time, per observation, invested in foraging over other activities. This provides a description of time allocation decisions made by individuals in each specific observation bout. We used LMMs with Animal ID included as a random effect to account for repeated measures. Fixed effects included treatment, treatment period and the interaction between the two terms. We also included several key covariates in the LMMs, including time of day, age, group size and season. Initial models included the interactions between treatment and each covariate, but because none of these variables emerged as significant predictors of behaviour ratios we dropped them from the final models. All behaviour ratios were log transformed and model residuals were tested for normality. Statistical analyses were performed in JMP 4.0.2 (SAS Institute, 2000), and results were considered significant at $P \leq 0.05$. Finally, because of interpretive difficulties with ratio data, we report the untransformed mean and variance of the numerator (i.e. foraging) and denominator (i.e. the ‘other’ behaviour variables) by treatment group to facilitate interpretation of the underlying causes of any significant changes in ratios (Allison, Paultre, Goran, Poehlman, & Heymsfield, 1995).

RESULTS

Treatment Effect on Parasite Load

Individuals assigned to the treatment and control groups did not differ in age (ANOVA: $F_{1,17} = 0.09$, $P = 0.77$) or body mass ($F_{1,17} = 0.01$, $P = 0.91$). Prior to anthelmintic treatment, there was also no difference between treated and control females in strongyle nematode or lungworm counts (strongyle: $F_{1,17} = 0.36$, $P = 0.56$; lungworm: $F_{1,17} = 0.0005$, $P = 0.98$; Fig. 1). After treatment, treated females shed significantly fewer strongyle eggs and lungworm larvae than did control females, as evidenced by a main effect of treatment (Table 1). However, the difference between the two treatment groups disappeared after the 120-day treatment period and we found a significant treatment $*$ treatment period interaction for both parasite taxa. Treated females shed fewer strongyle eggs and lungworm larvae than control females, but only during the

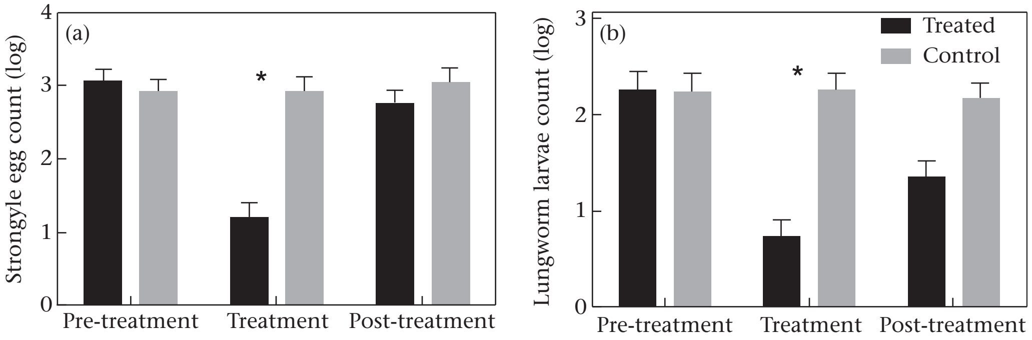

Figure 1. Mean ± SE (a) strongyle egg count (log) and (b) lungworm larvae count (log) for anthelmintic-treated and control female Grant's gazelles during each treatment period. $^*P \leq 0.05$.

treatment period (≤120 days post treatment) and not during the post-treatment period (>120 days post treatment; Table 1, Fig. 1). Neither age, group size nor season had significant effects on strongyle and lungworm counts (Table 1).

Gazelle Daily Activity and Effects of Treatment on Time Budgets

On average, untreated, naturally infected (control) females devoted 28% of their time to foraging, 31% to resting, 21% to moving, 16% to vigilance and 3% to other activities. Treated females spent significantly more time foraging than did controls during the treatment period (Wilcoxon signed-ranks test: $Z = -2.21$, $N = 18$, $P = 0.03$; Fig. 2a), but this effect disappeared during the post-treatment period ($Z = -1.01$, $N = 17$, $P = 0.31$; Fig. 2b). There was also a significant negative effect of treatment on vigilance during the treatment period ($Z = 2.3$, $P = 0.02$; Fig. 2a), but not during the post-treatment period ($Z = 1.3$, $P = 0.2$; Fig. 2b). Treatment had no significant effect on any other behaviour during either period (treatment period: resting: $Z = 1.15$, $P = 0.25$; moving: $Z = -0.88$, $P = 0.38$; other: $Z = 0.44$, $P = 0.66$; Fig. 2a; post-treatment period: resting: $Z = 0.14$, $P = 0.89$; moving: $Z = -0.05$, $P = 0.96$; other: $Z = -1.01$, $P = 0.31$; Fig. 2b).

Treatment Effects on Behavioural Time Allocation

When examining the relative proportion of time that females invested in foraging compared to competing activities, we found that treated females devoted more time to foraging over vigilance than did control females. While this effect was present during the treatment period (behaviour: mean (variance); treated females: foraging: 0.42 (0.07), vigilance: 0.12 (0.02); control females: foraging: 0.27 (0.06), vigilance: 0.19 (0.03); Table 2), it disappeared during the post-treatment period, as illustrated by a significant treatment∗treatment period interaction (treated females: foraging: 0.36 (0.07), vigilance: 0.12 (0.01); control females: foraging: 0.29 (0.06), vigilance: 0.14 (0.02); Table 2). There was no effect of treatment on the ratio of foraging to any other behaviour (Table 2).

In addition to parasite treatment, group size and season were also significant predictors of behavioural time allocation in female gazelles. Group size was a significant predictor of the foraging:vigilance ratio and the foraging:resting ratio. Females allocated relatively more time to foraging over both vigilance and resting when they were in larger groups (Table 2). Season was a predictor of the foraging:moving ratio; females allocated relatively more time to moving over foraging during the wet season compared to the dry season (Table 2).

DISCUSSION

Several factors can affect how much time animals allocate to competing activities. Here, we show that parasite removal influenced time allocation to core activities in female Grant's gazelles. Over 90% of female gazelle daily activity was devoted to four key behaviours: foraging (28%), resting (31%), moving (21%) and vigilance (16%). Other behaviours such as reproductive, agonistic and maintenance behaviours (e.g. grooming) comprised less than 4% of daily activity. Females relieved of gastrointestinal and pulmonary nematodes adjusted their daily time budgets. At the group level, parasite removal was associated with an increase in foraging and a decrease in vigilance. This effect was also apparent at the individual level. During individual focal observations, treated females allocated more time to foraging at the expense of vigilance, suggesting that parasites directly affect host time allocation decisions.

The pattern of daily activity observed for female Grant's gazelles is similar to what has been reported for other wild bovids (Hamel & Cote, 2008; Neuhaus & Ruckstuhl, 2002; Smith & Cain, 2009). Importantly, we found that the anthelmintic treatment disrupted these activity patterns. In particular, treatment affected the relative amount of time that females allocated to foraging. During the

Table 1
Predictors of strongyle nematode and lungworm counts in female Grant's gazelle following anthelmintic treatment

Variables	Strongyle eggs, *N*=251			Lungworm larvae, *N*=251		
	Estimate	F_1	*P*	Estimate	F_1	*P*
Treatment (treated)	**−0.5**	**15.11**	**0.002**	**−0.59**	**27.47**	**<0.0001**
Treatment period (post)	**0.42**	**53.29**	**<0.0001**	**0.13**	**6.93**	**0.009**
Treatment (treated)∗treatment period (post)	**0.35**	**86.21**	**<0.0001**	**0.18**	**27.13**	**<0.0001**
Age	0.02	2.71	0.11	0.01	1.04	0.31
Group size	−0.003	0.06	0.8	−0.008	0.47	0.49
Season (dry)	0.02	0.11	0.74	−0.06	1.56	0.21

Significant effects are shown in bold. Reference levels are indicated in parentheses.

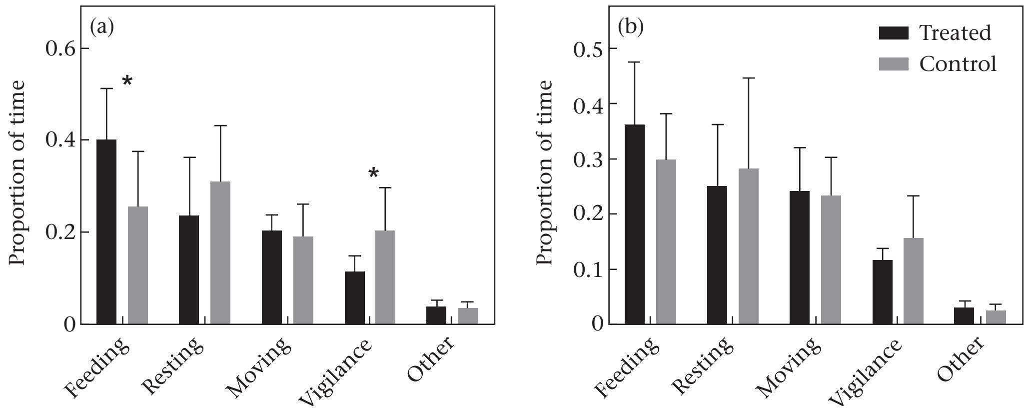

Figure 2. Mean ± SD proportion of time that anthelmintic-treated and control female Grant's gazelles devoted to feeding, resting, moving, vigilance and other behaviour during (a) the treatment period ($\leq$120 days after applying the treatment) and (b) the post-treatment period (>120 days after applying the treatment). $^*P \leq 0.05$.

treatment period, treated females spent a significantly larger proportion of their time foraging compared to controls. However, during the post-treatment period the difference disappeared such that treated and control females spent similar amounts of time foraging. The difference in foraging behaviour between treated and control females during the treatment period and the disappearance of this effect during the post-treatment period suggest that parasites are likely responsible for the differences in female foraging behaviour.

Although we cannot rule out other ecological and environmental factors as potential causes of the difference in foraging behaviour observed between treated and control females during the treatment period, this effect is consistent with previous studies on domestic ruminants showing that nematode infection can induce reductions in forage intake (Forbes et al., 2000; Fox, 1997; Gunn & Irvine, 2003; Kyriazakis et al., 1998). In our study, we monitored two parasite taxa that were affected by the anthelmintic treatment: strongyle nematodes, of which genera such as *Haemonchus*, *Cooperia*, *Gazellostrongylus* and *Trichostrongylus* have been recorded in Grant's gazelles (Ezenwa, 2003; Round, 1968), and pulmonary nematodes, most likely from the family Protostrongylidae (Bowman, 2009). The pathogenic effects of these parasites have not been described for Grant's gazelles, and we could not tease apart the likely effect of each parasite taxon on gazelle foraging behaviour. In livestock, severe infections with many strongyle nematodes are known to cause reductions in food intake (Kyriazakis et al., 1998; Lankester, 2001), but the effects of pulmonary nematodes on host feeding behaviour are largely unknown (Lankester, 2001). However, in wild bighorn sheep, *Ovis canadensis*, lungworm burdens were found to be negatively correlated with foraging time (Pelletier & Festa-Bianchet, 2004), suggesting that these parasites may also negatively affect host food intake to some degree. More generally, nematode-induced suppression of feeding in ruminants is thought to be associated with immune and endocrine responses that can lead to the release of appetite inhibitors or the suppression of appetite enhancers (Forbes, 2008; Fox et al., 1989; Greer, Stankiewicz, Jay, McAnulty, & Sykes, 2005; Zaralis, Tolkamp, Houdijk, Wylie, & Kyriazakis, 2008). Whether this occurs in Grant's gazelles is unknown. As such, future work is needed to explicitly link specific nematode parasites to feeding depression in this species and to explore the physiological mechanisms underlying any effects.

Treated and control females also differed in the relative proportion of time devoted to vigilance. Treated females allocated less time to vigilance than control females during the treatment period but not during the post-treatment period. The fact that treated females increased time invested in foraging and simultaneously decreased time invested in vigilance suggests that individuals without nematode infections may have substituted foraging for vigilance. This idea is supported by our behaviour ratio models, which showed that, at the level of individual focal observations, treated females increased foraging time at the expense of vigilance. The mean foraging:vigilance ratio for treated females was 10.7 compared to 3.4 for control females, indicating that, on average, treated females allocated three-fold more time to foraging over vigilance during a typical 20 min focal observation. This suggests that parasite removal may have induced a major reallocation of host time. The fact that the difference between treated and control females disappeared during the post-treatment period further implicates parasite removal as a factor driving this time reallocation. Once the treatment wore off, the foraging:vigilance ratio was 8.3 for treated females versus 5.6 for control females. Importantly,

Table 2
Predictors of relative time allocation to foraging versus other activities in female gazelles following anthelmintic treatment

Variables	Foraging vs Vigilance N=424			Foraging vs Resting N=396			Foraging vs Moving N=427			Foraging vs Other N=382		
	Estimate	F_1	P	Estimate	F_1	P	Estimate	F_1	P	Estimate	F_1	P
Treatment (treated)	**0.15**	**7.0**	**0.02**	0.06	0.34	0.57	0.06	1.45	0.25	0.04	0.61	0.44
Treatment period (post)	0.008	0.03	0.86	−0.01	0.04	0.84	0.002	0.002	0.97	0.03	0.34	0.56
Treatment (treated)∗treatment period (post)	**−0.06**	**3.93**	**0.05**	0.003	0.004	0.95	−0.004	0.02	0.9	−0.05	1.67	0.2
Age	0.006	0.62	0.44	0.001	0.006	0.94	−0.003	0.2	0.66	−0.005	0.41	0.53
Group size	**0.02**	**5.15**	**0.02**	**0.04**	**5.65**	**0.02**	0.001	0.02	0.89	0.008	0.59	0.44
Season (dry)	−0.07	3.24	0.07	−0.06	0.83	0.36	**−0.07**	**4.03**	**0.04**	0.05	1.14	0.29
Time of day	–	1.52	0.21	–	1.24	0.3	–	1.16	0.32	–	2.37	0.07

Significant effects are shown in bold. Reference levels are indicated in parentheses.

some species with laterally placed eyes and wide lateral fields of view can gather information about predators while their heads are down (Fernández-Juricic, 2012). Since we used a ‘head-up’ definition of vigilance that did not account for the possibility that gazelles with their heads down might also be vigilant, we may have underestimated the amount of time that treated animals, in particular, were investing in vigilance behaviours. Interestingly, ‘head-up’ vigilance is thought to be more effective for detecting predators than ‘head-down’ vigilance (Lima & Bednekoff, 1999), so it is possible that treated gazelles may have swapped more effective ‘head-up’ vigilance for less disruptive, but less effective, ‘head-down’ vigilance.

It is noteworthy that time reallocation associated with parasite treatment and foraging behaviour was observed for vigilance and no other behaviour. Investing time in antipredator behaviour is crucial for survival, but time allocated to highly effective ‘head-up’ vigilance incurs a cost since it interrupts active foraging. For this reason, inherently vulnerable individuals are predicted to invest more time in costly antipredator behaviours compared to individuals that are less vulnerable to predation (Elgar, 1989). Predator vulnerability is often linked to individual traits such as age, sex, reproductive status and body condition, and a number of studies suggest that these traits can determine how animals allocate their time between foraging and vigilance behaviours (Edwards et al., 2013; Elgar, 1989; Rieucau & Martin, 2008). In European rabbits, *Oryctolagus cuniculus*, for example, females increase vigilance time at the expense of foraging during late pregnancy, possibly because of their reduced capacity to evade predators (Monclús & Rödel, 2009). Similarly, yellow-bellied marmots, *Marmota flaviventris*, in poor body condition at the end of the summer invest more time in foraging activities at the expense of vigilance to enhance overwinter survival (Lea & Blumstein, 2011). Both examples suggest that aspects of an animal's physical condition can influence relative time allocation to foraging versus vigilance behaviours. The fact that parasite removal significantly altered foraging:vigilance ratios in Grant's gazelles suggests that parasites might also act as important drivers of behavioural time allocation decisions. Since treated females reallocated time spent vigilant to foraging, it seems likely that parasite removal reduced female vulnerability to predators. One way the change in vulnerability could have occurred is if treated females were in better condition and thus better able to escape predators. These ‘good condition’ females may therefore have the flexibility to invest less time in costly antipredator activities with no negative consequences. We did not have data on female body condition in this study, but one interesting direction for future studies would be to examine how parasite-induced changes in body condition can affect time allocation to foraging and antipredator behaviours.

In addition to treatment, group size influenced time allocation to foraging and vigilance in gazelles. Specifically, females in larger groups allocated more time to foraging at the expense of vigilance. A reallocation of time towards foraging and away from vigilance with increasing group size has been observed in many other taxa ranging from birds to mammals (Blumstein, Daniel, & Sims, 2003; Childress & Lung, 2003; Hopewell, Rossiter, Blower, Leaver, & Goto, 2005; Lashley et al., 2014; Watson, Aebischer, & Cresswell, 2007). Such effects of group size on vigilance are thought to be a consequence of the presence of ‘more eyes’ (Pulliam, 1973), where animals in larger groups benefit from increased group vigilance. Another possibility is that individual time investment in vigilance declines in larger groups because of the decline in individual predation risk via a dilution effect (Hamilton, 1971). More generally, group size and season emerged as significant predictors of gazelle time allocation to foraging relative to other activities such as resting and moving. These results highlight the role of social and environmental factors in shaping individual time allocation.

There is considerable interest in understanding how social, ecological and environmental factors influence variation in an animal's behavioural repertoire and the fitness consequences of these behavioural differences. For example, predation studies have shown that exposure to predators can result in a major reallocation of prey behaviours (Creel, Winnie, Maxwell, Hamlin, & Creel, 2005), highlighting the importance of natural enemies in shaping individual behaviour. Our work demonstrates that another type of natural enemy, parasites, may also affect host time allocation decisions. Specifically, we found that female gazelles relieved of gastrointestinal and pulmonary nematodes increased time invested in foraging at the expense of vigilance. In our study, group size also predicted how much time individuals invested in foraging versus vigilance, and interestingly the magnitude of the parasite treatment effect was of similar size to the effect observed for group size ($F = 7.0$ versus 5.1). This suggests that parasites may induce changes in host behaviour that are equivalent in magnitude to some of the most commonly studied social drivers of behavioural variation, reinforcing the importance of parasitism as a key process shaping animal behaviour in the wild.

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