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

Katherine E. L. Worsley-Tonks [a,*], Vanessa O. Ezenwa [a,b]

[a] *Odum School of Ecology, University of Georgia, Athens, GA, U.S.A.*
[b] *Department of Infectious Diseases, College of Veterinary Medicine, University of Georgia, Athens, GA, U.S.A.*

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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

* Correspondence: K. E. L. Worsley-Tonks, Odum School of Ecology, University of Georgia, Athens, GA 30602, U.S.A.
E-mail address: katherine.worsley.tonks@gmail.com (K. E. L. Worsley-Tonks).

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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