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From parasite encounter to infection: multiple-scale drivers of parasite richness in a wild social primate population

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39 **Abstract**

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41 Host parasite diversity plays a fundamental role in ecological and evolutionary processes, yet
42 the factors that drive it are still poorly understood. A variety of processes, operating across a
43 range of spatial scales, are likely to influence both the probability of parasite encounter and
44 subsequent infection. Here, we explored eight possible determinants of parasite richness,
45 comprising rainfall and temperature at the population level, ranging behavior and home range
46 productivity at the group level, and age, sex, body condition, and social rank at the individual
47 level. We used a unique dataset describing gastrointestinal parasites in a terrestrial subtropical
48 vertebrate (chacma baboons, *Papio ursinus*), comprising 662 faecal samples from 86
49 individuals representing all age-sex classes across two groups over two dry seasons in a desert
50 population. Three mixed models were used to identify the most important factor at each of the
51 three spatial scales (population, group, individual); these were then standardised and
52 combined in a single, global, mixed model. Individual age had the strongest influence on
53 parasite richness, in a convex relationship. Parasite richness was also higher in females and
54 animals in poor condition, albeit at a lower order of magnitude than age. Finally, with a
55 further halving of effect size, parasite richness was positively correlated to day range and
56 temperature. These findings indicate that a range of factors influence host parasite richness
57 through both encounter and infection probabilities, but that individual-level processes may be
58 more important than those at the group or population level.

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3 60 Understanding the forces driving the spread of infectious diseases in wild animal
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5 61 populations is becoming increasingly important. From a theoretical perspective, parasites and
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8 62 pathogens are thought to play a primary role in driving population dynamics and evolutionary
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10 63 processes (Anderson and May 1978; Tompkins 2001). In population dynamics, wildlife
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12 64 diseases can lead to rapid declines in threatened species (Smith et al. 2009) and pose a
13
14 65 growing threat as a source of human zoonoses (Jones et al. 2008). In evolutionary processes,
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16 66 infectious diseases have long been proposed as a significant pressure in the shaping of mating
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18 67 and social systems (Freeland 1976), partly because frequent contact rates between mates and
19
20 68 social partners might greatly facilitate the transmission of pathogens.
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24 69 Since most animals are infected by several parasite species, and even individually
25
26 70 benign infections can have a cumulative pathogenic impact (McCallum 1994; McCallum and
27
28 71 Dobson 1995), an understanding of the factors that determine the number of parasites an
29
30 72 individual carries (i.e. host parasite richness) may be crucial to elucidating patterns of host
31
32 73 vulnerability and the wider impacts of parasitism on host ecology and evolution (Bordes and
33
34 74 Morand 2009). Indeed, host parasite richness has been linked to a diverse range of micro- and
35
36 75 macro-ecological and evolutionary processes, such as adult mortality rates (Simkova et al.
37
38 76 2006), the population-level maintenance of polymorphisms in immune genes such as the
39
40 77 major histocompatibility complex (mammals: Goüy de Bellocq et al. 2008; Simkova et al.
41
42 78 2006), and species diversification (e.g. primates: Nunn et al. 2004). Parasite richness is also
43
44 79 becoming an increasingly important metric for understanding the impacts of anthropogenic
45
46 80 disturbance on threatened taxa (e.g. primates: Chapman et al. 2005b; Gillespie et al. 2005;
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48 81 Valdespino et al. 2010).
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53 82 Despite its importance, we know surprisingly little about the determinants of host
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55 83 parasite richness. Indeed, theoretical progress in this area is constrained by the dearth of
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57 84 empirical research - and this is particularly true for field data - and a lack of information
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3 85 necessary for modeling (Tompkins et al. 2010). Within species, a variety of forces can
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5 86 potentially interact with host susceptibilities to shape parasite transmission across a range of
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8 87 ecological scales, from populations to individuals (Tompkins et al. 2010). At the population
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10 88 level, seasonal environmental factors, such as increasing rainfall and temperature, are
11
12 89 expected to increase parasite richness (Nunn and Altizer 2006), along with intrinsic factors
13
14 90 such as population size and density, number of groups (for social species), and degree of
15
16 91 population fragmentation (Chapman et al. 2005b; Morand and Poulin 1998; Nunn and Altizer
17
18 92 2006). At the group level (in socially structured populations), the group size, area and
19
20 93 productivity of the home range, and daily travel distance might all affect parasite richness
21
22 94 (Nunn and Altizer 2006; Vitone et al. 2004) (but see also Bordes et al. 2009; Snaith et al.
23
24 95 2008). Finally, at the individual level, a wide range of traits might influence parasite richness
25
26 96 including body mass, age, social rank, reproductive state, hormone levels, immune status, and
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28 97 genetic constitution (for reviews, see : Nunn and Altizer 2006; Tompkins et al. 2010).
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30 98 However, identifying independent, contemporaneous, effects of such myriad factors across
31
32 99 spatial scales, and assessing their relative importance, remains a substantial challenge –
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34 100 especially when the complexity of factors involved necessitates an integrative approach, using
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36 101 concurrent monitoring of individuals and their environment through a longitudinal, rather than
37
38 102 cross-sectional, design (Tompkins et al. 2010).
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48 **[Please insert Table 1 here]**
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53 106 Here we investigate the relative importance of a range of factors that might influence
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55 107 host parasite richness. We structure our analysis to recognise the multiple spatial scales over
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57 108 which these factors operate (i.e. the population, group, and individual), and specify whether
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59 109 their mode of action is most likely to affect parasite richness through the probability of
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3 110 encounter with parasites or the susceptibility to infection following encounter (sensu Nunn &
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5 111 Altizer, 2006). Our analysis focuses on patterns of gastrointestinal parasite richness in a wild
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8 112 social primate population of chacma baboons (*Papio ursinus*). While individually-based
9
10 113 parasite studies in wild primates are uncommon (Nunn and Altizer 2006), they are of
11
12 114 particular interest for at least three reasons. First, wild primates are perhaps the most serious
13
14 115 wild source of cross-species disease transmission to humans, with sometimes catastrophic
15
16 116 consequences for public health (e.g. ebola: Leroy et al. 2004). Second, primates are a taxon of
17
18 117 high conservation concern, with disease posing a serious threat in some populations
19
20 118 (Chapman et al. 2005a). Finally, studying a social species will contribute to our understanding
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22 119 of the dynamics of parasite transmission in group-living organisms that may be especially
23
24 120 vulnerable to infectious diseases (Altizer et al. 2003).

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29 121 In Table 1, we detail the eight hypotheses tested. At the population level, our
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31 122 hypotheses predicted that parasite richness would increase with wet (H1) or hot (H2)
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33 123 conditions. At the group level, we predicted that parasite richness would be higher in more
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35 124 productive home ranges (H3), or in association with more extensive ranging behavior (H4).
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37 125 At the individual level, we predicted that parasite richness would be influenced by age (H5),
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39 126 sex (H6), physical condition (H7), and social rank (H8). Finally, we investigated the relative
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41 127 magnitude of the effects of all those factors that influence parasite richness, across spatial
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43 128 scales, in a single global model.
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MATERIALS AND METHODS

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Study system

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Our study was carried out on wild chacma baboons on the edge of the Namib Desert, in central Namibia, at Tsaobis Leopard Park (22°23'S 15°45'W). Tsaobis is characterized by

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3 135 mountains and rocky foothills that descend to rolling gravel and alluvial plains. Vegetation is
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6 136 sparse, comprising grasses and herbs, shrubs and dwarf trees, although patches of aquifer-
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8 137 dependent woodland grow along the ephemeral Swakop River bordering Tsaobis to the north.
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10 138 The landscape is arid and strongly seasonal: annual rainfall is low (mean \pm SD: 123 ± 77 mm,
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12 139 $n=68$ years) and falls only during the austral summer, primarily between December and April.
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14 140 The altitudinal range is 683–1445m. Shade temperatures can approach zero on winter nights,
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16 141 but exceed 40°C on summer days.

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20 142 Data were collected during two field seasons (June to December 2005, May to October
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22 143 2006) on two social groups. These comprised, in October 2006, 9 adult or subadult males, 16
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24 144 adult females, and 32 juveniles for the larger group (Troop J) and 7 adult or subadult males, 9
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26 145 females and 16 juveniles for the smaller group (Troop L). All subjects were fully habituated
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28 146 and individually identifiable.

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33 34 148 **Faecal sampling and analysis**

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36 149 A total of 662 faecal samples were collected immediately after defecation from 86
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38 150 individuals. The faeces were homogenized and a portion (mean \pm SEM: 0.73 ± 4.10^{-3} g) was
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40 151 weighed and stored in 4 ml of 10% buffered formalin solution immediately after collection, at
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42 152 room temperature. A mean of 8.1 samples per individual (SD=6.40, median=7, range: 1-37),
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44 153 and 53.4 samples per month (SD=27.8, median=61, range: 17-104), were collected through
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46 154 the study period. Faecal analysis was carried out using the modified formol-ether
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48 155 sedimentation technique (Allen and Ridley 1970), using merthiolate-formalin as a stain.
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50 156 Parasitic eggs, larvae, trophs, and cysts were recorded by species or morphotype, with
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52 157 measurements made to the nearest 0.1 mm using an ocular micrometer fitted to a compound
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54 158 microscope (further details on parasite identification see Appleton et al. 1991; Appleton et
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56 159 al. 1986) Due to difficulties in identifying rounded-up trophozoites or pre-cystic stages within

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3 160 small-sized amoebae, *Entamoeba hartmanni*, *Endolimax nana*, and *Dientamoeba fragilis*
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6 161 were pooled together into a morphotype designated as “small amoebae” (Fiennes 1972).
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8 162 Similarly, *Entamoeba chattoni*, *Entamoeba histolytica*, *Entamoeba dispar* and *Iodamoeba*
9
10 163 *buetchlii* were pooled as “medium amoebae”. Host parasite richness was estimated for each
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12 164 faecal sample by the number of different species/morphotypes recorded. We assumed that
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15 165 when species/morphotypes were present we were able to detect them, but some false
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17 166 negatives may have occurred if a species was harder to detect when its intensity of infection
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20 167 or reproductive output were lower.
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24 169 **Population-level environmental conditions (H1-H2)**

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26 170 Rainfall was monitored on a daily basis. Similarly, maximal temperatures (Tmax) in
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29 171 the shade were recorded on a daily basis and were available for 179 days (78 % of the study
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31 172 period). Tmax varied across the study period (maximal mean \pm SD = 31.9 ± 4.8 , range = [20-
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33 173 41]), with maximal values during summer (December) and minimal values in winter (July) in
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35
36 174 both years. Minimal and maximal daily temperatures were strongly correlated (Pearson’s
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38 175 correlations: $\rho = 0.71$, $n = 283$, $P < 2 \cdot 10^{-16}$), so only Tmax was used here.
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43 177 **Group-level range productivity and ranging behavior (H3-H4)**

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45 178 Group location waypoints were taken at half-hour intervals over at least 100 full-day
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48 179 follows for each group conducted between May and November, thus covering periods of both
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50 180 high and low plant productivity in the late austral summer and winter. Minimum convex
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52 181 polygons (Heupel et al. 2004), were constructed around these waypoints in ArcMap Version
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55 182 9.3 using HawthTools extension package (<http://www.spatial ecology.com/htools/>) to provide
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57 183 a simple estimation of the home range boundaries over the study period. Within the home
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60 184 ranges, plant production was estimated using the Normalized Difference Vegetation Index

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3 185 (NDVI: Pettorelli et al. 2011): a satellite-based vegetation index based on the information
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5 186 collected by the Satellite Pour l'Observation de la Terre-Vegetation (SPOT VGT). NDVI is
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7
8 187 derived from the red to the near-infrared reflectance ratio [NDVI = (NIR-RED)/(NIR+RED)],
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10 188 where NIR and RED are the amounts of near-infrared and red light, respectively, reflected by
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12 189 the vegetation and captured by the satellite sensor (Jensen 2006). We use a spatial resolution
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14 190 of 1×1 km available at 10-day intervals in each troop's home range (J and L). The home range
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16 191 boundaries were also used to determine the monthly home range size for each group (J:
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18 192 mean± SD= 12.3± 6.5 km², range = [5-27], L: 26.8 ± 13.5 km², [8-49]), while the waypoint
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20 193 locations were also converted into paths to measure daily travel distance for 208 days (92% of
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22 194 the study period) (J: mean ± SD = 5.9 ± 0.8, range = [5.2-8.0], L: 5.9 ± 1.5, [2.6-7.3]). In the
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24 195 analyses, we use the mean daily travel distance per month.
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197 **Individual traits (H5-H8)**

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34 198 We investigated the influence of age, sex, body condition, and dominance rank on
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36 199 parasite richness. Age and condition were determined through individual inspection during
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38 200 troop captures: in J troop, 42 individuals (of 52) were captured in July 2005 and 55 (of 57) in
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40 201 October 2006, in L troop 32 individuals (of 32) were captured in October 2006. Briefly,
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42 202 troops were captured using individual cages baited with corn cobs and set-up at dusk. The
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44 203 baboons were captured at dawn, anaesthetised using tiletamine-zolazepam, and all processed
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46 204 within a day to be released together the following morning when fully awake. Age was
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48 205 estimated through dentition: tooth eruption schedules for wild baboons were used to assign
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50 206 age up to the eruption of the molars, while age beyond this point was estimated on the basis of
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52 207 molar wear (Huchard et al. 2009a). Body size was estimated by crown-rump length, measured
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54 208 during capture. Physical condition was measured through morphometric data. Because there
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56 209 is no consensus on the best way to index condition (Green 2001; Lukaski 1987), we used
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3 210 three different measures: (1) body mass, (2) mean skinfold thickness (MST), averaged across
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5 211 the triceps, abdominal, and subscapular regions, and (3) mid upper-arm fat (MUAF), a
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7 212 combination of the triceps skinfold thickness and the mid upper-arm circumference:
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11 213
$$MUAF = \frac{SC}{2} - \frac{\pi S^2}{4}$$

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13

14 214 where S = triceps skinfold thickness and C = upper-arm circumference (Gibson 2005). In
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16 215 order to summarize these three measures into one general index, we conducted a principal
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18 216 component analysis (PCA). This analysis included all data from all individuals across 2005
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20 217 and 2006 for which the three indices were available (49 out of 51 individuals). The
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22 218 contribution of each measure to the first component (estimated through PCA square cosinus)
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24 219 was 0.71, 0.75 and 0.91 for MUAF, MST and body mass, respectively. The first principal
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26 220 component of the PCA accounted for 81 % of the total condition variation, and was then used
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28 221 as the body condition variable in our analyses. The mean time difference between our
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30 222 assessment of parasite richness (i.e. a given faecal sample) and the closest estimate of
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32 223 age/condition (at capture) was 73.4 ± 46.9 days.
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38 224 Sex was determined by visual inspection. To establish dominance ranks, agonistic and
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40 225 approach/avoid interactions (following Smuts 1985) were collected using *ad libitum* and focal
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42 226 observations across the study period (for details see: Huchard et al. 2009b). In order to control
43
44 227 for differences in troop size, an animal's absolute rank is divided by the total number of
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46 228 individuals in the group – thus alpha animals have the smallest rank. Ranks were estimated
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48 229 for sexually mature individuals (females reach sexual maturity around 4 years of age and
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50 230 males around 5 years of age: e.g. Altmann and Alberts 2003).
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54 231 In summary, the data available for each individual variable were as follows: 86
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56 232 individuals (662 samples) for sex, 76 individuals (613 samples) for age, 73 individuals (456
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58 233 samples) for body condition, and 44 individuals (298 samples) for dominance rank.
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3 235 **Statistical analyses**
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5 236 To test the influence of socio-ecological factors on individual parasite richness, we ran five
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7
8 237 sets of Linear Mixed Models (LMMs) with parasite richness as the response variable.
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10 238 Although our response variable was discrete, we used LMMs rather than Generalized Linear
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12 239 Mixed Models (GLMMs) due to the need to incorporate temporal autocorrelation in the
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15 240 analysis (see below) which is so far only possible using LMMs fitted with a Gaussian
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17 241 distribution (Pinheiro and Bates 2000). The residuals of all models were constant and normally
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19
20 242 distributed as checked by Q-Q plots and Shapiro-Wilk normality tests ($P > 0.05$ in all
21
22 243 models). However, we also ran our models using GLMMs with a Poisson distribution (but
23
24
25 244 without the autocorrelation term) and obtained the same results. All models tested include
26
27 245 “baboon identity” nested in “troop membership” as random effects, to account for the non-
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29 246 independence of multiple data collected from the same individual within a troop. Because
30
31 247 estimations of parasite richness can increase (in a non-linear way) with faecal sample weight
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33
34 248 (Walther et al. 1995), we also controlled in each model for a potential effect of sample weight
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36 249 by introducing it as a fixed factor at the third polynomial degree. This degree was selected
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38
39 250 using an information theoretic approach: briefly, for each of the five models presented below,
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41 251 we initially compared the Akaike Information Criterion (AIC) scores of three alternative
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43 252 models with faecal sample weight fitted at the first, second and third order, and found that the
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46 253 latter consistently performed best (i.e. presented an AIC score at least two points lower than
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48 254 the alternative models). This third order relationship was further confirmed graphically by an
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51 255 asymptotic curve linking parasite richness to faecal sample weight. As a final statistical
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53 256 control, we also included the year of sample collection as a fixed effect. However, this was
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55 257 not found to be significant in any model examined and was therefore excluded in the final set
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57
58 258 of analyses, for simplicity.
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3 259 The first set of analyses occurred in three successive stages, exploring the effects of
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5
6 260 the different variables at each considered scale (population, group, individual). The first
7
8 261 model was designed to investigate the effect of a population-level factor on host parasite
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10 262 richness, specifically the effects of the maximum daily temperature (Tmax) averaged over the
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12 263 seven-day period during which the individual was sampled (Hypothesis H2; the effects of
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14
15 264 rainfall, Hypothesis H1, were tested independently due to the limited number of rainfall
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17 265 events: see below). We further explored if Tmax collected before the time of faecal collection
18
19
20 266 predicted parasite richness better than contemporary measures by using an additional subset
21
22 267 of lagged models for Tmax. These models included maximum daily temperature averaged
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24 268 across the seven-day period occurring one, two, three, four or five weeks before the sampling
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26
27 269 date, compared by AIC and the Tmax p-value. The model including Tmax averaged four
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29 270 weeks before sampling performed best (see Supporting Information Table S1), and was
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31 271 therefore used in further analyses (the global model).

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33
34 272 The second model was designed to investigate the group-level effects of home range
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36 273 productivity (H3) and ranging behavior (H4.a,b) on host parasite richness. Therefore, it
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38 274 included home range NDVI, home range area, and daily travel distances as fixed effects. As
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40
41 275 for Tmax, we also tested the NDVI measure lagged for 10, 20 and 30 days before sampling
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43 276 (as NDVI data were available for 10 days intervals), but found that contemporary NDVI
44
45 277 performed best (see Supporting Information Table S2).

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47
48 278 The third model was designed to investigate the first three of our four individual-level
49
50 279 effects, namely age (H5), sex (H6), and body condition (H7), on host parasite richness. These
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52 280 variables were all included as fixed effects in the same model. Age was introduced at the third
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54
55 281 polynomial degree to account for a potential non-linear effect, which was suggested by
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57 282 graphical exploration of the raw data and by a model AIC score 2 points lower than the
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59 283 alternative models (i.e. with first or second polynomial degrees). Crown-rump length was

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2
3 284 additionally introduced in the model, to control for body size when investigating condition
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5 285 effects (Jakob et al. 1996). To investigate the effects of our fourth individual-level factor on
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8 286 host parasite richness, namely social rank (H8), we ran the individual-level model again for
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10 287 the subset of animals for whom social ranks were available (N = 44 adults), adding social
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12 288 rank as a fixed effect. We also included a sex*rank interaction term to account for profound
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14
15 289 sex differences in the acquisition of rank in this species (stable and heritable ranks among
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17 290 females; fluctuating ranks determined by fighting ability among males).

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20 291 Following our analyses of the factors determining host parasite richness at each of the
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22 292 three spatial scales, we ran a final model to integrate our findings and to explore the relative
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24 293 importance of each of these factors across scales. This global model included all the variables
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26 294 that were found to be significant in the single-scale models, and was run using the full sample
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28
29 295 (juveniles and adults). In order to compare the effect sizes of each variable in this global
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31 296 model, all variables were standardized to have a mean of zero and a standard deviation of one.
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33
34 297 In each model, we controlled for the temporal dependence of observations (i.e. temporal
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36 298 autocorrelation) by including a temporal correlation structure of the residuals. We compared
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38 299 the AIC of models having an autoregressive structure of order 1 to 7 (i.e. 1 to 7 lags of
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40 300 dependence between observations). In all the model sets described above, the final model
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43 301 with order 5 obtained the lowest AIC and was therefore selected. This was implemented using
44
45 302 the correlation structure corARMA (Pinheiro and Bates 2000) in the nlme package of R 2.8.0
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47
48 303 (R Development Core Team, 2003). The significance of fixed effects was evaluated using F-
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50 304 tests according to the principle of marginality, testing each fixed effect coefficient when all
51
52 305 other fixed effects are present in the model. Statistical significance is reported for full models
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54
55 306 (i.e. inferences were drawn with all predictors present) throughout (Mundry and Nunn 2009;
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57 307 Whittingham et al. 2006). The significance of random effects was tested by performing
58
59 308 likelihood ratio tests (following a χ^2 distribution) comparing two models differing only in the

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2
3 309 presence of this effect. In all models, the random effect “troop identity” did not significantly
4
5 310 affect individual parasite richness (Likelihood Ratio Test, $P > 0.05$) whereas “baboon
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7 311 identity” always had a significant effect (Likelihood Ratio Test, $P < 0.001$).
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RESULTS

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17 315 A total of 11 species or morphotypes of intestinal parasites including five nematodes,
18
19 316 one acanthocephalan and nine protozoan, were found in the faeces of *P. ursinus* at Tsaobis
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21 317 (Table 2). One type of nematode egg, that occurred in 6% of individuals, could not be
22
23 318 identified further (named Egg 1 hereafter). Based on species/morphotype, the median
24
25 319 individual parasite richness was 3.00 (range= 0-8, mean \pm SD= 3.2 ± 1.3).
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32 321 **[Please insert Table 2 here]**33
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323 **Population-level environmental determinants of parasite richness (H1-H2)**

35
36
37 324 Host parasite richness decreased across the dry season (Fig. 1). However, a peak was
38
39 325 observed in November 2005 (median= 4.0; mean \pm SD= 3.8 ± 1.3), 10 days after the first and
40
41 326 only rain recorded in the study period (16mm, 29/10/05). During November, average
42
43 327 individual values of parasite richness were significantly higher than in October 2005
44
45 328 (median= 3.0, mean \pm SD= 2.9 ± 1.1 , Mann-Whitney test: $W = 1345.5$, $n = 86$ individuals, $P =$
46
47 329 0.002), supporting our hypothesis that parasite richness increases after rainfall (H1). This
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49 330 difference was driven by protozoans (analyses excluding protozoans: $W = 3435$, $n = 86$, $P =$
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51 331 0.25).
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3 332 The best temperature predictor was Tmax averaged across the fourth week preceding
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5 333 the sampling date (Table 3, Table S1), suggesting a lagged response of parasite richness.
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7
8 334 Thus, host parasite richness was higher following hot weather four weeks earlier (Fig. 2).
9

10 335 11 12 336 **Group-level ranging determinants of parasite richness (H3-H4)**

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14
15 337 Host parasite richness increased when groups travelled further, as predicted by
16
17 338 hypothesis H4.b. In contrast, there was no effect of home range NDVI (H3, for either
18
19 339 contemporary or lagged measures, Table S2) or home range area (H4.a) (Table 3).
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22 340 23 24 341 **Individual-level trait determinants of parasite richness (H5-H8)**

25
26 342 Across all individuals, host age, sex, and body condition (together with body size,
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28 343 included as a control variable for condition) influenced host parasite richness (Table 3). Host
29
30 344 parasite richness initially increases with age (supporting H5.a), but then peaks around sexual
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32 345 maturity, following which it declines (supporting H5.b) (Fig. 3). The sex effect indicated that
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34 346 parasite richness was higher in females than in males (contrary to H6), while the condition
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36 347 effect suggested that animals in better condition exhibited lower parasite richness (in support
37
38 348 of H7.b) (Table 3, Fig. 4). Among adults only, we found no evidence that dominance rank
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40 349 affected parasite richness (failing to support H8), while the effects of age and sex were no
41
42 350 longer significant ($P > 0.05$ in each case). The age effect remained non-significant when age
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44 351 was included at the first or second order (instead of the third) in this last model (after sexual
45
46 352 maturity, the relationship between age and parasite richness appears roughly linear, Fig. 3).
47
48 353 However, adults in better condition still exhibited lower parasite richness than those in poor
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50 354 condition ($F = 4.43$, $P = 0.03$).
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60 356 **[Please insert Table 3 here]**

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5 358**Integrated global model for multiple-scale effects on parasite richness**6
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23 367**[Please insert Table 4 here]**24
25 36826
27 369**DISCUSSION**28
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Identifying the determinants of multiple parasite infections in wild animals is crucial for both fundamental and applied, conservation-based, reasons, since they may represent important drivers of both evolutionary change and population dynamics. However, there are surprisingly few studies of the drivers of parasite richness in wild populations (Tompkins et al. 2010), and most of these have worked at a single spatial scale. In this study, we found that gut parasite richness in a wild primate population increases with higher rainfall and maximum daily temperature at the population level, and with longer daily travel distances at the group level, as well as showing more complex covariation with age, sex, and body condition at the individual level. These findings, and how they compare to previous studies on parasite richness in wild populations, are summarised in Table 5. Finally, integrating our analyses

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3 381 across the three scales of population, group, and individual, suggests that host age is the
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5 382 primary predictor of parasite richness.
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10 384 **[Please insert Table 5 here]**
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15 386 At the population level, we observed significant effects of rainfall and maximum daily
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17 387 temperature on host parasite richness, indicating an important influence of climatic conditions
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19 388 on parasite encounter rates. The increase in water-borne protozoan parasites associated with
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21 389 rainfall represents a preliminary result since it is based on only a single rainfall event.
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23 390 Nevertheless, it provides circumstantial evidence that precipitation can increase parasite
24
25 391 richness on a short timescale (H1). Parasite richness also increased following a period of hot
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27 392 weather but with a four-week lag (H2). The mechanisms linking temperature to gastro-
28
29 393 intestinal parasite prevalence have been extensively studied, with several species of helminths
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31 394 requiring a minimum temperature for development (Boag 1985), having shorter generation
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33 395 times at relatively high temperatures, and/or producing more intermediate stages in their life
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35 396 cycle when temperature increases (Pietroock and Marcogliese 2003). Protozoan taxa are
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37 397 similarly affected, commonly displaying higher reproductive rates at higher temperatures
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39 398 (Rodriguez-Zaragoza 1994). The lagged response most likely reflects the cumulative time
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41 399 required by the free-living stages of parasites to react to environmental variation and for the
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43 400 host to be exposed to, and contaminated by, the growing populations of infectious parasitic
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45 401 forms.
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48 402 At the group level, we found that longer daily travel distances (H4.b) but not larger
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50 403 home ranges (H4.a) were associated with higher host parasite richness. This supports the idea
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52 404 that more intensive movement patterns within a relatively stable home range, rather than
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54 405 variation in the home range area itself, are associated with increased parasite exposure and
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3 406 subsequent infection with parasites that accumulate in the environment and mature in the host
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5 407 to produce ova (Nunn and Altizer 2006). The lack of association between home range NDVI
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7 408 and parasite richness (H3) further suggests that group-level changes in parasite encounter
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9 409 rates primarily result from the group's behavioral response to environmental variation rather
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11 410 than fluctuations in the density of infectious parasite stages, i.e. the baboons encounter more
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13 411 parasites because their groups are travelling further, not because there are more parasites to
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15 412 encounter per unit distance travelled.

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19 413 At the individual level, we found co-variation between parasite richness and age, sex
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21 414 and body condition. Previous research on the age-parasite richness relationship (H5) has
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23 415 produced inconsistent results when assuming a linear pattern (Table 5). Our finding of a non-
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25 416 linear relationship, positive before sexual maturity but negative afterwards, might help to
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27 417 explain these inconsistencies – and reflect a combined effect of both encounter and infection
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29 418 probabilities. In the first case, the positive part of the curve might reflect cumulative exposure
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31 419 to parasites if the probability of encountering new parasite species is constant over time
32
33 420 (Nunn and Altizer 2006). This would suggest a relatively slow rate of acquisition of new
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35 421 infections by young animals in this population. In the second case, the negative part of the
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37 422 curve, exhibiting a weaker slope, might reflect an improved adaptive immune response
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39 423 following repeated exposures to parasites (Hudson and Dobson 1997) and/or better
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41 424 survivorship of those individuals possessing stronger immune defenses against multiple
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43 425 infections. This hypothesis is supported by a recent study in this same population, where
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45 426 MHC heterozygotes (class II *Mhc*-DRB region) appeared to show higher survivorship
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47 427 (Huchard et al. 2010). Heterozygosity at MHC class II loci has already been found to mediate
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49 428 individual parasite richness in natural populations (Goüy de Bellocq et al. 2008; Oliver et al.
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51 429 2009). Multiple infections might thus constitute the selective pressure increasing the mortality
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53 430 rate of individuals with low MHC diversity, if they display limited ability to fight multiple
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3 431 parasites, as previously found in fish hosts (Simkova et al. 2006). Notably, a recent
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5 432 comparative primate study found that parasitic nematode richness associated positively with
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8 433 the nonsynonymous nucleotide substitution rate at the functional part of the MHC molecule,
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10 434 but not with MHC allelic diversity (Garamszegi and Nunn 2011). It is also possible that the
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12 435 weaker relationship linking age to parasite richness after sexual maturity might at least
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15 436 partially reflect the stabilization of individual parasite communities when they have reached a
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17 437 given threshold, mediated through competitive interactions among multiple co-infecting
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19 438 parasites (decreasing the probability of subsequent infection by additional parasite species)
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22 439 (Graham 2008).

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24 440 We also found that females harbour more parasite species than males (H6). Although
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26 441 males are generally found to be more susceptible to parasitism than females (e.g. Klein 2004),
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28 442 results from primate field studies have been less consistent, with several reported cases of
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30 443 female-biased parasitism (e.g. Clough et al. 2010; reviewed in Nunn and Altizer 2006). In this
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32 444 case, there is no reason to expect female baboons to have a higher probability of encounter
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34 445 with parasites than males, so the most likely explanation for this difference is that females
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36 446 have a higher susceptibility to infection. One possibility is a social effect, given that all adult
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38 447 males outrank all adult females, but the lack of a sex*rank interaction does not support this.
39
40 448 Alternative explanations may relate to the costs of reproduction in females, including the
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42 449 production of exaggerated sexual swellings when cycling and the nutritional stress associated
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44 450 with pregnancy and lactation, or to complex interactions between sex hormones and immune
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46 451 status. A recent field study in lemurs reported immune-enhancing effects of testosterone on
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48 452 parasite species richness, suggesting that differences in immune responses due to sex steroids
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50 453 might potentially lead to female-biased parasitism, at least in the case of host parasite richness
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52 454 (Clough et al. 2010).
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3 455 Parasite richness was higher in poor-condition animals (H7.b) but there was no
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6 456 evidence that dominant animals carried more or fewer parasite taxa (H8). Our findings for the
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8 457 effects of physical condition corroborate the results of the one previous study to date that has
9
10 458 also explored this relationship (Lello et al. 2005). The negative association between body
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12 459 condition and parasite richness suggests a role of infection rather than encounter probability,
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15 460 but the direction of the causal arrow remains uncertain: while poor condition might reflect a
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17 461 host's weak capacity to fight parasites on the one hand, it's also possible that the deleterious
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19 462 effects of multiple infections could lead to poor condition on the other. In the latter case,
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21
22 463 although most of the parasites reported here are not thought to be highly pathogenic, some
23
24 464 might still impact baboon health (Ruch 1959). The amoeba *E. histolytica* can cause severe
25
26 465 diarrheal and dysenteric diseases, and affect the liver, lungs, brain, and other areas; while
27
28 466 others like *B. coli* can become pathogenic if the host's natural resistance is depleted by a poor
29
30 467 diet (Ruch 1959). Whatever the causal direction, the observed association may help to explain
31
32 468 why females in better condition in this population display a higher reproductive success
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34 469 (Huchard et al. 2009b). Our lack of rank effect was in contrast to theoretical expectations but
35
36 470 consistent with most previous empirical studies in primates (Table 5), and may reflect
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38 471 confounding co-variation between rank and condition.
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43 472 When focusing solely on adults, body condition remained the only individual trait
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45 473 influencing parasite richness. In comparison with the full model including juveniles, the
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47 474 disappearance of both age and sex effects reflects either decreased statistical power arising
48
49 475 from a smaller sample, or a weaker influence of such traits after sexual maturity. The latter
50
51 476 hypothesis is plausible in the case of age, since the slope of the relationship linking age to
52
53 477 parasite richness weakens in adulthood (Fig. 3), but seems counter-intuitive in the effect of
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55 478 sex, which is usually reinforced among sexually mature individuals. Given that sex ratios are
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57 479 relatively balanced in both our full and restricted sample, the disappearance of this effect
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3 480 among adults might reflect a genuine pattern. Post-hoc interpretation is necessarily
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5 481 speculative, but could involve parental investment or maternal effects preferentially biased
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8 482 towards male offspring, which might translate into improved parasite resistance in early life
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10 483 (Hayward et al. 2010) - although the hypothesis of sex-biased maternal investment has not
11
12 484 been strongly supported by empirical studies of non-human primates so far (Bercovitch 2002;
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14
15 485 Brown 2001).

16
17 486 The final global model integrating variables across scales largely confirmed the results
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19 487 obtained within scales (all variables previously found to be significant in their respective
20
21 488 single-scale models remained significant in the multi-scale model), but also emphasized the
22
23 489 importance of working at multiple ecological scales. Comparing the effect sizes of each
24
25 490 variable in the global model suggests that the individual-level factors have a higher influence
26
27 491 on patterns of variation in parasite richness than population- or group-level factors. In fact,
28
29 492 age had by far the biggest effect on parasite richness, followed by sex and body condition, and
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31 493 finally by maximal daily temperature and daily travel distance. As such, the global model
32
33 494 suggests that, while variation in encounter probability at both the population and group level
34
35 495 do influence host parasite richness, the strongest effects are related to both encounter and
36
37 496 infection probabilities at the individual level. Two areas of uncertainty in this interpretation
38
39 497 should be highlighted. First, due to the difficulties involved in working at wider spatial scales
40
41 498 with large social vertebrates, our sample of groups and populations is necessarily small.
42
43 499 Similarly, we only sample one season (the dry winter season) over two years, and it is
44
45 500 possible that in other seasons and/or years different patterns would be obtained. Extrapolation
46
47 501 of our conclusion (that individual-level processes play the predominant role) beyond the
48
49 502 sample and conditions investigated here should therefore be made with caution. Second,
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51 503 estimation of the relative importance of encounter and infection probabilities at the individual
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53 504 level is challenging. On the one hand, the effects of body condition (and probably sex)

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3 505 emphasize the importance of susceptibility to infection at the individual level. On the other,
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5 506 the age effect includes both encounter and susceptibility to infection, with the former having
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7 507 the strongest effect (since the negative relationship between age and parasite richness after
8
9 508 maturity is relatively weak). While neither of these uncertainties can be fully resolved here,
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11 509 they do help to highlight those areas that might be prioritized for further research.
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15 510 In conclusion, these findings demonstrate that host parasite richness in animal
16
17 511 populations may be associated with a range of factors operating on multiple scales. In this
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19 512 case, parasite richness is highest in poor-condition females at the time of sexual maturity,
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21 513 when their social group is travelling longer daily distances, and when environmental
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23 514 conditions are characterized by high rainfall and temperature. This study also suggests that
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25 515 individual traits, acting through both encounter and infection rates, can have a higher impact
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27 516 on parasite richness than group- or population-level factors acting through encounter rates
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29 517 alone. Our results emphasise the value of integrative approaches based on the longitudinal
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31 518 sampling of known animals in well-documented ecological contexts, and suggests that such a
32
33 519 design can provide unique insights into the relative importance of different factors shaping
34
35 520 host parasite richness and its impact in wild populations.
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41 521

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4
5
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7
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Table 1. Potential factors influencing host parasite richness explored in this study. Factors are grouped by the scale at which they operate (population, group, and individual). Further information is also provided on the proposed mechanism (whether each factor is more likely to influence parasite richness through the probability of parasite encounter or susceptibility to infection following encounter). The positive effect of a considered factor is noted (+), and a negative effect is noted (-).

Scale	Factor	Hypotheses under test	
Population	Rainfall	H1	(+) encounter probability ~ due to the accelerated development, replication or survival of parasites in wetter conditions (Nunn and Altizer, 2006).
	Temperature	H2	(+) encounter probability ~ due to the accelerated development, replication or survival of parasites in hotter conditions (Nunn and Altizer, 2006).
Group	Home range productivity	H3	(+) encounter probability ~ because vegetation can be a surrogate measure of environmental moisture and thermal conditions for parasites (Bavia et al., 2001) or can represent a breeding or sheltering site for parasites (Ceccato et al., 2005; Lindsay et al., 1991)
	Ranging behavior	H4.a	Home range size: (+) encounter probability ~ due to an increased probability of encounters with parasites in a larger home range (Nunn and Altizer, 2006).
		H4.b	Daily travel distance: (+) encounter probability ~ due to an increased probability of encounters with parasites in a more intensively used home range (Nunn and Altizer, 2006).
Individual	Age	H5.a	(+) encounter probability ~ due to an accumulation of parasites in older individuals resulting from a stable probability of encounters with new parasites over time (Nunn and Altizer, 2006)
		H5.b	(-) susceptibility to infection ~ due to a reinforced immunity in older individuals following repeated contacts with multiple parasites (Hudson and Dobson, 1997)

Sex	H6	(+ males) encounter probability ~ higher parasite richness in males due to higher consumption of food and thus more opportunity to eat contaminated items (Nunn and Altizer, 2006) ⁶
		(+ males) susceptibility to infection ~ higher parasite richness in males (Zuk and McKean, 1996), due to immunosuppression typically resulting from elevated testosterone levels (Roberts et al., 2004)
Physical condition	H7.a	(+) exposure probability ~ animals that eat more are in better physical condition but also have more opportunity to eat contaminated items (Nunn and Altizer, 2006)
	H7.b	(-) susceptibility to infection ~ due to a better ability to resist infections for animals in good physical condition (Irvine et al., 2006)
Social rank ¹	H8.a	(+) encounter probability ~ higher parasite richness in dominant individuals due to higher consumption of food and thus more opportunity to eat contaminated items (Nunn and Altizer, 2006)
	H8.b	(-) susceptibility to infection ~ higher parasite richness in subordinate individuals due to stress compromising immunocompetence (Nunn and Altizer, 2006)

¹ Here assuming high social rank for dominant individuals, low social rank for subordinates

Table 2. Individual patterns of parasite infection (662 samples, 86 individuals), with species/morphotypes ordered by prevalence. The “Medium Amoebae” category includes *E. histolytica*, *E. dispar* and *I. buetchlii*. The “Small Amoebae” category includes *E. hartmanni*, *E. nana*, and *D. fragilis*. “Egg 1” corresponds to an unidentified nematode species. For nematodes, the median and range of intensity of infection is expressed in egg per gram. For protozoans, the intensity of infection is expressed as a score on a 5-point semi-quantitative scale (0-4). Parasite prevalence is expressed as the number of individuals infected by a given parasite species (or category in the case of medium and small amoebae) divided by the total number of individuals, and is given in percentage.

Species	Median	Range	Prevalence (%)	Parasite phylum
<i>Streptopharagus pigmentatus</i>	153.4	0.0-4431.5	77.5	Nematode
<i>Entamoeba coli</i>	1.6	0.0-3.0	77.1	Amoeboid
<i>Balantidium coli</i>	1.3	0.0-4.0	66.6	Ciliate
Small-sized amoebae	0.4	0.0-3.0	30.3	Amoeboid
<i>Chilomastix mesnili</i>	0.3	0.0-1.7	23.1	Flagellate
Medium-sized amoebae	0.5	0.0-2.0	21.9	Amoeboid
<i>Physaloptera caucasia</i>	0.0	0.0-464.5	14.6	Nematode
Unidentified species (Egg1)	0.0	0.0-30.7	5.8	Nematode
<i>Ascaris sp.</i>	0.0	0.0-81	0.02	Nematode
<i>Subulura sp.</i>	0.0	0.0-98	0.01	Nematode
<i>Macracanthorhynchus hirudinaceus</i>	0.0	0.0-1	0.01	Acanthocephalan

Table 3. Influence of environmental factors, ranging behavior, and individual traits on individual baboon parasite richness. Each model represents a different scale: population-level factors (524 samples, 82 individuals, AIC=1685.28), group-level factors (599 samples, 86 individuals, AIC=1955.47) and individual-level factors (456 samples, 73 individuals, AIC=1437.07).

Model	Variables	Estimate	SE	F-value	df	P-value
Population level	Sample weight ³	2.06	1.17	3.16	3	0.03
	Tmax ¹	4.83	1.73	7.75	1	<0.01
Group level	Sample weight ³	2.20	1.19	3.02	3	0.03
	Home range NDVI	3.31	4.28	0.6	1	0.44
	Home range area	-0.01	0.01	1.44	1	0.23
	Travel distance	0.28	0.07	15.95	1	<0.001
Individual level	Sample weight ³	3.30	1.06	4.32	3	<0.01
	Age ³	3.45	1.58	2.85	3	0.03
	Sex ²	-0.53	0.19	7.5	1	<0.01
	Body condition	-0.18	-0.08	5.08	1	0.02
	Body size	0.01	0.01	4.45	1	0.04

¹ Daily maximum temperature is averaged over the seven-days occurring four weeks before sample collection (see results)

² The reference category for sex is female.

Table 4. Multiple-scale influences on baboon parasite richness (386 samples, 72 individuals, AIC= 1170.02). All variables were standardised (mean of zero, standard deviation of one) and are ordered by their effect size.

Variables	Estimate	SE	F-value	df	P-value
Age ³	3.92	1.46	4.41	3	<0.01
Sample weight ³	2.75	1.03	5.79	3	<0.001
Body size	0.48	0.19	6.24	1	0.01
Sex ¹	-0.47	0.19	5.97	1	0.02
Body condition	-0.43	0.13	11.22	1	<0.001
Tmax (with four-week lag) ²	0.22	1.07	5.79	1	<0.01
Travel distance	0.21	0.06	10.56	1	0.001

¹ The reference category for sex is female.

² Daily maximum temperature is averaged over the seven-days occurring four weeks before sample collection (see results)

Table 5. Evidence from previous empirical studies. Previous studies in captivity, or studies examining other parasitic measures such as prevalence or load, are not reported here. The positive effect of a considered factor is noted (+), a negative effect is noted (-), and no effect is noted by (0).

Scale	Factor	Evidence from previous empirical studies	This study
Population	Rainfall	(+) comparative studies: bacteria across human populations (Guernier et al., 2004); gamasid mites across small mammals (Krasnov et al., 2008) (0) field study of helminths in red foxes (Barbosa et al., 2005)	(+)
	Temperature	(+) comparative study of fungi in French forest (Vacher et al., 2008); field study of helminthes in red-legged partridge (Calvete, 2003) (0) comparative studies: all parasite types in humans at large geographical scale (Guernier et al., 2004); endo- and ectoparasites in fish (Rohde and Heap, 1998); field study of helminthes in red foxes (Barbosa et al., 2005)	(+)
Group	Home range productivity	No previous studies	0
	Home range size	(0) comparative study of gut parasites in mammals (Watve and Sukumar, 1995) (-) comparative study of helminths in mammals (Bordes et al., 2009)	0
	Daily travel distance	(+) comparative study of helminths in primates (Nunn and Dokey, 2006); field study of chigger infections in California meadow mice (Mohr and Stumpf, 1964)	(+)
Individual	Age	(+) Longevity: comparative studies of Protozoans across primates (Nunn et al., 2003); ectoparasites across Pericidae fish (Ranta, 1992); helminths across freshwater fish (Bell and Burt, 1991); field study of endo- and ectoparasites in coral-reef fish (Lo et al., 1998) (0) Longevity: comparative study of ectoparasites across cyprinid fish (Simkova et al., 2006); field studies of gut parasites: red-fronted lemurs (Clough et al., 2010); mandrills (Setchell et al., 2007); chimpanzees (Muehlenbein, 2005) (-) Longevity: comparative study of helminths across mammals (Morand and Harvey, 2000)	Polynomial relationship with (+) effect before sexual maturity and a (-) effect for adults
	Sex	(+ males) comparative study: ectoparasites in small mammals (Morand et al., 2004); field study of fleas in desert rodents (Krasnov et al., 2005) (+ females) field studies: fleas in rodent <i>Acromys russatus</i> (Krasnov et al., 2005); lice in neotropical birds (Clayton et al., 1992) (0) No bias: field study of gut parasites in red-fronted lemurs (Clough et al., 2010)	(+ females)
	Physical condition	(-) field study of helminths of the wild rabbit (Lello et al., 2005)	(-)
	Social rank ¹	(+) field study of gut parasites in chimpanzees (Muehlenbein, 2005) but analyses not shown. (0) field studies: gut parasites in ursine colobus (Teichroeb et al., 2009); red-fronted lemurs (Clough et al., 2010); mandrills (Setchell et al., 2007)	0

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¹ Here assuming high social rank for dominant individuals, low social rank for subordinates

Figure legends

Fig. 1. Temporal variation of parasite richness during the study period. Monthly variation in parasite richness for the 2005 and 2006 study periods (means and standard errors) are displayed in the top panel. Monthly parasite prevalence (expressed as a fraction of total individuals) for each parasite species or morphotype for the 2005 study period are displayed on the bottom panel.

Fig. 2. Relationship between host parasite richness and daily maximum temperature (T_{max}), averaged over the seven-days occurring four weeks before sample collection. The means and standard errors of T_{max} for each parasite richness score are shown.

Fig. 3. Relationship between host parasite richness and age. Circles represent the mean parasite richness for an individual. The fitted line was drawn using a locally weighted polynomial regression (Cleveland, 1979) with the `lowess` command in R 2.8.0 (R Development Core Team, 2003).

Fig. 4. Relationship between host parasite richness and physical condition. The means and standard errors of physical condition for each parasite richness score are shown.

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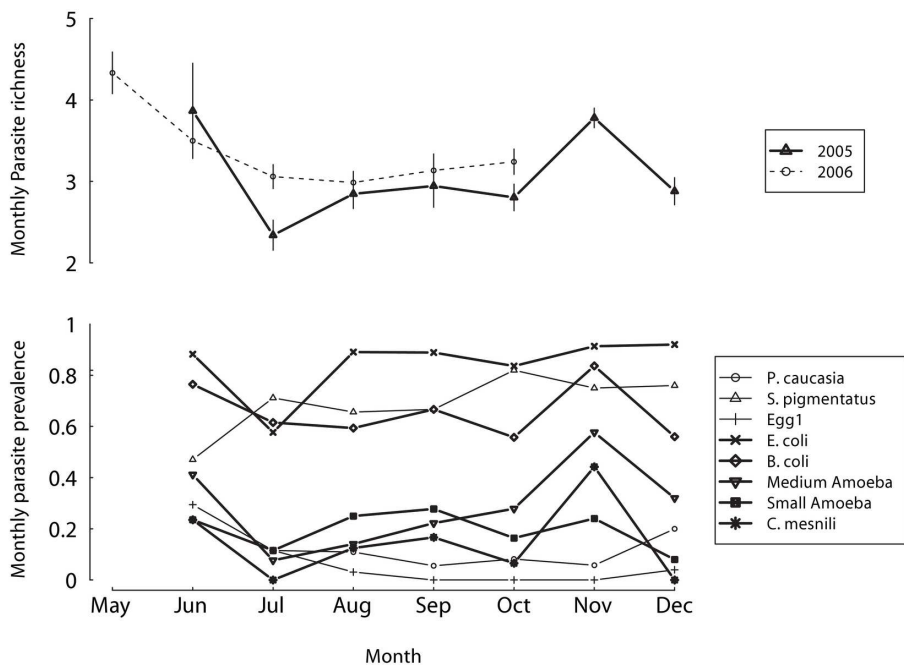


Fig1
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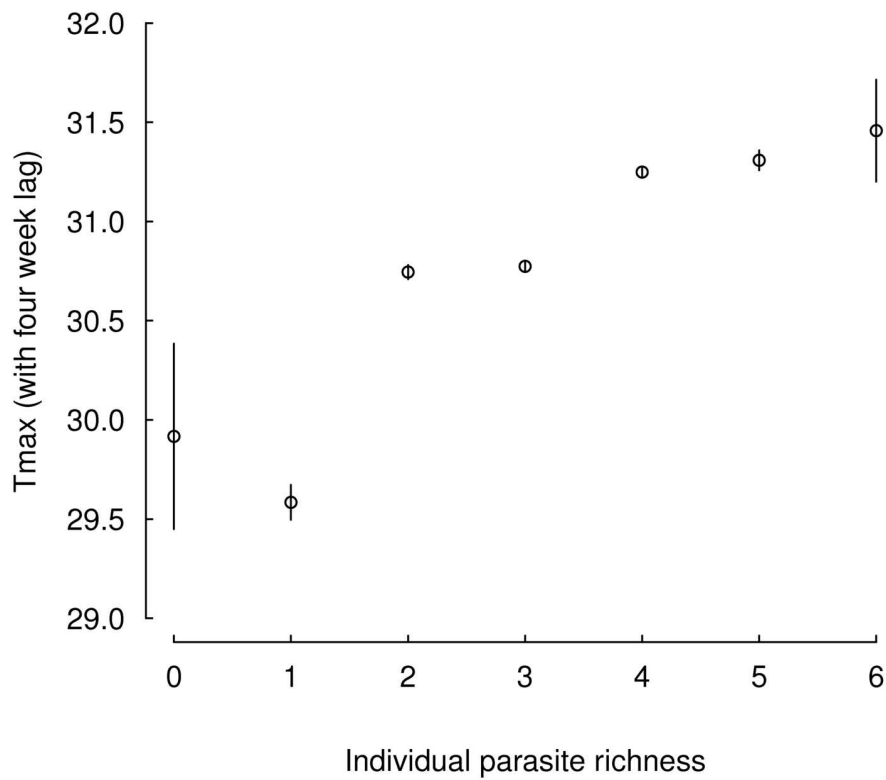


Fig2
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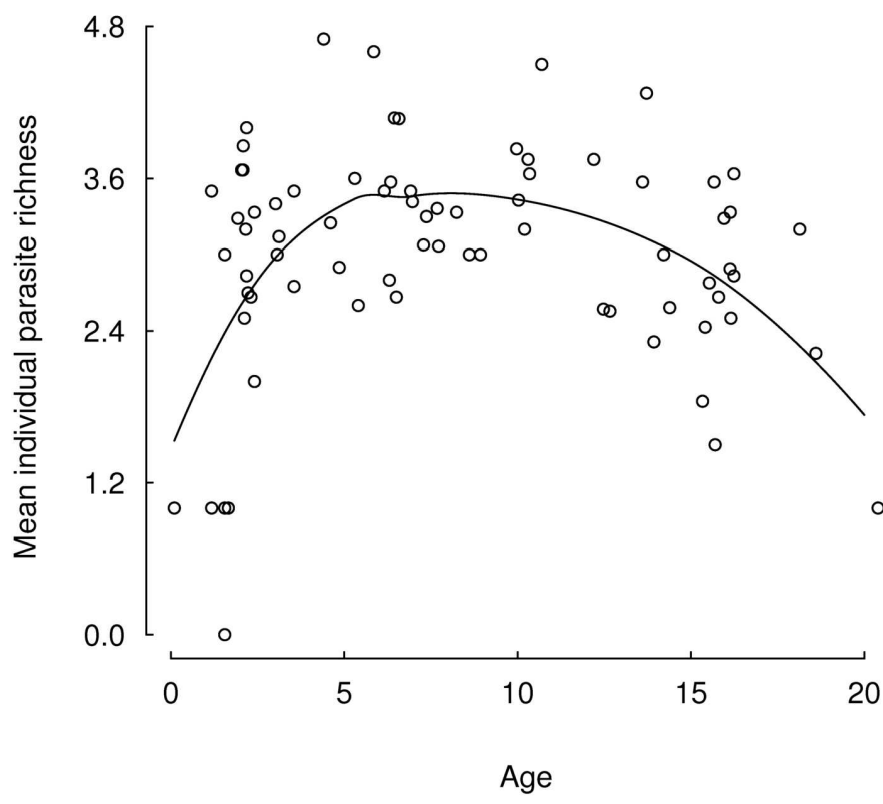


Fig3
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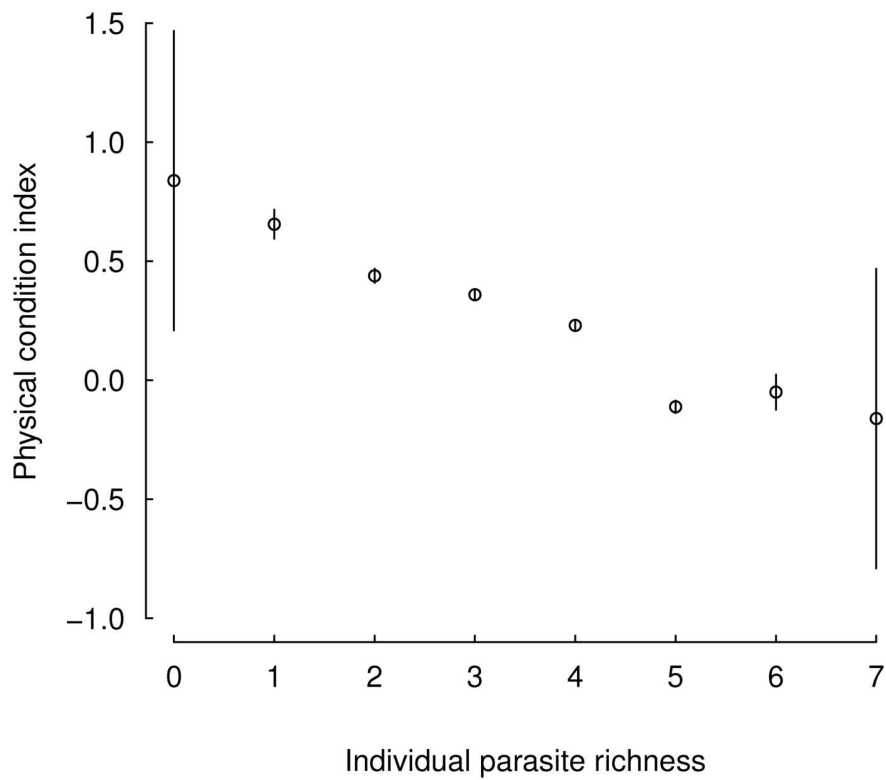


Fig4
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