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4 Social contact behaviors are associated with infection status for whipworm (*Trichuris* sp.)
5 in wild vervet monkeys (*Chlorocebus pygerythrus*)

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40 **Abstract**

41 Social grooming in the animal kingdom is common and serves several functions,
42 from removing ectoparasites to maintaining social bonds between conspecifics. We
43 examined whether time spent grooming with others in a highly social mammal species
44 was associated with infection status for gastrointestinal parasites. Of six parasites
45 detected, one (*Trichuris* sp.) was associated with social grooming behaviors, but more
46 specifically with direct physical contact with others. Individuals infected with *Trichuris*
47 sp. spent significantly less time grooming conspecifics than those not infected, and time
48 in direct contact with others was the major predictor of infection status. One model
49 correctly predicted infection status for *Trichuris* sp. with a reliability of 95.17% overall
50 when the variables used were time spent in direct contact and time spent grooming
51 others. This decrease in time spent grooming and interacting with others is likely a
52 sickness behavior displayed by individuals with less energy or motivation for non-
53 essential behaviors. This study highlights the need for an understanding of a study
54 population's parasitic infections when attempting to interpret animal behavior.

55

56 **Introduction**

57 Grooming is widespread in the animal kingdom, from insects [1-4] to rodents [5-
58 8], birds [9-13], and primates [14-17]. Grooming is generally classified into two types:
59 self-grooming, in which individuals groom themselves, and social grooming or
60 allogrooming in which individuals groom others or are groomed by others [18]. Both
61 self-grooming and social grooming have hygienic benefits including removal of parasites

62 and debris [19-21], as well as physiological benefits like releasing endorphins and
63 lowering heart rate [22,23]. Social grooming specifically also has social, reproductive,
64 and resource acquisition benefits [24-28]. Grooming with others can also be costly,
65 however, because it may lead to transmission of viruses, bacteria, and other pathogens
66 [29-34]. Studies of rodents [35] and primates [36,37] have even suggested that social
67 grooming may increase likelihood of infection with parasites that are not typically
68 transmitted between hosts.

69 Grooming and sociality in general have an influence on reproductive fitness. For
70 example, social integration (often measured largely by grooming behaviors) was
71 associated with increased reproductive success in feral mares [38]. Social integration was
72 also positively correlated with survival of infants of female savannah baboons (*Papio*
73 *cynocephalus*) [39]. Allopreening was related to an increase in reproductive fitness in
74 common guillemots (*Uria aalge*) [40].

75 Grooming and social contact are known to provide health benefits as well. When
76 horses are groomed on favored body parts, they exhibit reduced heart rates [23]. In a case
77 study of a pigtail macaque (*Macaca* sp.), being groomed by others resulted in a
78 significantly lower heart rate but self-grooming and initiating grooming with others did
79 not [41]. In rhesus macaques (*Macaca mulatta*), being groomed mitigated anxiety
80 regarding a dominant conspecific as revealed by faster heart rate deceleration when being
81 groomed [42]. It is common for individuals to become so relaxed that they fall asleep
82 when being groomed [personal observations]. A study on Barbary macaques (*Macaca*

83 *sylvanus*) suggested that grooming others can reduce stress, as indicated by assessments
84 of fecal glucocorticoids [43].

85 Research supports claims that social grooming can help reduce numbers of
86 ectoparasites, often termed the hygiene hypothesis [14]. In one study of Japanese
87 macaques, researchers concluded that the main function of grooming was to eliminate
88 ectoparasites, specifically lice [19]. Another study revealed that wild savannah baboons
89 (*Papio cynocephalus*) that were groomed more frequently had fewer ticks [44]. Further,
90 research suggests that social grooming may reduce mortality risk from the fungus
91 *Metarhizium anisopliae* among termite hosts (*Zootermopsis angusticollis*) [45].

92 However, this approach does not fully acknowledge the complexity of all host-
93 parasite relationships and the multifaceted relationship between grooming and health.
94 Understanding host-parasite ecology means understanding the complex interplay of a
95 number of factors including distribution of parasites in the environment and likelihood of
96 encountering them, age, sex, physiology, and social behavior [46,47]. Dunbar [25]
97 concluded that the hygiene hypothesis alone could not account for primate social
98 grooming behaviors because a meta-analysis revealed that amount of time spent
99 grooming with others correlated more with group size than with body size across the
100 Order Primates overall. Dunbar's work suggested that social grooming may serve more
101 of a hygienic function among New World monkeys (among whom grooming time
102 correlated more precisely with body weight than group size) while serving more of a
103 social function among Old World monkeys and apes (among whom grooming time
104 correlated more precisely with group size than body weight). Further, some studies have

105 found that parasite loads do not correlate with grooming behaviors. For example,
106 grooming behaviors in the Seychelles warbler (*Acrocephalus sechellensis*) were not
107 correlated with feather mite load [48]. Observers also noted that chacma baboons (*Papio*
108 *ursinus*) did not always remove ticks (*Rhipicephalus* sp.) from partners when grooming
109 with them, even when researchers could see from afar that ticks were engorged [49]. It is
110 also worth noting that tick infestations were estimated to cause over half of known infant
111 deaths among that study population.

112 Some parasites may be more likely to be transmitted when two individuals groom,
113 and it is not uncommon for some types of pathogens, like viruses, to be transmitted
114 through social contact. This is being increasingly acknowledged as societies around the
115 world have dealt with the COVID-19 pandemic, and researchers have noted these
116 connections between social proximity and the spread of infectious disease in both humans
117 and other animal species [50]. Social contact in western lowland gorillas (*Gorilla gorilla*
118 *gorilla*) – largely observed as grooming – was associated with death from the Ebola-Zaire
119 virus in a study population in Congo [30]. One study on meerkats (*Suricata suricatta*)
120 revealed that those who groomed others more frequently were more likely to become
121 infected with tuberculosis (*Mycobacterium bovis*) than those that groomed others less
122 frequently [51]. Social grooming in ants (*Lasius* sp.) resulted in transmission of the
123 potentially pathogenic fungus *Metarhizium anisopliae*, however this ultimately aids in
124 developing immunity to the fungus [52]. Examples like this highlight the complexity of
125 the host-parasite relationship and the need for a more nuanced approach to understanding
126 host-parasite dynamics.

127 Some studies even suggest that grooming may play a role in transmission of
128 macroparasites like nematodes which are not typically considered to be capable of host-
129 to-host transmission. For example, grooming among mice (*Mus* sp.) was associated with
130 infection with the gastrointestinal parasite *Heligmosomoides polygyrus* [35]. Grooming
131 behaviors in vervet monkeys (*Chlorocebus aethiops* [*pygerythrus*]) also varied with
132 infection status with hookworm species [36].

133 Behavioral ecology theory predicts that an adaptation is selected for when the
134 costs of a behavior are exceeded by the benefits. Social grooming presents significant
135 benefits including removal of ectoparasites and debris, increased likelihood of future
136 social support or tolerance, increased likelihood of future mating opportunities, and
137 improved reproductive fitness. However, social grooming also presents significant costs
138 (e.g., increased likelihood of contracting an infectious pathogen leading to death) because
139 of the close contact. While much is known about the benefits of social grooming, much
140 less is known about the costs of it among nonhuman primates.

141 The aim of this study was to determine whether grooming behaviors in a highly
142 social mammal species varied with respect to infection status with gastrointestinal
143 parasites. We examined various dimensions of vervet monkey (*Chlorocebus pygerythrus*)
144 grooming behavior, including time spent grooming others, time spent being groomed by
145 others, and time spent in direct contact with others. We tested fecal samples for
146 gastrointestinal parasites, specifically protozoa and helminths. We then tested whether
147 individuals who were infected with parasites spent similar relative amounts of time
148 grooming and/or receiving grooming from other individuals. We predicted that if social

149 grooming or direct social contact facilitates the transmission of any gastrointestinal
150 parasite species in our study population, then those individuals that spend more time
151 grooming with others should be more likely to exhibit infection with parasites.

152

153 **Materials and methods**

154 **Study site and subjects**

155 Data were collected from three social groups of wild vervet monkeys
156 (*Chlorocebus pygerythrus*) at Loskop Dam Nature Reserve (LDNR), South Africa
157 (Figure 1). LDNR is located in the Olifants River Valley within Mpumalanga and
158 Limpopo provinces (25°25'S, 29°18'E), and is managed by the Mpumalanga Tourism
159 and Parks Agency (MTPA). The reserve is 225 km² and surrounds Lake Loskop, a
160 reservoir of 23.5 km². The reserve encompasses both highveld and bushveld ecological
161 zones, and habitat ranges from open grasslands to dense woodlands [53]. Common
162 woody species throughout the three groups' ranges include a variety of species of
163 *Combretum*, *Acacia*, *Rhus*, *Grewia*, and *Ficus*, as well as *Dichrostachys cinerea*,
164 *Mimusops zeyheri*, and *Olea europa* [54,55]. Altitude in LDNR ranges from 990-1450 m
165 and the reserve exhibits a highly seasonal climate. Annual rainfall during the study was
166 914.5 mm, most of which fell between October and January [2009-2010, LDNR,
167 unpublished. *data*]. Average minimum and maximum temperatures during the study
168 period were 13.5°C and 26.1°C, respectively [2009-2010, LDNR unpublished. *data*;
169 2009-2010, Wren unpublished. *data*].

170 We chose *Chlorocebus pygerythrus* as the study species because individuals
171 exhibit variation in grooming behaviors [56], allowing us to examine differences in the
172 relationship between social behaviors and parasite infection status. Groups of *Ch.*
173 *pygerythrus* in LDNR – and much of the surrounding region – typically vary in size from
174 13-25 individuals [54,55,57]. Six groups of *Ch. pygerythrus* at LDNR are habituated, and
175 researchers have been conducting studies of these groups semi-regularly for more than a
176 decade [58-61]. We collected data from three of the six habituated groups at LDNR:
177 Blesbok group, Donga group, and Bay group. At the commencement of the study there
178 were 14 individuals in the Blesbok group, 16 in the Donga group, and 17 in the Bay
179 group; the total study population fluctuated due to births, migrations, and deaths, and was
180 54 at the conclusion of the study. Here we present data on a total of 55 subjects as well as
181 a subset of 38 of those study subjects. Information on group composition for each social
182 group can be found in Wren [55] and Wren et al. [36,62]. We located groups using
183 known sleeping sites and home ranges. Data were recorded for only the Blesbok group
184 from July – October 2009 because other researchers were studying the Donga and Bay
185 groups during that time. Data were collected from all three social groups for the
186 remainder of the project.

187 **Behavioral data collection**

188 From July 2009 through July 2010 we followed *Ch. pygerythrus* groups and
189 collected observational data [63]. Although most data were collected between 07:00 h
190 and 16:00 h, observations were conducted between 05:00 h and 19:00 h. We performed
191 30-min focal follows on each individual. Some follows were terminated early because

192 monkeys were lost from sight, but we kept data from all follows longer than 5 min. We
193 used continuous recording for all behavioral data [63].

194 We recorded data on the following variables for all bouts of social grooming: start
195 and stop times, whether grooming was given or received, and identity of grooming
196 partner. A grooming bout was considered to be a new bout when any of the following
197 conditions were met: the focal individual stopped grooming or being groomed for 30
198 seconds or more, the direction of grooming switched (i.e., the individual being groomed
199 began grooming its partner or vice versa), or the individual switched grooming partners.
200 We also recorded data on start and stop times for direct physical contact with another
201 individual and identification of direct social contact partners.

202 **Fecal sample collection and analysis**

203 We collected 332 fecal samples non-invasively from identified individuals
204 directly following defecation, and samples were immediately preserved in a 10%
205 buffered formalin solution. We recorded data on the following variables for each sample:
206 date, individual, social group, location (GPS coordinates), consistency and color of feces,
207 and whether adult worms were visible in the stool. Fecal samples varied from
208 approximately 3 to 7 g.

209 We used three methods to detect parasite eggs and cysts in samples in order to
210 reduce the risk of false negatives: fecal flotation, fecal sedimentation, and
211 immunofluorescence microscopy. We isolated helminth eggs and protozoan cysts and
212 oocysts from fecal material using fecal flotation with double centrifugation (at 1800 rpm
213 for 10 min) in NaNO₃ solution and fecal sedimentation with dilute soapy water [64]. We

214 also used immunofluorescence microscopy with a Merifluor *Cryptosporidium/Giardia*
215 Direct Immunofluorescent Detection Kit (Meridian Bioscience Inc., Cincinnati, Ohio,
216 USA) to detect *Cryptosporidium* sp. oocysts and *Giardia* sp. cysts [65]. Parasite eggs
217 and cysts were identified by egg or cyst shape, size, color, and contents for flotation and
218 sedimentations, and measurements of eggs and cysts were taken with an ocular
219 micrometer fitted to a compound microscope. For the immunofluorescence microscopy,
220 we scored fecal samples for the presence or absence of *Cryptosporidium* sp. oocysts and
221 *Giardia* sp. cysts.

222 **Data analysis**

223 Although we collected 511 h of behavioral data and 332 fecal samples from 55
224 individual vervet monkeys, we analyzed 477.66 h of data and 272 fecal samples from 38
225 individuals. Some behavioral data were not used in the final analyses because there were
226 no corresponding fecal samples for some study subjects, and vice versa.

227 We calculated measures of parasite infections following Bush et al. [66]. Richness
228 refers to the number of parasite species detected in a host or group. Prevalence refers to
229 the number of hosts infected with a specific parasite species divided by the number of
230 hosts examined.

231 We used analysis of variance (ANOVA) to examine whether social groups
232 differed by sampling effort, grooming behaviors, or parasite infections. We planned
233 contrasts to compare each group and each combined grouping of groups to identify
234 statistically significant differences in each observed variable. We further explored
235 significant results from the ANOVA using a logistic regression model from calculated z-

236 scores for each independent variable. We set the presence of *Trichuris* sp. as the binary
237 outcome variable with the following observed variables: time observed, total seconds
238 observed, number of grooming partners, number of grooming partners giving grooming,
239 number of grooming partners receiving grooming, number of total contact partners, time
240 spent giving grooming, time spent receiving grooming, time spent self grooming, time in
241 direct contact, and time spent playing.

242 We used GNU PSPP 1.2.0 for all statistical tests. We set the significance level at
243 $p < 0.05$ and considered all tests two-tailed.

244

245 **Ethical note**

246 This study was conducted with approvals from LDNR, MTPA, Applied
247 Behavioural Ecology and Ecosystem Research Unit of the University of South Africa,
248 and Purdue University's Animal Care & Use Committee (approval #07-609). We
249 followed all guidelines for the study of nonhuman primates set forth by the International
250 Primatological Society.

251

252 **Results**

253 **Descriptive statistics**

254 Mean time observed per individual for the entire study sample was 9.3 hours ($n =$
255 55, minimum = 0.18, maximum = 37.04, SD = 8.84). Age of individuals ranged from 1 to
256 11 years ($n = 55$, mean = 4.80, SD = 2.67) at the end of the study, and 42% of subjects
257 were female (35/55) while 64% were male (35/55).

258 For parasitological hypothesis testing, we used a subset of the entire study sample
259 that consisted of 38 individuals from the three social groups. This included only
260 individuals for which both behavioral and parasitological data were available and
261 complete. Mean time observed per individual in this subset used for parasitological
262 hypothesis testing was 12.57 hours ($n = 38$, minimum = 1.343, maximum = 37.04, SD =
263 8.83).

264 Mean number of fecal samples collected per individual was 7.16 ($n = 38$,
265 minimum = 1, maximum = 25, SD = 8.84). For this subset of individuals for which
266 parasitological results were obtained, groups differed significantly in regard to total time
267 observed ($F_{(2,35)} = 28.242, p < 0.001$) and number of fecal samples collected ($F_{(2,35)} =$
268 $27.929, p < 0.001$). Age of individuals ranged from 3 to 11 years ($n = 38$, mean = 5.6,
269 SD = 2.29) at the end of the study, and 42% of subjects were female (16/38) while 58%
270 were male (22/38).

271 **Behavioral results**

272 Mean proportion of time spent grooming others was 5.0% of total time observed
273 ($n = 55$, mean = 0.05, minimum = 0.0, maximum = 0.29, SD = 0.06). (Table 1) Mean
274 proportion of time spent being groomed for the entire study sample was 4.0% of total
275 time observed ($n = 55$, mean = 0.04, minimum = 0.0, maximum = 0.01, SD = 0.03).
276 (Table 2) Social groups did not differ in regard to mean time spent grooming others
277 ($F_{(2,52)} = 0.39, p = 0.677$) or being groomed by others ($F_{(2,52)} = 0.93, p = 0.401$). Time in
278 direct contact, while not grooming, accounted for an average of 20% of the total time
279 observed and did not differ among groups ($F_{(2,52)} = 0.03, p = 0.971$).

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Table 1: Mean percentage of time spent grooming others among vervet monkeys (*Chlorocebus pygerythrus*) at Loskop Dam Nature Reserve, South Africa

	Infected, Mean Time Observed	Not Infected, Mean Time Observed	t-value	P-value
<i>Trichuris</i>	4%	14%	-3.17	0.003
Hookworm	6%	4%	0.87	0.388
Spirurids	5%	6%	-0.90	0.375
<i>Oesophagostomum</i> sp.	4%	9%	-1.74	0.090
<i>Strongyloides</i> sp.	3%	6%	-1.45	0.156
<i>Entamoeba coli</i>	3%	5%	-0.76	0.454

Degrees of freedom = 36 in all cases.

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Table 2: Mean percentage of time spent being groomed among vervet monkeys (*Chlorocebus pygerythrus*) at Loskop Dam Nature Reserve, South Africa

	Infected, Mean Time Observed	Not Infected, Mean Time Observed	t-value	P-value
<i>Trichuris</i> sp.	4%	4%	0.02	0.987
Hookworm	4%	4%	0.80	0.430
Spirurids	4%	4%	-0.39	0.698
<i>Oesophagostomum</i> sp.	4%	5%	-0.69	0.496
<i>Strongyloides</i> sp.	4%	4%	-0.44	0.660
<i>Entamoeba coli</i>	3%	4%	-0.50	0.622

Degrees of freedom = 36 in all cases.

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For the subset of the study sample used in the parasitological hypothesis testing, mean proportion of time spent being groomed was also 4.0% of total time observed ($n = 38$, mean = 0.04, minimum = 0.0, maximum = 0.01, SD = 0.025). Mean proportion of

289 time spent grooming others was 5.1% of total time observed ($n = 38$, mean = 0.05,
290 minimum = 0.0, maximum = 0.29, SD = 0.059). Social groups did not differ in regard to
291 mean time spent grooming others ($F_{(2,35)} = 0.172$, $p > 0.05$) or being groomed by others
292 ($F_{(2,35)} = 0.517$, $p > 0.05$). Groups also did not differ in mean time spent in direct contact
293 ($F_{(2,35)} = 2.6$, $p > 0.05$).

294 **Parasitological results**

295 Analyses revealed six types of parasites: *Trichuris* sp. (92% prevalence in the
296 study sample), hookworm (71% prevalence), spirurids (68% prevalence),
297 *Oesophagostomum* sp. (84% prevalence), *Strongyloides* sp. (24% prevalence), and
298 *Entamoeba coli* (92% prevalence) ($n = 38$). Descriptions of these can be found in Wren et
299 al. [35,53,60]. We did not detect presence of *Cryptosporidium* sp. or *Giardia* sp. with
300 immunofluorescence microscopy.

301 Social group differences are presented in Table 3. These differences are likely due
302 to the different sampling efforts for each social group as noted in the methods section.
303 Social groups were significantly different regarding richness of parasite species detected
304 ($F_{(2,35)} = 5.0804$, $p = 0.012$). The Bay group differed significantly from the Donga group
305 ($t(35) = 2.98$, $p = 0.005$) and the Blesbok from the Donga group ($t(35) = 2.58$, $p = 0.014$).
306 The combination of the Bay and Blesbok group differed significantly from the Donga
307 group ($t(35) = 2.05$, $p = 0.048$) while the combination of the Blesbok and Donga group
308 differed significantly from the Bay group ($t(35) = 3.16$, $p = 0.003$).

309 Groups differed significantly in the presence of hookworm ($F_{(2,35)} = 1.35$, $p =$
310 0.272), The Bay group differed from the Blesbok group ($t(35) = 3.45$, $p = 0.001$) and the

311 Donga group ($t(35) = 2.44, p = 0.020$). The combination of the Bay and Donga groups
312 differed from the Blesbok group ($t(35) = 2.65, p = 0.012$). The combination of the
313 Blesbok and Donga group differed significantly from the Bay group ($t(35) = 3.34, p =$
314 0.002).

315 Groups did not differ significantly in the presence of *Trichuris* sp. ($F_{(2,35)} = 1.35, p$
316 $= 0.272$), spirurids ($F_{(2,35)} = 2.80, p = 0.075$), *Oesophagostomum* sp. ($F_{(2,35)} = 0.91, p =$
317 0.412), *Strongyloides* sp. ($F_{(2,35)} = 0.17, p = 0.842$), or *Entamoeba coli* ($F_{(2,35)} = 1.35, p =$
318 0.272).

319

320 **Hypothesis testing results**

321 **Group differences**

322 One-way analysis of variance (ANOVA) was conducted to examine group
323 differences in observed behaviors. Levene's test of homogeneity of variance revealed
324 only the number of grooming partners, time receiving grooming, and time in direct
325 contact met this assumption (Table 3). However, because ANOVA is robust with respect
326 to violations of homogeneity of variance analyses could still be performed. There were
327 statistically significant differences among groups for: total seconds observed ($F_{(2, 52)} =$
328 $22.79, p < 0.001$); number of grooming partners ($F_{(2, 52)} = 15.70, p < 0.001$); number of
329 grooming partners giving ($F_{(2, 52)} = 8.11, p = 0.001$); number of total partners ($F_{(2, 52)} =$
330 $19.08, p < 0.001$); time self-grooming ($F_{(2, 52)} = 3.54, p = 0.036$) (Table 4).

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Table 3: Levene's Test of Homogeneity of Variance for Behavioural Variables in Vervet Monkeys (*Chlorocebus pygerythrus*) at Loskop Dam Nature Reserve, South Africa

Variable	Levene's Statistic	df1	df2	<i>p</i>
Total Seconds Observed	6.27	2	52	0.004
Number of Grooming Partners	5.52	2	52	0.007
Number of Grooming Partners (Giving)	4.89	2	52	0.011
Number of Grooming Partners (Receiving)	3.16	2	52	0.051
Number of Total Partners (Contact)	3.81	2	52	0.029
Time Giving Grooming	2.68	2	52	0.078
Time Receiving Grooming	2.90	2	52	0.064
Time Self-Grooming	8.80	2	52	0.001
Time in Direct Contact	0.28	2	52	0.756
Time Playing	4.79	2	52	0.012

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Table 4: ANOVA Summary for Behavioural Variables in Vervet Monkeys (*Chlorocebus pygerythrus*) at Loskop Dam Nature Reserve, South Africa

Variable	SS	df	MS	F	p
Total Seconds Observed	25571402466.39	2	12785701233.20	22.79	<0.001
	29172783930.95	52	561015075.60		
	54744186397.35	54			
Number of Grooming Partners	243.56	2	121.78	15.70	<0.001
	403.24	52	7.75		
	646.80	54			
Number of Grooming Partners (Giving)	126.13	2	63.07	8.11	0.001
	404.30	52	7.78		
	530.44	54			
Number of Grooming Partners (Receiving)	142.37	2	71.19	12.36	<0.001
	299.37	52	5.76		
	441.75	54			
Number of Total Partners (Contact)	311.25	2	155.63	19.08	<0.001
	424.09	52	8.16		
	735.35	54			
Time Giving Grooming	0.00	2	0.00	0.39	0.677
	0.20	52	0.00		
	0.20	54			
Time Receiving Grooming	0.00	2	0.00	0.93	0.401
	0.04	52	0.00		
	0.04	54			
Time Self-Grooming	0.00	2	0.00	3.54	0.036
	0.01	52	0.00		
	0.01	54			
Time in Direct Contact	0.01	2	0.00	0.03	0.971
	5.02	52	0.10		
	5.03	54			
Time Playing	0.00	2	0.00	1.16	0.322
	0.00	52	0.00		
	0.00	54			

341

342 Planned contrasts revealed specific differences among groups and combinations

343 of groups (Tables 5 & 6). There were statistically significant differences for all

344 combinations of groups with respect to total seconds observed. There were statistically

345 significant differences for all combination of groups with respect to the number of

346 grooming partners except between the combination of the Bay and Blesbok groups
347 compared to the Donga group, ($t(22.12) = 0.86, p = 0.398$). There were statistically
348 significant differences for all combination of groups with respect to the number of
349 grooming partners giving grooming except between the combination of the Bay and
350 Blesbok groups compared to the Donga group, ($t(36.79) = 0.63, p = 0.543$). There were
351 statistically significant differences for all combination of groups with respect to the
352 number of grooming partners receiving grooming except between the combination of the
353 Bay and Blesbok groups compared to the Donga group, ($t(52) = 0.1.03, p = 0.310$). There
354 were statistically significant differences for all combination of groups with respect to the
355 number of total partners except between the combination of the Bay and Blesbok groups
356 compared to the Donga group, ($t(34.10) = 1.21, p = 0.236$). There were no statistically
357 significant differences for any combination of groups with respect to time giving
358 grooming. There were no statistically significant differences for any combination of
359 groups with respect to time receiving grooming. There were statistically significant
360 differences for all combinations of groups with respect to time spent self-grooming
361 except for: the Bay group compared to the Donga group, ($t(32.88) = 0.54, p = 0.59$); the
362 combination of the Bay and Blesbok groups compared to the Donga group, ($t(32.62) = -$
363 $0.79, p = 0.435$); the Bay group compared to the combination of the Blesbok and Donga
364 groups, ($t(23.03) = -1.60, p = 0.123$). There were no statistically significant differences
365 for any combination of groups with respect to the time spent playing except between the
366 combination of the Bay and Blesbok groups compared to the Donga group, ($t(28.23) =$
367 $2.07, p = 0.048$).

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Table 5: Contrast Coefficients for ANOVA of Behavioural Variables in Vervet Monkeys (*Chlorocebus pygerythrus*) at Loskop Dam Nature Reserve, South Africa

Contrast	Group		
	1 (Bay)	2 (Blesbok)	3 (Donga)
1	1	0	-1
2	1	-1	0
3	0	1	-1
4	1	1	-2
5	1	-2	1
6	-2	1	1

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Table 6: ANOVA Follow-up Results for Behavioural Variables in Vervet Monkeys (*Chlorocebus pygerythrus*) at Loskop Dam Nature Reserve, South Africa

Variable	Variance	Contrast	Value of Contrast	Standard Error	t	df	p-value
Total Seconds Observed	Equal Variance Not Assumed	1	-	5271.92	-2.28	28.49	0.030
		2	12006.79	8892.15	-5.78	18.99	<0.001
		3	51396.45	9661.11	4.08	24.80	<0.001
		4	39389.66	12774.58	2.14	36.86	0.039
		5	27382.87	17805.10	-5.10	19.12	<0.001
		6	90786.11	10972.24	5.78	36.97	<0.001
Number of Grooming Partners	Equal Variance Not Assumed	1	-1.89	0.76	-2.51	29.29	0.018
		2	-5.17	0.96	-5.41	22.10	<0.001
		3	3.28	1.09	3.01	30.35	0.005
		4	1.38	1.61	0.86	34.50	0.398
		5	-8.45	1.90	-4.43	22.12	<0.001
		6	7.07	1.34	5.29	48.05	<0.001
Number of Grooming Partners (Giving)	Equal Variance Not Assumed	1	-1.37	0.73	-1.87	31.43	0.070
		2	-3.72	0.99	-3.76	22.31	0.001
		3	2.35	1.09	2.16	28.54	0.039
		4	0.98	1.57	0.63	36.79	0.543
		5	-6.07	1.95	-3.12	21.37	0.005
		6	5.09	1.36	3.75	46.38	<0.001
Number of Grooming Partners (Receiving)	Equal Variance Not Assumed	1	-1.26	0.78	1.62	52	0.111
		2	-3.92	0.80	4.9	52	<0.001
		3	0.66	0.80	3.32	52	0.002
		4	1.40	1.36	1.03	52	0.310
		5	-6.58	1.40	4.70	52	<0.001
		6	5.19	1.36	3.81	52	<0.001

Number of Total Partners (Contact)	Equal	1	-1.89	0.85	-2.22	32.98	0.033
	Variance Not Assumed	2	-5.80	0.95	-6.12	27.26	<0.001
		3	3.91	1.06	3.70	32.50	0.001
	Assumed	4	2.02	1.67	1.21	34.10	0.236
		5	-9.72	1.82	-5.34	25.27	<0.001
		6	7.70	1.46	5.27	47.60	<0.001
Time Giving Grooming	Equal	1	0.01	0.02	0.62	52	0.538
	Variance Not Assumed	2	0.02	0.02	0.85	52	0.397
		3	-0.01	0.02	0.25	52	0.801
	Assumed	4	0.01	0.04	0.21	52	0.838
		5	0.02	0.04	0.63	52	0.529
		6	-0.03	0.04	0.86	52	0.395
Time Receiving Grooming	Equal	1	-0.01	0.01	1.35	52	0.182
	Variance Not Assumed	2	-0.01	0.01	0.81	52	0.419
		3	0.00	0.01	0.50	52	0.620
	Assumed	4	-0.02	0.02	1.07	52	0.291
		5	0.00	0.02	0.18	52	0.857
		6	0.02	0.02	1.25	52	0.216
Time Self-Grooming	Equal	1	0.00	0.01	0.54	32.88	0.590
	Variance Not Assumed	2	0.01	0.00	2.70	19.26	0.014
		3	-0.01	0.00	-2.76	20.36	0.012
	Assumed	4	-0.01	0.01	-0.79	32.62	0.435
		5	0.02	0.01	3.73	38.52	0.001
		6	-0.02	0.01	-1.60	23.03	0.123
Time in Direct Contact	Equal	1	0.02	0.10	0.18	52	0.860
	Variance Not Assumed	2	-0.01	0.10	0.06	52	0.954
		3	0.02	0.10	0.23	52	0.818
	Assumed	4	0.04	0.18	0.24	52	0.813
		5	-0.03	0.18	0.17	52	0.869
		6	-0.01	0.18	0.07	52	0.947
Time Playing	Equal	1	0.00	0.00	1.35	18.22	0.192
	Variance Not Assumed	2	0.00	0.00	0.31	27.22	0.759
		3	0.00	0.00	1.87	16.68	0.079
	Assumed	4	0.00	0.00	2.07	28.23	0.048
		5	0.00	0.00	-0.45	33.68	0.657
		6	0.00	0.00	-0.83	20.59	0.419

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373 **Generalized linear model**

374 All behavioral variables from all observed individuals were converted to z-scores

375 for inclusion in the generation of a multivariate logistic regression equation, with the

376 dependent variable modeled as the presence or absence of *Trichuris* sp. The only

377 individual statistically significant effect was time in direct contact ($\beta = -4.63, p = 0.02$;

378 Table 7). The model shows excellent fit based on the -2 Log likelihood (24.22) and

379 Nagelkerke pseudo- R^2 (0.73) (Table 8). This equation was able to correctly predict 100%

380 of observed absence of *Trichuris* sp. and 94.44% of observed presence of *Trichuris* sp.,

381 for a total of 95.17% of cases correctly predicted (Table 9).

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Table 7: Logistic Regression Summary Table for Univariate and Equations Predicting *Trichuris* infection status in Vervet Monkeys (*Chlorocebus pygerythrus*) at Loskop Dam Nature Reserve, South Africa

Z-score of Variable	β	SE	Wald	p	Exp(β)
Multivariate Equation:					
Total Seconds Observed	-2.64	1.8	2.16	1.42	0.07
Number of Grooming Partners	-0.21	4.69	0.00	9.65	0.81
Number of Grooming Partners Giving	-0.74	2.85	0.07	7.96	0.48
Number of Grooming Partners Received	3.33	2.91	1.31	0.253	27.95
Number of Total Partners	2.58	2.66	0.94	0.332	13.14
Time Giving Grooming	-.034	2.51	0.147	0.225	0.05
Time Receiving Grooming	0.14	0.77	0.03	0.858	1.15
Time Self Grooming	-0.83	0.79	1.10	0.294	0.44
Time in Direct Contact	-4.63	1.99	5.42	0.020	0.01
Time Playing	-0.74	0.60	1.53	0.216	0.48

Bivariate Equation:					
Number of Total Partners	0.79	0.46	2.29	0.084	2.21
Time in Direct Contact	-2.76	0.84	10.88	0.001	0.06
Univariate Equation:					
Time in Direct Contact	-4.63	1.99	5.42	0.020	0.01

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Table 8: Logistic Regression Fit Statistics for Univariate and Multivariate Equations Predicting *Trichuris* infection status in Vervet Monkeys (*Chlorocebus pygerythrus*) at Loskop Dam Nature Reserve, South Africa

Statistic	Equation	Value
-2 Log Likelihood	Univariate	37.68
	Bivariate	34.11
	Multivariate	24.22
Cox and Snell pseudo- R^2	Univariate	0.37
	Bivariate	0.43
	Multivariate	0.55
Nagelkerke pseudo- R^2	Univariate	0.50
	Bivariate	0.57
	Multivariate	0.73

391

Table 9: Logistic Regression Classification by Univariate and Multivariate Equations for predicting *Trichuris* infection status in Vervet Monkeys (*Chlorocebus pygerythrus*) at Loskop Dam Nature Reserve, South Africa

	Predicted Present	Predicted Absent	Percent Correctly Predicted

	Observed Present	5	0	100
Multivariate	Observed Absent	2	34	94.44
	Total	7	34	95.12
	Observed Present	3	2	60
Bivariate	Observed Absent	2	34	94.44
	Total	5	36	90.24
	Observed Present	3	2	60.00
Univariate	Observed Absent	5	31	86.11
	Total	8	33	82.93

392 A bivariate logistic regression was conducted using only the z-score of time in
 393 direct contact and the total number of grooming partners to predict the presence of
 394 *Trichuris* sp. This regression indicated that time in direct contact with others had a
 395 statistically significant negative effect on infection status ($\beta = -2.76, p = 0.001$). Total
 396 number of grooming partners had a non-statistically significant positive effect on
 397 infection status ($\beta = 0.79, p = 0.084$). The model fit for this equation is worse than for the
 398 multivariate equation, based on a higher -2 Log likelihood (34.11) and lower Nagelkerke
 399 pseudo- R^2 (0.73) (Table 8). This equation was able to correctly predict 60% of observed
 400 absence of *Trichuris* sp. and 94.44% of observed presence of *Trichuris* sp., for a total of
 401 90.24% of cases correctly predicted (Table 9).

402 A univariate logistic regression was conducted using only the z-score of time in
 403 direct contact and the presence of *Trichuris* sp. This regression indicated that time in
 404 direct contact with others had a statistically significant effect on infection status ($\beta = -$
 405 $2.73, p = 0.001$). The model fit for this equation is worse than for the multivariate

406 equation, based on a higher -2 Log likelihood (37.68) and lower Nagelkerke pseudo-R²
407 (0.50) (Table 8). This equation was able to correctly predict 60% of observed absence of
408 *Trichuris* sp. and 86.11% of observed presence of *Trichuris* sp., for a total of 82.93% of
409 cases correctly predicted (Table 9).

410

411 **Discussion**

412 Vervet monkeys at LDNR that are infected with *Trichuris* sp. tend to spend
413 significantly less time grooming conspecifics as well as less time in direct contact with
414 others when compared to those that are not infected. Infected individuals at LDNR spent
415 an average of 4% of their observed time grooming others, while those not infected with
416 this parasite spent an average of 14% of their observed time grooming others. However,
417 no differences existed in time spent being groomed by others. Overall, for the entire
418 sample ($n = 55$), study subjects spent about 20% of their time in direct contact with
419 another individual. The subset used for parasitological analysis spent 6.5% ($n = 38$) of
420 their time in direct contact with another individual. This large difference is primarily
421 influenced by the inclusion of infants and mothers with infants in the entire sample of $n =$
422 55, but only mothers in the smaller subset of $n = 38$. These mother-infant dyads remain in
423 almost constant contact for the first weeks of a monkey's life and this inflates the overall
424 mean for the group. Because there were not enough fecal samples from these infants,
425 their behavioral data was not included in hypothesis testing. One model that we built was
426 able to correctly predict infection status for *Trichuris* sp. with a reliability of 95.17%
427 overall, but the major factor for prediction was time spent in direct contact.

428 These results do not support the hypothesis that social grooming facilitates
429 transmission of this type of gastrointestinal parasite. One possible explanation for these
430 results is that individuals that are infected with *Trichuris* sp. experience degraded health
431 and/or less motivation to groom others and interact with others. Red colobus monkeys
432 (*Procolobus rufomitratu*s) in Uganda that were infected with *Trichuris* sp. decreased their
433 time spent performing a number of behaviors, including grooming others [67]. Those
434 same individuals spent more time resting as well as ingesting plant species and/or parts
435 that suggest self-medicative behavior. Whipworm is known to cause anemia, chronic
436 dysentery, rectal prolapse, and poor growth in humans with symptomatic infections [68],
437 so less energy, motivation, or interest for behaviors like social grooming should not be
438 surprising in other species.

439 Another possible explanation is that *Trichuris* sp. more directly alters host
440 behavior in vervet monkeys. Gastrointestinal parasites are known to alter host behavior in
441 some host-parasite relationships, an idea referred to as the manipulation hypothesis [69-
442 72]. For example, *Toxoplasma gondii* causes intermediate rodent hosts to be more
443 attracted to the scent of felid predators, which are also the definitive host for the parasite
444 [73]. *Dicrocoelium dendriticum* causes infected ants to wait on the tips of blades of grass
445 where they can be ingested by sheep, the parasite's definitive host. Because manipulation
446 of host behavior usually serves to facilitate transmission of the parasite from an
447 intermediate host to a definitive host, and vervet monkeys do not serve as intermediate
448 hosts for *Trichuris* sp., the manipulation hypothesis does not adequately explain the
449 results of this study.

450 Other studies have found multiple morphotypes of *Trichuris* sp. in nonhuman
451 primate hosts in captivity in Nigeria [74,75], suggesting that potentially multiple species
452 of *Trichuris* sp. may infect nonhuman primates. The major implication of this has been
453 seen as relevant for public health because it may mean that the species of *Trichuris* sp.
454 that infect humans and nonhuman primates are not the same, suggesting that transmission
455 of *Trichuris* sp. between humans and other primates is not as severe a public health
456 concern as previously considered. However, it could also have implications for how
457 primate hosts respond to or become infected with *Trichuris* sp.

458 Hart [76] noted that ill or infected animals display altered behavior, and argued
459 that these sickness behaviors can be adaptive. One study of chimpanzees (*Pan*
460 *troglydytes schweinfurthii*) revealed that infected individuals exhibit altered behavior,
461 most fittingly described as lethargy [77]. Behavioral changes due to parasitic infections in
462 fish have been observed and range from mating behaviors to foraging efficiency
463 (reviewed in Barber et al. [78]). The Ghai et al. [67] study that revealed that *Trichuris* sp.
464 was associated with a reduction in grooming and mating and also found that individuals
465 infected with this parasite took longer to switch behaviors than those individuals that
466 were not infected. These studies make it increasingly clear that host-parasite dynamics
467 have far-reaching consequences for animal behavior.

468 This study suggests that the gastrointestinal parasite *Trichuris* sp. is associated
469 with behavioral differences, specifically decreased time spent grooming others and time
470 spent in direct contact with others, in vervet monkey hosts. These behavioral differences
471 are extreme enough to influence group means when assessing behavior. Further, if an

472 individual is less likely to groom or interact with conspecifics, then they may also
473 experience lower social status and thus lower reproductive fitness. These results highlight
474 the need for parasitological analyses for a complete and nuanced understanding of animal
475 behavior.

476

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484

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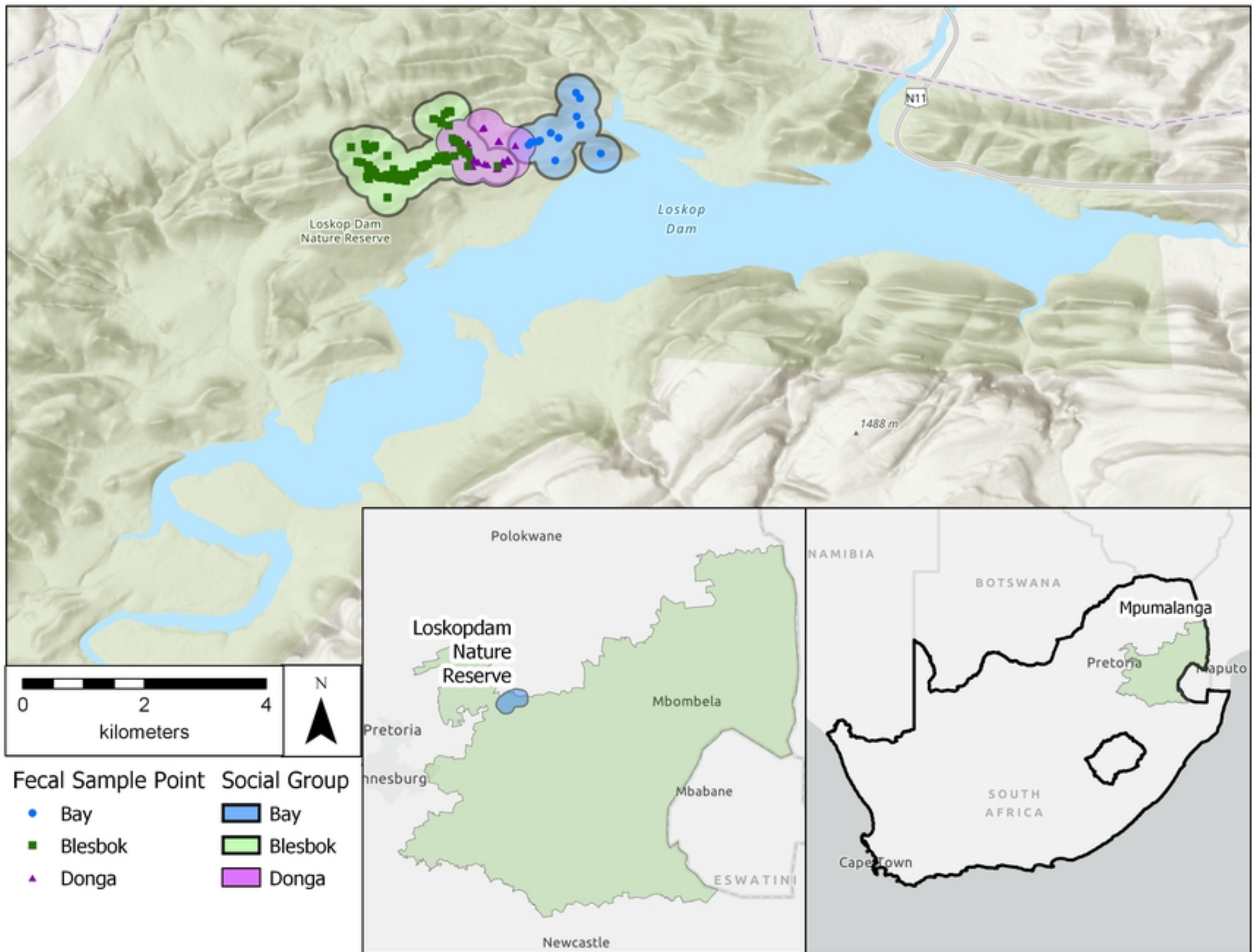


Figure 1: Loskop Dam Nature Reserve, South Africa.