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1 Helminth parasites are associated with reduced survival probability in young red
2 deer

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14 **Abstract**

15 Helminths are common parasites of wild ungulates that can have substantial costs for growth,
16 mortality, and reproduction. Whilst these costs are relatively well documented for mature
17 animals, knowledge of helminths' impacts on juveniles is more limited. Identifying these
18 effects is important because young individuals are often heavily infected, and juvenile mortality
19 is a key process regulating wild populations. Here, we investigated associations between
20 helminth infection and overwinter survival in juvenile wild red deer (*Cervus elaphus*) on the
21 Isle of Rum, Scotland. We collected faecal samples non-invasively from known individuals
22 and used them to count propagules of three helminth taxa (strongyle nematodes, *Fasciola*
23 *hepatica*, and *Elaphostrongylus cervi*). Using generalised linear models, we investigated
24 associations between parasite counts and overwinter survival for calves and yearlings.
25 Strongyles were associated with reduced survival in both age classes, and *F. hepatica* was
26 associated with reduced survival in yearlings, whilst *E. cervi* infection showed no association
27 with survival in either age class. This study provides observational evidence for fitness costs
28 of helminth infection in juveniles of a wild mammal, and suggests that these parasites could
29 play a role in regulating population dynamics.

30

31 **Key words:** disease ecology, helminths, wild mammal, survival, ungulate, fitness costs

32

33

34 **Key Findings**

- 35 • Non-invasive faecal parasite egg counts predict overwinter survival of wild young red
36 deer.
- 37 • Strongyle nematode infection is associated with decreased survival probability in calves
38 and yearlings
- 39 • *Fasciola hepatica* infection is associated with decreased survival probability in
40 yearlings

41

42 **Introduction**

43 Parasites are ubiquitous in natural populations and are often costly to the hosts they infect
44 (Hudson *et al.*, 2002). Whilst the consequences of parasitism in mammals are well documented
45 for domestic livestock, evidence of their effects in wild populations is far more limited due to
46 the practical difficulties of collecting long-term parasitological data from wild hosts –
47 particularly large, long-lived mammals (Coulson *et al.*, 2018; Wilson *et al.*, 2003). Wild
48 mammals are typically infected with gastrointestinal helminth parasites; a paraphyletic clade
49 of macro-parasitic worms, including tapeworms (Cestoda), roundworms (Nematoda), and
50 flukes (Trematoda) (Taylor *et al.*, 2015b). These parasites display a variety of life histories and
51 induced pathologies in their hosts (McSorley and Maizels, 2012). Most frequently, helminths
52 invade their host via the gastrointestinal tract, after free-living larval stages are consumed by
53 the host (Taylor *et al.*, 2015b). Adult helminths live, feed, and reproduce within their hosts,
54 and their propagules are excreted into the environment with the faeces, from which they spread
55 to other hosts either directly or indirectly via an intermediate host (Taylor *et al.*, 2015b).
56 Quantification of infection is possible by counting these propagules within a host's faeces using
57 a method known as faecal egg counts (FECs) (Taylor *et al.*, 2015a). This non-invasive measure
58 can be used as a proxy for an individual's parasite burden, defined as the actual quantity of

59 adult helminths within the host (Budischak *et al.*, 2015). Parasite count often varies with both
60 extrinsic and intrinsic host factors. Age-dependent parasitism is common; juveniles are often
61 the most heavily parasitised members in a population, predominantly attributed to their naïve
62 immune systems and prioritisation of resources for growth rather than immunity (Ashby and
63 Bruns, 2018; Wilson *et al.*, 2003). Juveniles are a key demographic group, and any parasite-
64 mediated effects on their survival could play a role in population regulation (Gaillard *et al.*,
65 2000).

66 The European red deer (*Cervus elaphus*) is a large ungulate that has great ecological
67 importance as a wide-ranging herbivore and source of livestock diseases (Böhm *et al.*, 2007;
68 Fuller and Gill, 2001). Red deer are abundant in Scotland, and culling regimes for population
69 regulation have provided the basis for many parasitological investigations. These studies have
70 documented the prevalence of endoparasites in Scottish red deer, including multiple species of
71 strongyle nematodes (a family of worms whose eggs are indistinguishable by microscopy and
72 so grouped together in assays), lungworms (*Dictyocaulus* spp.), the tissue nematode
73 (*Elaphostrongylus cervi*), *Sarcocystis* spp., and the common liver fluke (*Fasciola hepatica*)
74 (Böhm *et al.*, 2006; Irvine *et al.*, 2006; French *et al.*, 2016). The study population of wild red
75 deer on the Isle of Rum provide an excellent system for investigating the fitness consequences
76 of parasitism. Longitudinal individual-based monitoring enables collection of complete life
77 history information and parasite data from non-invasive faecal sampling (Albery *et al.*, 2021).
78 The population hosts a variety of helminth parasites, the most prevalent taxa being strongyle
79 nematodes, *F. hepatica* and *E. cervi* (Albery *et al.*, 2018). Juvenile deer tend to be more heavily
80 parasitised than adults, with calves (≤ 12 months old) showing the highest strongyle intensities
81 and yearlings (13-24 months old) showing the highest *F. hepatica* and *E. cervi* intensities
82 (Albery *et al.*, 2018). Mortality rates are high among juveniles, with many of these deaths
83 occurring over the winter months (January-March) when environmental conditions are harshest

84 and food is limited (Clutton-Brock *et al.*, 1987; Coulson *et al.*, 1997). Juvenile overwinter
85 survival may be influenced by the extent of parasite infection. In other wild ungulates, helminth
86 infection in juveniles has been shown to cause mortality over winter periods, exacerbating the
87 effects of food shortage (Coltman *et al.*, 1999). Strongyle infection negatively impacts future
88 reproductive success and survival in adult female deer in the Rum study population (Albery *et*
89 *al.*, 2021), but to date there have been no investigations into the fitness costs of juvenile
90 parasitism in this population.

91 Here, we investigate associations between survival probability of juvenile red deer on the
92 Isle of Rum, and infection of strongyle nematodes, *F. hepatica* and *E. cervi*, quantified from
93 faecal samples collected at three different times of year. We predict that increases in helminth
94 parasite burden in young red deer will decrease their subsequent overwinter survival
95 probability.

96

97 **Materials and methods**

98 *Data collection*

99 This study used data collected between 2016 and 2020 from a wild population of red deer
100 situated on the North block of the Isle of Rum, Scotland. A detailed description of the study
101 system and field data collection can be found in Clutton-Brock *et al.* (1982). After many years
102 of study, the deer are relatively habituated to human presence. The ‘deer year’ begins on May
103 1st, marking the start of the calving season (May-July). During this time pregnant female deer
104 are monitored daily for when they give birth to a single calf. Within a few hours of birth, calves
105 are caught, sex determined, weighed, and marked with a combination of collars, tags, and ear
106 punches, to allow individual identification throughout their lives. Regular censuses of the
107 population allow accurate individual life history data to be collected.

108 Faecal samples were collected in spring (April), summer (August), and autumn

109 (November). A detailed description of faecal sampling and parasitological methods can be
110 found in Albery *et al.* (2018). Individually recognised deer were observed defaecating from a
111 distance and the faeces were collected as quickly as possible without disturbing the deer. In
112 each season as many different individuals as possible were sampled. Faecal samples were kept
113 as anaerobic as possible in re-sealable plastic bags and refrigerated at 4°C to prevent the
114 hatching or development of parasite propagules until parasitological analysis was performed
115 (within 3 weeks of collection) (Albery *et al.*, 2018).

116 From a faecal subsample, parasite propagule counts were conducted for the three most
117 prevalent helminth taxa in the population; strongyle nematodes (including multiple species
118 whose eggs are indistinguishable by microscopy and so grouped at order-level), *Fasciola*
119 *hepatica* and *Elaphostrongylus cervi*, as detailed in Albery *et al.* (2018). Briefly, strongyle
120 nematode FECs were conducted via a sedimentation-salt flotation method, accurate to 1 egg
121 per gram (EPG) (Kenyon *et al.*, 2013; Albery *et al.*, 2018); faecal samples were homogenised
122 in water to suspend any eggs, then the suspension was filtered, centrifuged at 200× g for 2
123 minutes, and the supernatant was removed using a vacuum. Retentate was mixed with saturated
124 salt solution and then centrifuged again. The less dense strongyle eggs that floated to the surface
125 were collected and counted under 4× magnification. *F. hepatica* eggs were counted by a
126 sedimentation method (Taylor *et al.*, 2015a); faecal matter was homogenised with water and
127 filtered. The sample was then left to sediment; the dense eggs which sank to the bottom were
128 separated from the lighter material above and stained with methylene blue to facilitate counting
129 under 4× magnification. *E. cervi* larvae were counted by a baermannization method (Gajadhar
130 *et al.*, 1994); faecal matter was wrapped in muslin cloth, submerged in a tube of water and left
131 for 20-24 hours for the larvae to emerge and fall to the bottom of the tube. The supernatant was
132 then removed, and the remaining larvae were counted under 40× magnification. Propagule
133 counts were divided by the mass of the faecal subsample used, to give a measure of parasitic

134 burden as eggs per gram of faecal matter for strongyles and *F. hepatica* (EPG), or larvae per
135 gram of faecal matter for *E. cervi* (LPG). Our analysis used faecal propagule counts included
136 in Albery *et al.* (2018) collected in 2016, and additional samples collected in 2017, 2018 and
137 2019.

138

139 *Statistical analysis*

140 All statistical analysis was performed in R version 4.0.3 with the base package *stats* (RStudio
141 Team, 2021). All figures were plotted using the R package *ggplot2* (Wickham, 2016). For
142 calves and yearlings, we calculated prevalence (%) and mean FEC of strongyles, *F. hepatica*
143 and *E. cervi* in the spring (April), summer (August), and autumn (November). We do not
144 investigate parasite counts for yearlings sampled in the spring (April), as they have already
145 survived over the winter period and so are not informative for survival analysis. We used
146 binomial generalised linear models (GLM) to explore the association of parasitic burden with
147 subsequent overwinter survival in calves and yearlings. Parasite burden, determined by FECs,
148 was $\log(\text{count} + 1)$ transformed in all cases, to approximate normality. To investigate the
149 survival of a calf through their first winter, we conducted GLMs with a logit-link function using
150 faecal sample data from the summer (model A) and autumn (model B), before the calves' first
151 winter. In both models we included a response variable of first winter survival (binary; survived
152 (1) or died (0)), and explanatory variables of sex (categorical; female, male), sample deer year
153 (categorical), and strongyle count per gram of faeces (continuous). We included *F. hepatica*
154 count per gram of faeces (continuous) as an explanatory variable in model B but not model A,
155 as *F. hepatica* infection is prepatent and FECs are not meaningful when sampled from calves
156 in the summer at the age of two to three months. We did not fit *E. cervi* count in either model,
157 as infection is prepatent and FECs are not meaningful when sampled from calves aged up to
158 six months in the summer and autumn (Albery *et al.*, 2018; Gajadhar *et al.*, 1994). To

159 investigate yearlings' survival through their second winter, we conducted GLMs with a logit-
160 link function using faecal sample data from the spring (as calves; model C), summer (as
161 yearlings; model D), and autumn (as yearlings; model E) before the individuals' second winter.
162 In all three models we included a response variable of second winter survival (binary; survived
163 (1) or died (0)), and explanatory variables of sex (categorical; female, male), deer year
164 (categorical), strongyle count per gram of faeces (continuous), *F. hepatica* count per gram of
165 faeces (continuous), and *E. cervi* count per gram of faeces (continuous). The survival rate was
166 97.1% for calves and 98.1% for yearlings in deer year 2019, preventing us from fitting a
167 survival model to this year. For this reason, before running the models, we removed samples
168 corresponding to calf and yearling overwinter survival in the deer year 2019; samples taken in
169 the summer and autumn of the same deer year (August and November 2019) and samples taken
170 in spring of the previous deer year (2018; April 2019).

171

172 **Results**

173 Strongyle prevalence and mean intensities were higher in calves than yearlings, peaking in
174 calves sampled in the spring aged ten to eleven months. Strongyle prevalence and intensity was
175 lowest in the autumn. *F. hepatica* prevalence and intensity peaked in spring and dropped in
176 the summer and autumn. *E. cervi* showed the highest mean intensity across all parasite taxa,
177 with calves sampled in the spring displaying the highest mean counts. Prevalence of *E. cervi*
178 was highest in yearlings sampled in the autumn (Table 1).

179

180 A full listing of model effect sizes is displayed in Table 2. Below we provide mean parasite
181 effect sizes for each survival model, on the logistic-link scale as $\log(\text{parasite count} + 1)$.
182 Overall, 63.1% of calves survived through their first winter and 84% of yearlings survived
183 through their second winter (excluding data corresponding to overwinter survival in deer year

184 2019, which was not used in survival analysis). Calf and yearling survival models consistently
185 revealed a significant negative association between faecal strongyle count and subsequent
186 winter survival in each sampled season. A calf's summer strongyle FEC was negatively
187 associated with their first winter survival (model A, -0.513 ± 0.193 , $p=0.008$). Calves that had
188 the lowest summer strongyle FECs (0 EPG, 4.6% of samples) had a 90.0% probability of
189 surviving their first winter, whilst calves with the highest summer strongyle FECs (>40 EPG,
190 32.1% of samples) had a <57.3% probability of survival (Figure 1A). A calf's autumn strongyle
191 FEC was negatively associated with their first winter survival (model B, -0.858 ± 0.300 ,
192 $p=0.004$). Calves that had the lowest autumn strongyle FECs (0 EPG, 56.9% of samples) had
193 an 81.3% probability of survival, whilst calves with the highest autumn strongyle FECs (>10
194 EPG, 17.9% of samples) had a <35.7% probability of survival (Figure 1B).

195

196 An individual's spring strongyle FEC was significantly negatively associated with survival
197 over their second winter as yearlings (model C; -0.869 ± 0.372 , $p=0.019$). Individuals with the
198 lowest spring strongyle FECs (<10 EPG, 13.4% of samples) had a >95.4% probability of
199 survival over their second winter as a yearling, and those with the highest spring strongyle
200 FECs (>90 EPG, 26.9% of samples) had a <76.8% probability of survival (Figure 2A). A
201 yearling's summer strongyle FEC was also significantly negatively associated with their
202 overwinter survival (model D; -1.44 ± 0.565 , $p=0.011$). Yearlings with the lowest summer
203 strongyle FECs (<5 EPG, 10.9% of samples) had a >96.2% probability of survival over their
204 second winter, whilst those with the highest summer strongyle FECs (>30 EPG, 18.75% of
205 samples) had a <70.6% probability of survival (Figure 2B). A yearling's autumn strongyle FEC
206 was significantly negatively associated with survival over their second winter (model E; -1.88
207 ± 0.698 , $p=0.007$). Yearlings with the lowest autumn strongyle FECs (0 EPG, 53.8% of
208 samples) had a 97.1% probability of overwinter survival, whilst those with the highest autumn

209 strongyle FECs (10 EPG, 12.3% of samples) had a <26.7% probability of survival (Figure 2C).
210 A deer's *F. hepatica* FEC was negatively associated with subsequent overwinter survival only
211 in yearling summer samples (model D; -0.839 ± 0.365 , $p=0.022$). Yearlings with the lowest
212 summer *F. hepatica* FECs (0 EPG, 18.8% of samples) had a 97.4% probability of survival over
213 their second winter, whilst those with the highest summer *F. hepatica* FECs (>30 EPG, 18.8%
214 of samples) had a <67.5% probability of survival (Figure 2D). A deer's *E. cervi* FEC was not
215 significantly associated with subsequent overwinter survival in any sampled season (Table 2).
216 In this sample of deer, there was no significant difference in calf or yearling overwinter survival
217 between males and females (Table 2). Calf and yearling overwinter survival varied between
218 years in models using data sampled from autumn, with lower survival probabilities in 2016
219 compared to 2017 and 2018 (model B and model E, Table 2).

220

221 **Discussion**

222 We provide observational evidence that parasite infection is associated with substantially
223 reduced survival probability in young red deer. Individuals with higher strongyle nematode
224 intensities showed a reduced overwinter survival probability, consistent with the observation
225 that strongyle infection is negatively correlated with fitness in adult females (Albery *et al.*,
226 2021). Whilst our analysis cannot infer causality, adult strongyle nematodes are known to cause
227 damage to their hosts' abomasal mucosa, and consequently cause disruption to nutrient
228 absorption in ungulates (Hoberg *et al.*, 2001). Indeed, studies experimentally removing
229 helminths by administration of anthelmintic treatment have shown strongyle nematodes to
230 cause mortality in other wild mammals e.g. Soay sheep (*Ovis aries*) (Coltman *et al.*, 1999;
231 Gulland, 1992), reindeer (*Rangifer tarandus*) (Albon *et al.*, 2002), and snowshoe hares (*Lepus*
232 *americanus*) (Murray *et al.*, 1997). Taking this evidence together, it is therefore reasonable to
233 consider that strongyle nematodes are having negative impacts on the health of juvenile red

234 deer and are contributing towards overwinter mortality.

235 Studies of juvenile Soay sheep have uncovered a negative effect of strongyle nematodes
236 on survival, in addition to the effects of body weight, a correlate of body size (Sparks *et al.*,
237 2020). A similar effect may be occurring in red deer, but development of a non-invasive
238 measure of body size for the Rum study system would be necessary to disentangle size- and
239 parasite-dependent effects on survival. Nonetheless, our analysis shows a survival cost
240 associated with strongyle infection in juvenile red deer which may exert positive selection on
241 resistance to infection, as has been observed in other ungulate study systems (Hayward *et al.*,
242 2011). Furthermore, this negative association is observed despite low mean strongyle egg
243 counts in both calves and yearlings compared to the mean strongyle counts that are observed
244 in lamb and yearling Soay sheep (Craig *et al.*, 2008). Strongyle egg counts peaked in calves
245 sampled in spring (April), which may reflect a transmission strategy of coinciding maximum
246 propagule output with the influx of immunologically naïve calves in May. The low intensities
247 and prevalence of strongyle eggs in the autumn is likely due to a reduction in propagule output,
248 as colder temperatures decrease transmission, rather than reductions in actual burden (Albery
249 *et al.*, 2018). In general, calves had higher strongyle intensities than yearlings, agreeing with
250 previous findings, which may result from the negative effects of strongyle infection on juvenile
251 overwinter survival and/or the maturation of the naïve immune system (Albery *et al.*, 2018).

252 In the case of *F. hepatica*, yearling overwinter survival was predicted by the individual's
253 count in summer, but not by its count in spring or autumn. This may be true seasonal variation,
254 or a result of the selection of samples used in the yearling analysis (models C, D, and E). Only
255 ~16% of yearlings died in their second winter (in contrast to ~37% of calves in their first
256 winter), which may have reduced the models' ability to reliably detect an association between
257 *F. hepatica* FECs and survival. Ultimately, our analysis is restricted in estimating the
258 association between *F. hepatica* and juvenile survival; collection of further *F. hepatica* FECs

259 and fitness data from yearlings will be necessary to better understand their survival effects. *F.*
260 *hepatica* is known to have a negative effect on weight gain in domestic cattle and sheep
261 (Hayward *et al.*, 2021). Similar effects of *F. hepatica* infection in wild red deer may explain
262 their association with a reduced survival probability, as lighter individuals are less able to
263 survive over winter periods of poor nutrition (Loison *et al.*, 1999).

264 In contrast to strongyles and *F. hepatica*, *E. cervi* did not have any apparent survival
265 effects. *E. cervi* nematodes infect the central nervous system and skeletal muscles of their hosts,
266 and propagated larvae migrate through the bloodstream to the lungs prior to being swallowed
267 and excreted (Mason, 1989). Descriptions of the clinical symptoms of disease from *E. cervi*
268 infection have included paresis of hind limbs and pneumonia; however, pathogenicity is
269 relatively low in red deer in Scotland (Mason, 1989). Minimal pathology of *E. cervi* infection
270 in juvenile red deer may explain its lack of association with subsequent overwinter survival
271 probability. Furthermore, this result may reflect a host response of tolerance to *E. cervi*
272 infection, where minimising the damage caused by infection is prioritised over eradicating the
273 worms (McSorley and Maizels, 2012). This strategy could explain the high intensities and
274 prevalence, and lack of age-bias of this parasite in the population (Albery *et al.*, 2018). There
275 was also no sex disparity in survival probability, contrary to expected male-biased mortality
276 (Moore & Wilson, 2002). However, this observation is not likely due to sex differences in
277 parasite FECs, which were small in calves and yearlings for strongyles, and not observed for
278 *F. hepatica* (Albery *et al.*, 2018).

279 Host population density is predicted to positively affect helminth transmission (Tompkins
280 *et al.*, 2001); at higher population densities juveniles may show higher intensities of helminth
281 infection, as has been observed in another wild ungulate population, Soay sheep (Hayward *et*
282 *al.*, 2014). Considering the survival costs associated with strongyle infection in juveniles
283 demonstrated here, density-dependent parasitism could be involved in the density-dependent

284 juvenile survival that occurs in the deer (Coulson *et al.*, 1997). There is a limited understanding
285 of how parasites may regulate ungulate hosts populations; however, experimental studies of
286 wild reindeer suggest helminths may be capable of regulating the population via density-
287 dependent effects on host reproduction (Albon *et al.*, 2002). Strongyle nematodes are likely to
288 have mediating effects on population dynamics in red deer, by reducing juvenile survival, and
289 by reducing survival and future reproduction in adult females (Albery *et al.*, 2021). Whilst the
290 observational nature of the Rum red deer study system precludes the manipulation of helminth
291 infection necessary to determine a regulatory role, collection of further years of parasite and
292 fitness data, paired with population density data, would be valuable in developing a more
293 nuanced understanding of how helminths impact wild populations. Furthermore, additional
294 years of longitudinal parasite and fitness data collection will inform the long-term effects of
295 juvenile parasitism on future fitness, as deer are studied through to maturity and senescence.

296

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299

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304

305 **Conflicts of Interest**

306 The authors declare there are no conflicts of interest.

307

308 **Ethical Standards (mandatory)**

309 Not applicable

310

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427

428 **Table 1.** Prevalence (%) and mean faecal propagule counts of strongyles, *F. hepatica* (in eggs
429 per gram of faeces, EPG), and *E. cervi* (in larvae per gram of faeces, LPG) in calves and
430 yearling red deer sampled in the spring, summer, and autumn across all years (2016-2019). ‘P’
431 indicates parasite is prepatent in the sample and so prevalence and mean propagule counts are
432 not meaningful.
433

Sample	Strongyles		<i>F. hepatica</i>		<i>E. cervi</i>		
	Prevalence (%)	Mean count [range] (EPG)	Prevalence (%)	Mean count [range] (EPG)	Prevalence (%)	Mean count [range] (LPG)	
Summer	Calves (N=141)	87.2	31.1 [0-194.0]	P	P	P	P
	Yearlings (N=91)	89.0	14.8 [0-169.0]	83.5	11.5 [0-46.7]	85.7	40.5 [0-249.2]
Autumn	Calves (N=159)	47.2	3.91 [0-33.0]	81.1	8.86 [0-114]	P	P
	Yearlings (N=91)	42.9	3.40 [0-45.0]	83.5	11.3 [0-104.5]	49.3	49.3 [0-371.2]
Spring	Calves (N=90)	95.5	70.3 [0-468.0]	90	26.3 [0-132.0]	91.9	91.9 [0-817.4]

434

435 **Table 2.** Results from binomial generalised linear models predicting calf and yearling overwinter
 436 survival using parasite FEC data collected in different seasons prior to winter (as described in table
 437 subheadings). Estimates are given on the logistic scale. Negative estimates indicate a reduction in
 438 survival probability. Significant effects are given in bold text.

	Estimate	Std. Error	Z value	Pr(> z)
Model A (Summer, calf survival, n=109)				
(Intercept)	2.316	0.790	2.931	0.003
Log(Strongyles EPG + 1)	-0.513	0.193	-2.654	0.008
Sex [male]	-0.158	0.426	-0.372	0.710
Deer year [2017]	-0.536	0.481	-1.116	0.264
Deer year [2018]	0.555	0.581	0.954	0.340
Model B (Autumn, calf survival, n=123)				
(Intercept)	0.729	0.549	1.328	0.184
Log(Strongyles EPG + 1)	-0.858	0.300	-2.860	0.004
Log(<i>F. Hepatica</i> EPG + 1)	-0.002	0.181	-0.010	0.992
Sex [male]	-0.502	0.414	-1.212	0.225
Deer year [2017]	1.632	0.819	1.992	0.046
Deer year [2018]	1.714	0.703	2.438	0.015
Model C (Spring, yearling survival, n=67)				
(Intercept)	3.451	2.153	1.603	0.109
Log(Strongyles EPG + 1)	-0.869	0.372	-2.339	0.019
Log(<i>E. Cervi</i> LPG + 1)	0.212	0.218	0.974	0.330
Log(<i>F. Hepatica</i> EPG + 1)	-0.086	0.296	-0.291	0.771
Sex [male]	0.478	0.731	0.654	0.513
Deer year [2016]	0.803	0.784	1.025	0.305
Deer year [2017]	1.947	1.236	1.576	0.115
Model D (Summer, yearling survival, n=64)				
(Intercept)	5.964	2.277	2.620	0.009
Log(Strongyles EPG + 1)	-1.439	0.565	-2.548	0.011
Log(<i>E. Cervi</i> LPG + 1)	0.247	0.276	0.896	0.370
Log(<i>F. Hepatica</i> EPG + 1)	-0.839	0.365	-2.297	0.022
Sex [male]	0.746	0.817	0.914	0.361
Deer year [2017]	0.319	0.845	0.377	0.706
Deer year [2018]	0.576	1.231	0.468	0.640
Model E (Autumn, yearling survival, n=65)				
(Intercept)	0.801	1.425	0.562	0.574
Log(Strongyles EPG + 1)	-1.884	0.698	-2.697	0.007
Log(<i>E. Cervi</i> LPG + 1)	-0.046	0.258	-0.176	0.860
Log(<i>F. Hepatica</i> EPG + 1)	0.451	0.333	1.353	0.176
Sex [male]	-0.457	0.756	-0.605	0.545
Deer year [2017]	3.564	1.662	2.145	0.032
Deer year [2018]	3.394	1.999	1.698	0.090

440 **Figure 1:** Probability of calf survival over their first winter (1=survived, 0=died) as predicted
441 by their strongyle FEC ($\log(\text{EPG}+1)$) from samples taken in the (A) summer (model A) and
442 (B) autumn (model B). Solid black line = fitted logistic regression slope. Transparent grey lines
443 = 100 random draws from model estimates to display variation in the estimated slope.
444 Transparent grey dots = individual sample.

445

446

447 **Figure 2:** Probability of yearling survival over their second winter (1=survived, 0=died) as
448 predicted by their strongyle FEC ($\log(\text{EPG}+1)$) from samples taken in the (A) spring as calves
449 (model C), (B) summer as yearlings (model D), and (C) autumn as yearlings (model E). And
450 as predicted by (D) *F. hepatica* FEC ($\log(\text{EPG}+1)$) from samples taken in the summer as
451 yearlings (model D). Solid black line = fitted logistic regression slope. Transparent grey lines
452 = 100 random draws from model estimates to display variation in the slope. Transparent grey
453 dots = individual samples.