

Density dependent regulation of fecundity in *Syngamus trachea* populations in semi-naturally occurring ring-necked pheasants (*Phasianus colchicus*) and wild Carrion Crows (*Corvus corone*).

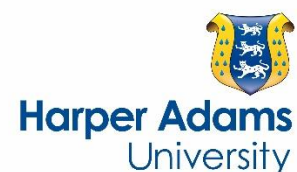
by Gethings, O.J., Sage, R.B. and Leather, S.R.

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DOI: 10.1017/S0031182016000135

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Gethings, O.J., Sage, R.B. and Leather, S.R. 2016. Density dependent regulation of fecundity in *Syngamus trachea* populations in semi-naturally occurring ring-necked pheasants (*Phasianus colchicus*) and wild Carrion Crows (*Corvus corone*). *Parasitology*, 143 (6), pp. 716-722.

1 **Density dependent regulation of fecundity in *Syngamus trachea* populations in semi-**
2 **naturally occurring ring-necked pheasants (*Phasianus colchicus*) and wild Carrion Crows**
3 **(*Corvus corone*).**

4

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9

10 **ABSTRACT**

11 Previous work has highlighted increased opportunities for the transmission of *Syngamus trachea*
12 within pheasant release pens, due in part to the highly aggregated distribution of the infectious
13 stages around feed hoppers and communal areas. Despite this, the distribution of adult worms
14 within their definitive hosts is not significantly different from predicted distributions under
15 Taylor's power law. Therefore, density-dependent processes are probably acting to regulate *S.*
16 *trachea* population dynamics. Patterns of nematode fecundity and parasite establishment were
17 investigated in a semi-naturally occurring population of ring-necked pheasants (*Phasianus*
18 *colchicus*) and a wild population of carrion crows (*Corvus Carone*).

19

20 Worm length was a reliable indicator of nematode fecundity, and an inverse relationship between
21 mean worm length and mean worm burden was identified within both species. The stunting of
22 worms at greater parasite densities was present in both immunologically naïve and previously
23 exposed pheasants, so is unlikely to be a function of age-dependent acquired immunity.
24 Interestingly, the effect of parasite crowding on mean worm length was stronger in the crow
25 population, apparently driven by a greater mean worm burden when compared with pheasants.
26 The findings of the present study are in agreement with previous work that pheasants do indeed
27 develop immunity to *S. trachea*, however nematode length and fecundity appear to be a function
28 of parasite density, and therefore parasite-mediated competition and not host-mediated
29 heterogeneities in immunocompetence.

30

31 **Keywords**

32 *Syngamus trachea; density dependence; Pheasant; Crow; Fecundity; Worm length; immunity*

33

34 *Introduction*

35 One recurring theme within parasite ecology is the relative stability of parasite populations in
36 domestic and wild animal hosts (Anderson & May, 1978; Tompkins & Hudson, 1999), which
37 suggests that some form of regulatory mechanism must be ensuring population stability. The
38 majority of these mechanisms are driven by parasite density, i.e. are a function of mean parasite
39 burden within individual hosts; thus acting on infra-populations as opposed to populations as a
40 whole. Indeed, density-dependent regulatory mechanisms act on many aspects of the parasite
41 lifecycle, such as parasite establishment, growth, fecundity, development and maturation times,
42 and adult survival (Walker *et al.*, 2009). Growth and fecundity for instance, being the two most
43 common aspects of the life cycle regulated by such mechanisms in helminth populations
44 (Tompkins & Hudson, 1999), are particularly important at regulating the abundance of the ‘free-
45 living’, infectious stages within the environment, and therefore determining the extent of future
46 infections. These density-dependent mechanisms are important for regulating and stabilising
47 transmission dynamics, and therefore the parasite-host relationship, by ensuring that infra-
48 populations do not become too over or underdispersed.

49

50 Despite knowledge of the existence of such regulation, the mechanisms underlying density-
51 dependence are poorly understood, as it is difficult to disentangle host and parasite responses to
52 increasing parasite challenge (Paterson & Viney, 2002). Host immune responses have been
53 demonstrated to reduce establishment, survivability and fecundity of parasitic nematodes, and it is
54 hypothesised that innate and adaptive immune responses, whose response to infection increases
55 with increasing parasite density, are responsible for the manifestation of density dependence
56 (Paterson & Viney, 2002). Similarly, intraspecific competition for space and resources once inside
57 the host has also been implicated as a driver of density-dependent regulation. Indeed, Michael and
58 Dunby (1989), hypothesised that parasite-mediated competition was responsible for *Trichuris*
59 *muris* establishment in the mouse, owing to the finite carrying-capacity of the caecum.

60

61 *Syngamus trachea* is a parasitic nematode occurring in a wide range of avian hosts (Gethings *et*
62 *al.*, 2015a;b). The non-specific nature of this parasite makes it possible to study differences in
63 host-mediated responses to a natural challenge of *S. trachea*. In a previous paper by Gethings *et al.*
64 (2015b), we highlighted the fact that despite increased opportunities for transmission of *S. trachea*
65 within pheasant release pens, relatively low numbers of adult worms are consistently recovered
66 upon post-mortem investigation. This is often the case in experimental infections using large
67 numbers of infective larvae (Olivier, 1944; Guildford & Herrick, 1954). Despite these previous
68 studies finding relationships between *S. trachea* establishment and host immunity, no such work

69 has been conducted in semi-naturally occurring pheasant populations using natural infections of *S.*
70 *trachea*. The aims of the present study were to determine firstly, whether worm length is a good
71 indicator of fecundity within *S. trachea* populations, and secondly, to determine whether fecundity
72 is impaired in response to increasing worm burden.

73

74 2. Materials and Method

75

76 2.1 Pheasants

77 Male and female ring-necked pheasants (*Phasianus colchicus*) were recovered from two pheasant
78 estates in the South West of England from January 2014 to November 2015. All birds were either
79 obtained during the shooting season or were found dead on the estates at various times of the year.

80

81

82 2.2 Corvids

83 Crows were opportunistically sampled throughout the season, as the sites were undertaking Corvid
84 control via the use of Larsen traps. Crows and Rooks are known to be commonly infected with *S.*
85 *trachea*, and any density-dependent effects would likely be more apparent as worm burdens tend
86 to be larger than in pheasants. Age was roughly estimated by presence/absence and size of the
87 bursa of fabricius, which has usually atrophied by 6 months (Williams & Newton, 1969); however
88 no formal analysis of the effects of age on either parasite burdens or length was undertaken during
89 this study.

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92 2.3 Adult worm recovery

93 Adult *Syngamus trachea* worms were recovered from the trachea of pheasants and crows. The
94 trachea was first resected from the underlying connective tissue and transected slightly above the
95 proximal bifurcation of the bronchi. The trachea was then incised longitudinally through the
96 tracheal cartilage and the worms recovered using fine-tipped forceps. Adult worms were
97 distinguished from juvenile (L4) worms by observation under a microscope at varying
98 magnifications in order to detect the presence of fertilised ova. Adult worms from both species
99 were assessed according to Lewis (1928), which confirmed that these worms were indeed *S.*
100 *trachea* and that the worms were identical between species justifying the between-species
101 comparisons.

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103

104 2.4 Worm length and fecundity

105 Fernando *et al.* (1971) conducted in-depth pathogenetic examinations detailing adult worm length
106 at various stages of development, and determined the number of days post-infection (PI) to the
107 production of fertilised ova. Female *S. trachea* worms are fertile by day 14 PI, with minimum
108 female length at the adult stage generally averaging 10-15mm. Once fertile, Guildford and Herrick
109 (1954) found no relationship between days PI and female worm length, so we concluded that the
110 number of days PI was not a significant confounding factor within this study. As several authors
111 have demonstrated that worm length is significantly correlated with worm fecundity (Michael &
112 Dunby, 1989; Stear *et al.*, 1997; Stear & Bishop, 1999; Tompkins & Hudson, 1999; Walker *et al.*,
113 2009), the same principle was applied in this study. One hundred female worms were selected at
114 random in order to estimate the effect of length on the number of eggs per worm. Each female
115 worm was measured using a digital calliper (accuracy to 0.01mm) and the number of eggs were
116 counted using a stereomicroscope. In order to ensure egg viability, eggs were recovered from each
117 worm and maintained in the laboratory at 24 ° C (Wehr, 1937). Eggs were cultured to the infective
118 stage (L3) and manually hatched by applying light pressure between two cover slips.

119

120

121 2.5 Condition of the trachea

122 It has been demonstrated that prolonged infections with *S. trachea* result in the formation of
123 hyperplastic tracheal cartilage in which the adult male worms are deeply embedded (Clapham,
124 1935). These nodules begin to form between 26 and 37 days PI and generally remain indefinitely;
125 meaning previous exposure and current infection length can be determined. To assess whether
126 previous exposure influenced mean worm length or mean worm burden in subsequent infections,
127 pheasant tracheas were examined for the present of nodules. These nodules do not form at the
128 point of attachment in corvids so previous exposure cannot be determined. Therefore, crows were
129 excluded from this part of analysis.

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131

132 2.6 Statistical analysis

133 All data were analysed using the R statistical package for Macintosh. The Mean number of worms
134 per bird and the mean number of eggs per female worm were transformed before analysis to
135 normalise the distribution by applying log(+1) transformation. Differences in the mean number of
136 worms and mean worm length between species were assessed using Welch's *t*-test for unequal
137 samples. The effect of parasite burden on mean parasite length was assessed using linear
138 regression analysis using the *lm* function in R. In order to determine the minimum parasite density

139 at which negative effects are observable, iterative backwards-stepwise deletion of the highest
140 parasite densities was conducted until the regression was no longer significant at the $P = < 0.05$
141 level.

142

143 3.0 Results

144 The trachea of 38 pheasants and 92 crows were recovered and examined for the presence of adult
145 *S. trachea* worms, of which 1307 pairs were recovered.

146

147 3.1 Worm length and number of eggs

148 *In-utero* egg counts were performed on 106 adult female worms recovered from 10 crows and 10
149 pheasants, with an average (\pm SEM) of 1066 (\pm 41.5). Worm length explained 86.2% of the
150 variation in the number of eggs per female worm, even after controlling for the number of worms
151 per trachea ($F_{1,102} = 646.5$, $R^2 = 0.862$, $p = < 0.001$).

152

153 3.2 Worm length and parasite intensity

154 Mean worm length was significantly correlated with parasite density for both pheasants and
155 crows, with a significant reduction in mean worm length at higher parasite densities ($F_{1,127} =$
156 393.3 , $R^2 = 0.759$, $P = < 0.001$) (Fig.1). For individual species, there was a stronger effect of mean
157 worm burden on mean worm length for crows ($F_{1,90} = 340.2$, $R^2 = 0.79$, $p = < 0.001$) than for
158 pheasants ($F_{1,35} = 64.21$, $R^2 = 0.64$, $p = < 0.001$). Stepwise data-point deletion of the highest
159 parasite densities revealed that density-dependent effects begin to manifest above 4 worms per
160 bird for pheasants, and 2 worms per bird for crows, with the regression model not reaching the
161 significance level of $p < 0.05$ below 5 worms per host.

162

163 3.3 Trachea length

164 The length of the trachea did not influence either the mean number of worms per bird or mean
165 worm length for either species.

166

167 3.4 Presence of nodules, mean worm length and number of adult worms

168 Crows were excluded from this part of analysis so results are not reported. Retrospective analysis
169 of the Guildford and Herrick (1954) data, and trachea condition in the present study revealed that
170 pheasants with hyperplastic tracheal nodules tended to have fewer adult worms present in the
171 trachea (Mean \pm SEM = 5.45 ± 1.16 worms per bird) than birds without nodules (Mean \pm SEM =
172 10.36 ± 1.29 worms per bird) ($n = 31$, $t^{28} = 3.45$, $p = < 0.001$). Interestingly, female worms in birds
173 with evidence of previous exposure tended to be longer (Mean \pm SEM = $15.42 \text{ mm} \pm 0.73$) when

174 compared with worms in birds that had no evidence of previous exposure (Mean \pm SEM = 10.43
175 mm \pm 0.79) ($n = 23$, $t^{13} = -3.13$, $p = < 0.001$).

176

177 *3.5 Mean worm length and mean worm burden between species*

178 The mean number of adult worms per trachea differed significantly between species, with crows
179 having a mean worm burden of 11.17 (\pm SEM = 0.10) and pheasants having an average of 7.54 (\pm
180 SEM = 1.39) worms per trachea ($t^{72.14} = 2.02$, $p = 0.04$). Similarly, mean worm length differed
181 significantly between species, with pheasants having a mean worm length of 17.97 mm (\pm SEM =
182 0.85) and crows having a mean worm length of 15.55 mm (\pm SEM = 0.55) ($t^{66.58} = 2.34$, $p = 0.02$).

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211 *4.0 Discussion*

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213 Density-dependent reductions in worm size and fecundity have been reported in a large number of
214 studies (Michael & Dunby, 1989; Stear *et al.*, 1997; Stear & Bishop, 1999; Tompkins & Hudson,
215 1999; Walker *et al.*, 2009), and density-dependent reductions in worm length, but not necessarily
216 fecundity, are reported in practically all nematode species (Mossinger & Wenk, 1986; Szalai &
217 Dick, 1989; Sinniah & Subramaniam, 1991; Skorpung *et al.*, 1991; Marcogliese, 1997; Dezfuli *et*
218 *al.*, 2002; Irvine *et al.* 2001; Richards & Lewis, 2001). A vast majority of studies concerning
219 density dependence have been laboratory-based experimental infections, which do not accurately
220 represent conditions facing free-living wild animal populations in terms of parasite load and
221 encounter rates. The present study provides reliable information concerning apparent density-
222 dependent regulation of fecundity in both an intensively-managed pheasant population, and a free-
223 living wild population of corvids. Although the fact that immune status is responsible for
224 regulating the establishment of *S. trachea* in ring-necked pheasants is not novel, this is first
225 mention of both parasite and host-mediated factors regulating *S. trachea* populations in any bird
226 species.

227

228 In agreement with previous studies (Olivier, 1944; Guildford and Herrick, 1954), immune function
229 is responsible for the establishment of *S. trachea* within the ring-necked pheasant. This is
230 demonstrated by a reduction in parasite abundance in birds that had evidence of previous
231 exposure. There was however, a trend for greater numbers of adult worms in crows, which
232 suggests that worm establishment is not constrained by size or length of the trachea, and therefore
233 overall host size, however is perhaps a function of host immunity. Indeed, Olivier (1944), found
234 that *S. trachea* establishment was dose dependent. He found that the number of worms
235 establishing was inversely proportional to the size of the infective dose, and attributed this to the
236 strength of the immune response (Olivier, 1944). This result is in stark contrast to the findings of
237 Michael and Dunby (1989), who found that *Trichuris muris* establishment in the murine host is
238 believed to be regulated by density-dependent infraspecific competition, owing to the finite space
239 in the caecum. It is unlikely however, that *S. trachea* establishment is regulated in a similar
240 manner as more worms have been found in crows with a shorter trachea, and there was no
241 relationship between trachea length and mean worm burden. This apparent immune-mediated
242 inhibition on worm establishment has also been identified for *S. trachea* in chickens, with a lower
243 mean worm burden generally identified in older, previously exposed chickens (Crawford, 1940). If

244 establishment was merely a result of parasite-mediated competition, worm establishment, and
245 therefore burden, would be similar in both immunological naïve and previously exposed birds
246 (Luong *et al.*, 2011).

247
248 One reason to explain the trend for higher worm abundance in crows is acquired-immunity.
249 Pheasants are known to develop moderate immunity to *S. trachea*, however, no such work has
250 been conducted in wild crow populations. Being a known reservoir for *S. trachea*, it may be that
251 crows have a higher parasite threshold for the stimulation of an immune response or they do not
252 develop significant immunity to subsequent infections. Indeed, pheasants appear to be more
253 susceptible to infection early on in the rearing process, whereas *S. trachea* adults have been
254 recovered from crows of varying ages (Personal unpublished data). Further work is however,
255 required in order to determine whether wild crows develop any immunity to *S. trachea*.

256
257 Although density-dependent reduction of worm fecundity was present in both species, the fact that
258 the effect of crowding on mean worm length was more profound within the crow population is
259 interesting. Mean worm burden explained 82% of the variation in mean worm length in crows,
260 compared with 64% in pheasants, with crows having a tendency for a greater mean worm burden
261 when compared with pheasants. Even so, the fact that worms tended to be shorter in crows, in
262 response to higher mean worm burdens, suggests that these effects are indeed density-dependent.
263 The inverse relationship between worm length and worm burden was present in both species, and
264 appears to be a result of parasite-mediated competition, for either space or resources. Indeed, these
265 effects were even observed in pheasants with no history of previous exposure. Similarly, as there
266 was a vast number of birds of different ages, it is unlikely that age-dependent acquired-immunity
267 was responsible for the manifestation of density dependence within these birds, as the effects were
268 identified in juveniles, as well as adult birds, with little to no acquired immunity. Conversely,
269 Paterson and Viney (2002), observed the absence of density-dependent mechanisms at regulating
270 survivability and fecundity of *Strongyloides ratti* infra-populations in immuno-compromised
271 hosts. These mechanisms were however, present in later primary infections, suggesting that host
272 mediated heterogeneities in immuno-competence are regulating population dynamics before
273 intraspecific competition for space and nutrients ever occurs in experimentally infected rats
274 (Paterson & Viney, 2002). Alternatively, worm length has been shown to be related to levels of
275 local parasite-specific immunoglobulin A (IgA) (Stear *et al.*, 1997). These responses are however,
276 often absent in immunologically-naïve animals, and only generally manifest in animals that have
277 been previously exposed (Craig *et al.*, 2014) so it is unlikely to be occurring within these study
278 populations.

279 The parasite threshold for the manifestation of density-dependence within this study was low
280 compared with other studies. For instance, the threshold for density-dependent reductions in
281 fecundity in the caecal nematode, *Heterakis gallinarum*, in pheasants is 96 worms (Tomkins &
282 Hudson, 1999). Similarly, this threshold for *Trichostrongylus colubriformis* in sheep is around 3000
283 worms per host (Dobson *et al.*, 1990). It is generally believed that density-dependent effects are of
284 greater importance for parasites that are large compared with their host (Poulin & Morand, 2000).
285 Indeed, *S. trachea* adults can grow up to ~33 mm in length in an 80-100mm long trachea (Crow).
286 In comparison, mean worm length of *Heterakis gallinarum* adults in the caecae of pheasants is
287 around 9.64 mm (± 0.11) (Tompkins & Hudson, 1999), in caecae ranging from 240.11 for male
288 and 213.84 for female pheasants respectively. Similarly, *Pterygodermatites peromysci*, a
289 nematode parasite of mice, is regulated by tight density-dependent restrictions on the number and
290 length of adult worms in the small intestine (Luong *et al.*, 2011). Similarly to *S. trachea*, *P.*
291 *peromysci* can grow up to 33 mm in a 250 mm mouse intestine (Luong *et al.*, 2011).

292
293 The findings of the present study are in agreement with previous work that pheasants do indeed
294 develop immunity to *S. trachea* (Olivier, 1944; Guildford & Herrick, 1954), however nematode
295 length and fecundity appear to be a function of parasite density, and therefore parasite-mediated
296 competition and not host-mediated heterogeneities in immunocompetence.

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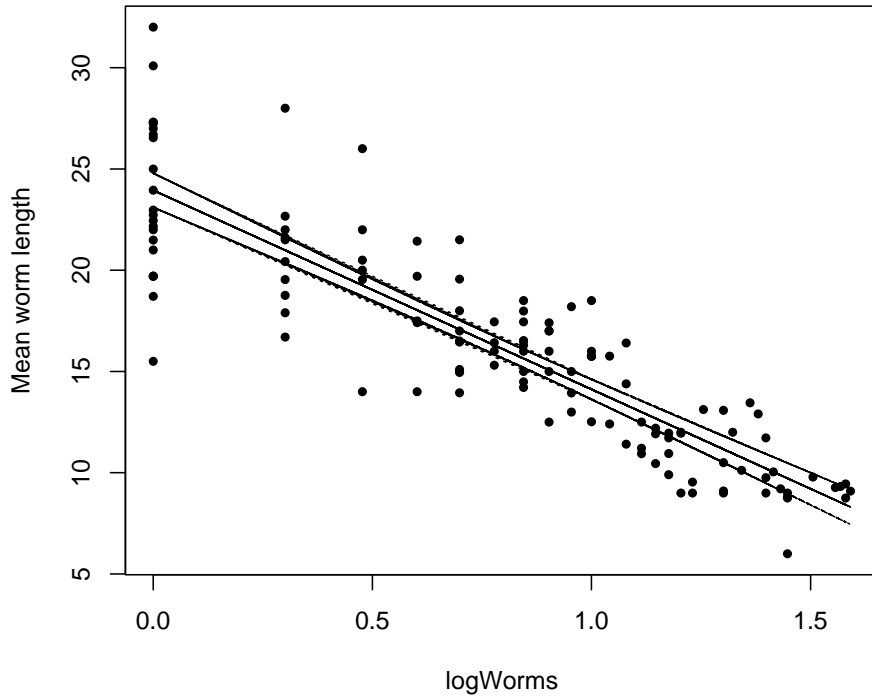
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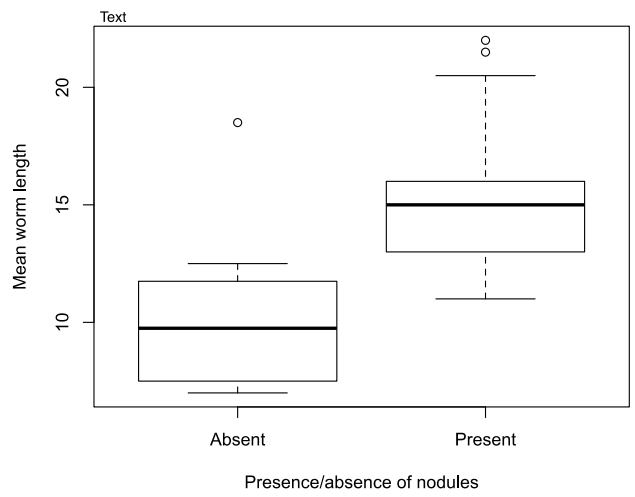
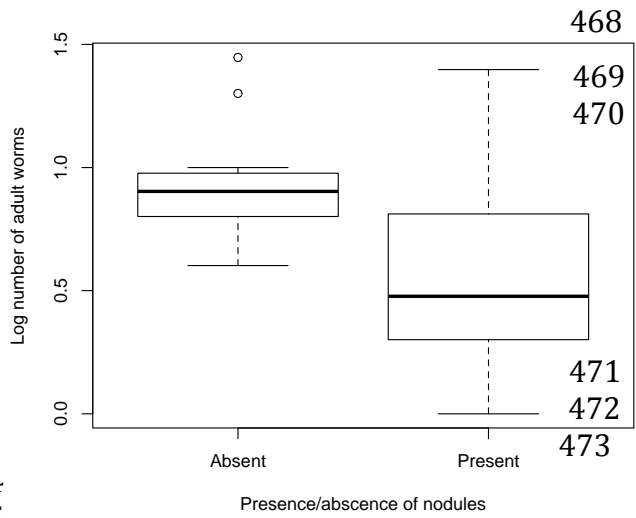
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451 **Figure 1 Relationship between log-mean number of worms and mean worm length for both species. Dashed line is**
452 **95% confidence interval.**

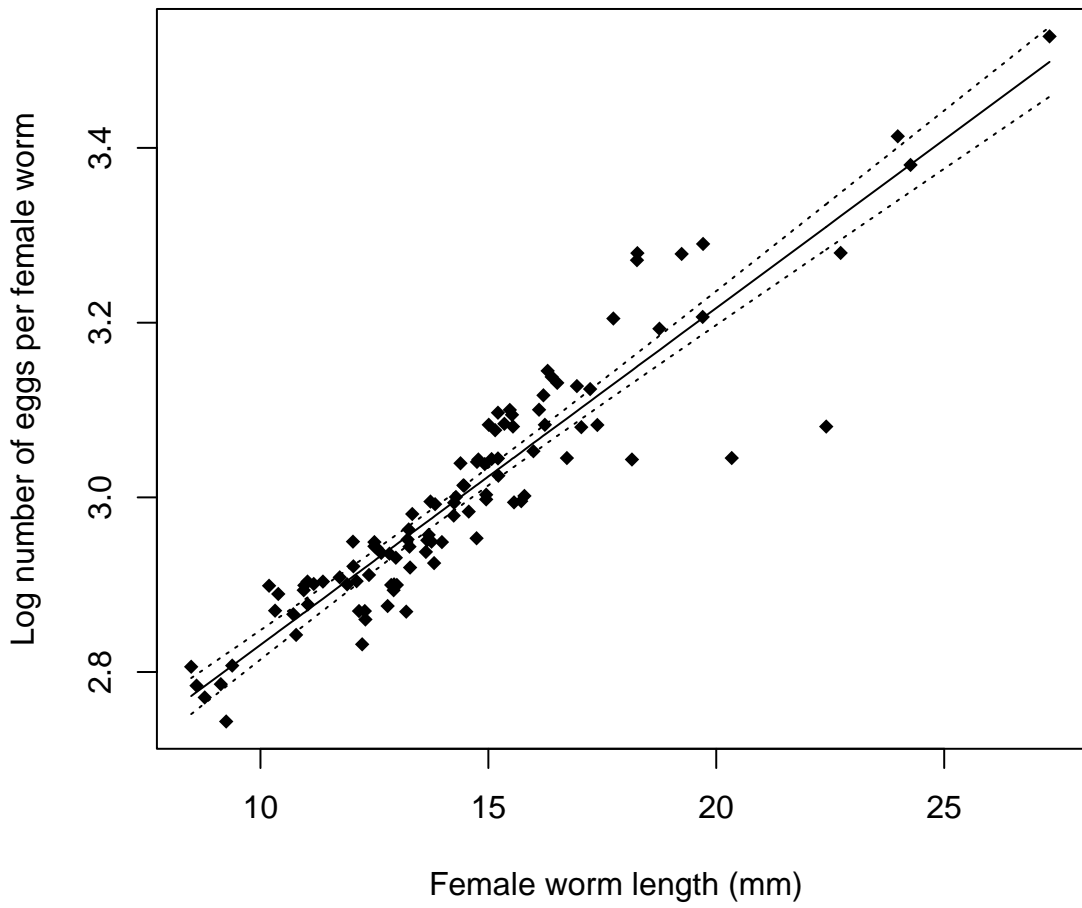
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Figure2 Relationship between the presence of nodules and mean worm burden and mean worm length in Pheasants.

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Figure 3?