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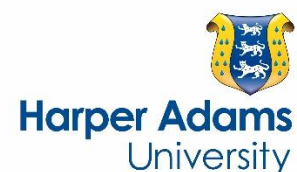
by Gethings, O.J., Sage, R.B. and Leather, S.R.

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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*).**

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5 O J Gethings[1], R B Sage[2] and S R Leather[1]

6 *[1]Department of Crop & Environment Sciences, Harper Adams University, Edgmond,*

7 *Newport, TF10 8NB UK;*

8 *[2]Game & Wildlife Conservation Trust, Burgate Manor, Fordingbridge, SP6 1EF, UK.*

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*).

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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

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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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.

130

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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 (±SEM) of 1066 (± 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 ± SEM = 5.45 ± 1.16 worms per bird) than birds without nodules (Mean ± 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 ± SEM = 15.42 mm ± 0.73) when

174 compared with worms in birds that had no evidence of previous exposure (Mean ± SEM = 10.43

175 mm ± 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 (± SEM = 0.10) and pheasants having an average of 7.54 (±

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 (± SEM =

182 0.85) and crows having a mean worm length of 15.55 mm (± 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; Skorping *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

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

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

Although density-dependent reduction of worm fecundity was present in both species, the fact that the effect of crowding on mean worm length was more profound within the crow population is interesting. Mean worm burden explained 82% of the variation in mean worm length in crows, compared with 64% in pheasants, with crows having a tendency for a greater mean worm burden when compared with pheasants. Even so, the fact that worms tended to be shorter in crows, in response to higher mean worm burdens, suggests that these effects are indeed density-dependent. The inverse relationship between worm length and worm burden was present in both species, and appears to be a result of parasite-mediated competition, for either space or resources. Indeed, these effects were even observed in pheasants with no history of previous exposure. Similarly, as there was a vast number of birds of different ages, it is unlikely that age-dependent acquired-immunity was responsible for the manifestation of density dependence within these birds, as the effects were identified in juveniles, as well as adult birds, with little to no acquired immunity. Conversely, Paterson and Viney (2002), observed the absence of density-dependent mechanisms at regulating survivability and fecundity of *Strongyloides ratti* infra-populations in immuno-compromised hosts. These mechanisms were however, present in later primary infections, suggesting that host mediated heterogeneities in immuno-competence are regulating population dynamics before intraspecific competition for space and nutrients ever occurs in experimentally infected rats (Paterson & Viney, 2002). Alternatively, worm length has been shown to be related to levels of local parasite-specific immunoglobulin A (IgA) (Stear *et al.,* 1997). These responses are however, often absent in immunologically-naïve animals, and only generally manifest in animals that have been previously exposed (Craig *et al.,* 2014) so it is unlikely to be occurring within these study 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 *Tricostrongylus 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 cecae 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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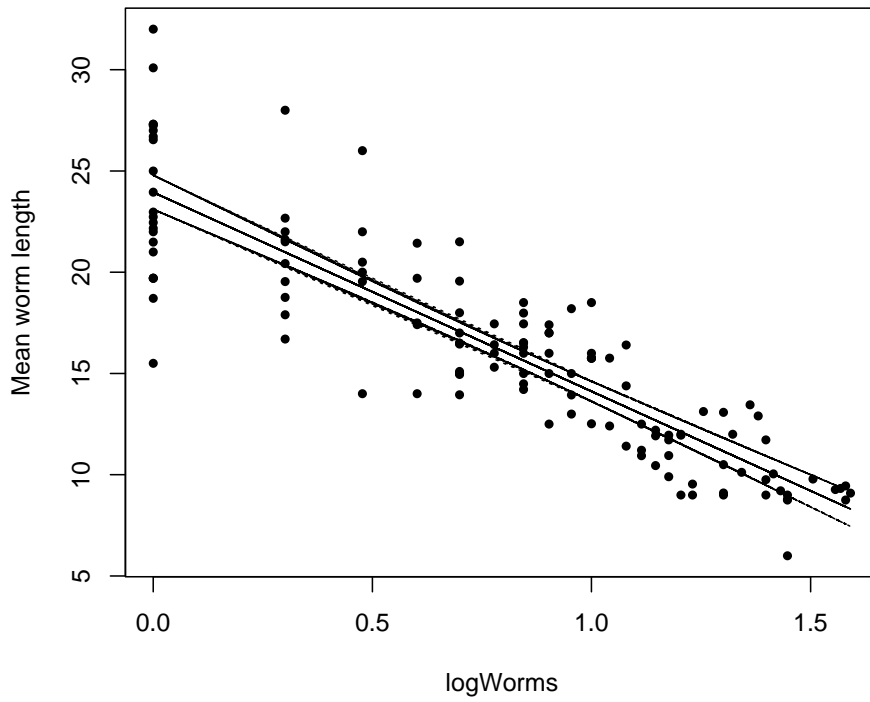
451   **Figure 1 Relationship between log-mean number of worms and mean worm length for both species. Dashed line is**
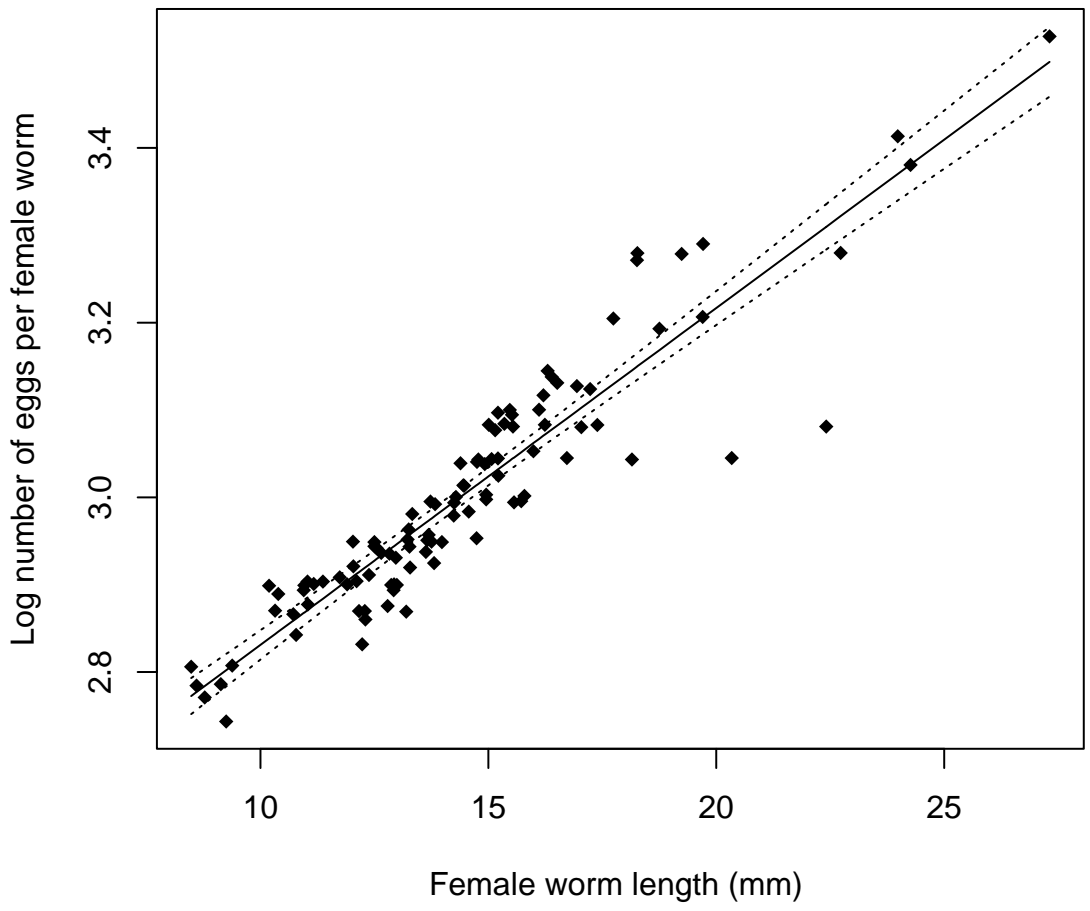452   **95% confidence interval.**

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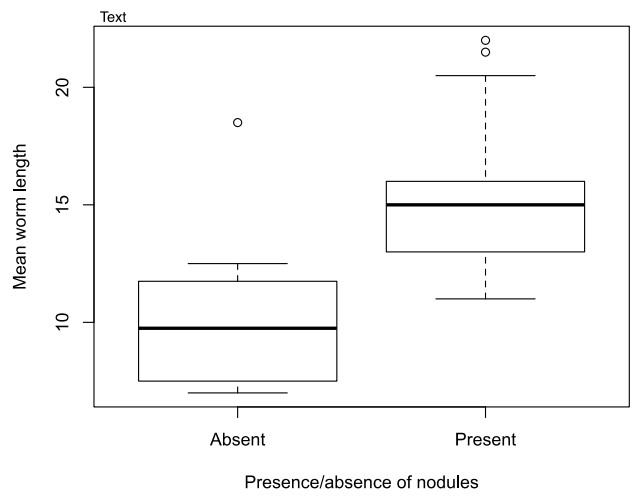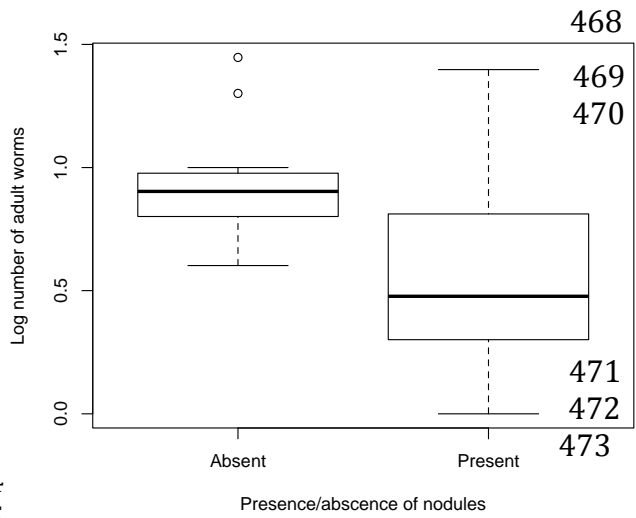
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Figure2 Relationship between the presence of nodules and mean worm burden and mean worm length in Pheasants.

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