Size dimorphism and sexual segregation in pheasants: tests of three competing hypotheses

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Fine scale sexual segregation outside of the mating season is common in sexually dimorphic and polygamous species, particularly in ungulates. A number of hypotheses predict sexual segregation but these are often contradictory with no agreement as to a common cause, perhaps because they are species specific. We explicitly tested three of these hypotheses which are commonly linked by a dependence on sexual dimorphism for animals which exhibit fine-scale sexual segregation; the Predation Risk Hypothesis, the Forage Selection Hypothesis, and the Activity Budget Hypothesis, in a single system the pheasant, *Phasianus colchicus*; a large, sedentary bird that is predominantly terrestrial and therefore analogous to ungulates rather than many avian species which sexually segregate. Over four years we reared 2400 individually tagged pheasants from one day old and after a period of 8-10 weeks we released them into the wild. We then followed the birds for 7 months, during the period that they sexually segregate, determined their fate and collected behavioural and morphological measures pertinent to the hypotheses. Pheasants are sexually dimorphic during the entire period that they sexually segregate in the wild; males are larger than females in both body size and gut measurements. However, this did not influence predation risk and predation rates (as predicted by the Predation Risk Hypothesis), diet choice (as predicted by the Forage Selection Hypothesis), or the amount of time spent foraging, resting or walking (as predicted by the Activity Budget Hypothesis). We conclude that adult sexual size dimorphism is not responsible for sexual segregation in the pheasant in the wild. Instead, we consider that segregation may be mediated by other, perhaps social, factors. We highlight the importance of studies on a wide range of taxa to help further the knowledge of sexual segregation.

1 Size dimorphism and sexual segregation in pheasants: tests of three competing hypotheses

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24   **Abstract**

25   Fine scale sexual segregation outside of the mating season is common in sexually

26   dimorphic and polygamous species, particularly in ungulates. A number of hypotheses predict

27   sexual segregation but these are often contradictory with no agreement as to a common cause,

28   perhaps because they are species specific.

30   We explicitly tested three of these hypotheses which are commonly linked by a

31   dependence on sexual dimorphism for animals which exhibit fine-scale sexual segregation; the

32   Predation Risk Hypothesis, the Forage Selection Hypothesis, and the Activity Budget

33   Hypothesis, in a single system the pheasant, *Phasianus colchicus*; a large, sedentary bird that is

34   predominantly terrestrial and therefore analogous to ungulates rather than many avian species

35   which sexually segregate.

37   Over four years we reared 2400 individually tagged pheasants from one day old and after

38   a period of 8-10 weeks we released them into the wild. We then followed the birds for 7 months,

39   during the period that they sexually segregate, determined their fate and collected behavioural

40   and morphological measures pertinent to the hypotheses.

42   Pheasants are sexually dimorphic during the entire period that they sexually segregate in

43   the wild; males are larger than females in both body size and gut measurements. However, this

44   did not influence predation risk and predation rates (as predicted by the Predation Risk

45   Hypothesis), diet choice (as predicted by the Forage Selection Hypothesis), or the amount of

46   time spent foraging, resting or walking (as predicted by the Activity Budget Hypothesis).

47

48   We conclude that adult sexual size dimorphism is not responsible for sexual segregation

49   in the pheasant in the wild. Instead, we consider that segregation may be mediated by other,

50   perhaps social, factors. We highlight the importance of studies on a wide range of taxa to help

51   further the knowledge of sexual segregation.

52

53 **Introduction**

54 Sexual segregation, in which females and males are separated in time and/or space outside of the

55 mating season, is common in a variety of birds, mammals, fish and reptiles (Bleich et al. 1997;

56 Ruckstuhl & Neuhaus 2005; Ruckstuhl & Neuhaus 2000). Fine scale sexual segregation, in

57 which segregation occurs within a small area, is particularly prevalent in species with strong

58 sexual dimorphism (Ruckstuhl & Neuhaus 2002) and those with polygynous mating systems

59 (Clutton-Brock 1989). However, there is little consensus about the underlying factors driving

60 sexual segregation (Alves et al. 2013; Bonenfant et al. 2007).

61

62   There are four main, but non-exclusive, hypotheses proposed to explain why sexual

63 segregation occurs in polygynous populations that are commonly linked by a dependence on

64 sexual (size) dimorphism (Bon & Campan 1996; Bowyer 2004; Ruckstuhl & Neuhaus 2005).

65 The first, the Predation Risk Hypothesis (PRH), or Reproductive Strategy Hypothesis, postulates

66 that sexual segregation results from each sex investing differentially in strategies to maximise

67 their own reproductive success (Main & Coblentz 1996). Females, perhaps accompanied by

68 dependent and vulnerable young, avoid higher predation risks and forage in places or at times

69 that offer lower nutrient intake (Corti & Shackleton 2002; Main & Coblentz 1996). In contrast,

70 males may opt to maximize their competitive advantage by investing in growth and therefore

71 exploit nutrient rich habitats despite the increased risk of predation (Clutton-Brock et al. 1982;

72 Prins 1989). The second, the Forage Selection Hypothesis (FSH), or Sexual Dimorphism Body-

73 size Hypothesis (Main 1996), predicts that allometric differences in body size, bite size, energy

74 requirements and/or fibre digestion between the sexes can lead to differences in diet selection

75 and habitat choice (Barboza & Bowyer 2000; Demment 1982; Main & Coblentz 1996).

76 Individuals with a smaller gut system are less able to digest lower quality food items and are

77 predicted to feed on higher quality diets than larger conspecifics (Barboza & Bowyer 2001;

78 Demment & Van Soest 1985). The third, the Activity Budget Hypothesis states that body size

79 dimorphism promotes differences in activity budgets and synchrony of these behaviours results

80 in aggregation of the sexes (Conradt 1998; Ruckstuhl & Neuhaus 2002; Ruckstuhl & Neuhaus

81 2000). Here, energetic requirements and digestive abilities predict that the smaller sex will spend

82 more time foraging and less time resting and digesting than the larger sex (Ruckstuhl 1999;

83 Ruckstuhl 1998), such that females will congregate to engage in foraging together while males

84   rest in areas with low risk of predation. A fourth, and much less studied hypothesis is the

85   Weather Sensitivity Hypothesis which suggests that animals could differ in their weather

86   sensitivity (e.g. Young & Isbell 1991), where larger individuals, often males, suffer higher

87   absolute heat loss and therefore opt for warmer habitats often at the expense of foraging

88   availability (Conradt et al. 2001)

89

90   There is little consensus as to what are the driving mechanisms underpinning sexual

91   segregation (Conradt & Roper 2000; Ruckstuhl et al. 2006). Typically, studies are unable to

92   tease apart which hypothesis best predicts why species segregate, often suggesting that multiple

93   hypothesis could be the cause (Alves et al. 2013; Bonenfant et al. 2007; Loe et al. 2006). One

94   reason for this could be that much of the research concentrates on ungulates (Alves et al. 2013;

95   Bon & Campan 1996; Bowyer & Kie 2004), in particular ruminants (Bowyer & Kie 2004) in

96   systems that are notoriously difficult to study in the wild (Michelena et al. 2004). It is not always

97   feasible in such free-ranging mammalian systems to collect the physiological and behavioural

98   data necessary to explicitly separate and test these competing hypotheses. Furthermore, in some

99   study locations, their natural predators have disappeared, rendering it difficult to explore the

100 effects of predation risk. Finally, many species that have been studied are dietary specialists,

101 meaning that variations in diet quality may chiefly depend on differences between particular

102 plants, even those of the same species, and thus dietary intake is difficult to determine accurately

103 without measuring the nutrient quality of each mouthful (Dove & Mayes 1996).

104

105   The pheasant, *Phasianus colchicus,* provides a novel, alternative system to ungulates to

106 try to tease apart hypotheses of segregation based on sexual size dimorphism. Many avian

107 species sexually segregate (e.g. northern giant petrels (*Macronectes halli*) (González-Solís et al.

108 2000) and Great bustards (*Otis tarda*) (Palacín et al. 2009)), however it is often attributed to

109 differential settlement of the sexes in discrete habitats, often over large distances, and is

110 primarily restricted to difference in migration behaviours or broad differences in habitat use

111 (Catry et al. 2006). Pheasants, however, exhibit a pattern of fine scale sexual segregation similar

112 to the regularly studied ungulate, in that they segregate, outside of the mating season, within the

113 same area as each other (Hill & Ridley 1987). Specifically, during the late autumn and winter,

114 females aggregate in same sex groups whereas males avoid both males and females (Whiteside et

115 al. 2018). Such segregation persists until early March (Hill & Ridley 1987; Hill & Robertson

116 1988) when harems of females visit and eventually join territory-holding males, which likely

117 reduces their harassment by other males (Ridley and Hill 1987) and allows females to decrease

118 their vigilance levels and so increase time spent foraging (Whiteside et al. 2016a), until they

119 independently start to nest and incubate their eggs (Taber 1949). Pheasants become sexually

120 dimorphic by three weeks of age (Whiteside et al. 2017), and chicks in captivity (<8 weeks old)

121 exhibit preference for their own sex (Whiteside et al. 2017). As adults, males have highly

122 conspicuous plumage and are 40% larger than the cryptic females (Wittzell 1991). Between

123 October and February, before the breeding season, released first year pheasants show increasing

124 levels of segregation (Whiteside et al. 2018). Therefore, pheasants present a system that is

125 analogous to the currently studied ungulates, yet being distantly related this may offer more

126 general insights as to how size-dimorphism may influence sexual segregation for species with

127 fine scale sexual segregation.

128

129   Mechanisms that drive sexual segregation of pheasants are poorly understood. In the

130 wild, sexual segregation of adults was observed at both a spatial and temporal scale that could

131 not be explained by crude measures of habitat structure, although the homogenous nature of the

132 study and reliance on data from supplementary feeding sites meant that fine scale differences in

133 habitat structure may have not been captured (Whiteside et al. 2018). During early life when the

134 sexes differ little in their size, juvenile pheasants reared in captivity in an environment that

135 controlled for habitat selection and diet, albeit under unnaturally high numbers but in a sex ratio

136 analogous to that observed in the wild, exhibited strong preferences for same-sex individuals in

137 binary choices which may drive segregation (Whiteside et al. 2017). It was suggested that at this

138 stage, females aggregate with other females in response to male aggression. When adults, body-

139 size dimorphism is more pronounced and the habitat is more heterogeneous and consequently we

140 may find other factors may influence sexual segregation. We excluded the possibility that

141 segregation in wild-living pheasants arises because of the Weather Sensitivity Hypothesis.

142 Pheasants typically spend the majority of their time in hedgerows (Hill & Robertson 1988), a

143 place that offers protection from the weather but also a site with a high abundance of natural

144 forage (e.g. insects, leaves, berries, wild fruit and nuts Lachlan & Bray 1973). This violates a

145 major assumption of the Weather Sensitivity Hypothesis in that a habitat should offer either

146   shelter or good foraging opportunity, not both. Often game-keepers will provide a designated

147   cover crop that is designed to provide both (Hill & Robertson 1988). Therefore, in this study we

148   tested the remaining three main hypotheses for sexual segregation that relate to sexual (size)

149   dimorphism in free-living adult pheasants.

150

151   Firstly, pheasants are at risk from terrestrial predators, such as the fox, *Vulpes vulpes*

152   (Hessler et al. 1970; Krauss et al. 1987), and aerial predators, such as goshawks, *Accipter*

153   *gentilis*, sparrow hawks, *Accipiter nicus,* and buzzards, *Buteo buteo,* (Kenward et al. 2001;

154   Kenward et al. 1981) producing high mortality rates of up to 80% in the first month after release

155   into the wild (Hessler et al. 1970). Sexual segregation occurs prior to the first breeding season

156   (Hill & Ridley 1987; Whiteside et al. 2018), and this therefore removes the possibility that

157   females caring for young are avoiding particularly risky sites or times. However, males may still

158   opt for a riskier foraging and movement strategy if there is a benefit for their growth. Therefore,

159   if the Predation Risk Hypothesis influences segregation then we expect that predation risk (in

160   terms of willingness to approach an area where predators have recently visited) and consequently

161   predation rates will differ between sexes.

162

163   Secondly, adult pheasants are dietary generalists (Hoodless et al. 2001) and dietary

164   choices can be assayed post-mortem from food that is well preserved and identifiable in the crop

165   of birds that have been shot during recreational hunting (Whiteside et al. 2015). Post-mortem

166   analyses of these shot birds also allows for the measurements of gut morphometrics. Both these

167   factors permit explicit testing of the Forage Selection Hypothesis. While gut size is likely to co-

168   vary with body size, with larger males possessing larger guts, allometric differences are

169   meaningful from a nutritional point of view as larger guts are more effective digesters and

170   absorbers of low quality diet (Barboza & Bowyer 2000). In addition, body size dimorphisms may

171   correspond to differences in food processing efficiency via bite size (Illius & Gordon 1987) or

172   grinding capacity in the gizzard (Putaala & Hissa 1995). If the Forage Selection Hypothesis

173   influences segregation then we expect that the larger sex (males in the case of pheasants) will

174   have larger guts and heavier gizzards, and this will be matched by a difference in diet

175   corresponding to spatial or temporal segregation.

176

177   Thirdly, adult pheasants are large, sedentary, diurnal and sexually distinct. Consequently,

178 their behaviours in the wild can be easily observed and their activity recorded. Differences in

179 behaviour between the sexes have been observed during the breeding season (Whiteside,

180 Langley et al 2016), however little is known about behavioural differences outside the breeding

181 season during the period when pheasants sexually segregate. If the Activity Budget Hypothesis

182 operates then we expect that during the periods of sexual segregation male and female pheasants

183 will differ in their behaviour, specifically state behaviours known to influence sexual segregation

184 in ungulates (e.g. foraging, locomotion or resting time (Ruckstuhl 1998)). Male pheasant chicks

185 in captivity were more aggressive than females and was a potential mechanisms driving

186 segregation (Whiteside et al. 2017). However, pheasants in the wild exhibit little aggression

187 during the periods that they sexually segregate, with male-male aggression rising from the start

188 of the breeding season and peaking mid-breeding season (Ridley 1983).

189

190   To tease apart these hypotheses we draw on two populations of individually identifiable

191 pheasants that were reared in captivity, had their morphometrics taken and then released into the

192 wild (see Table 1 for a description of each population and what was measured). The first

193 population was released into an environment that did not have predator control or recreational

194 shooting. Although initial release density was unnaturally high (~200 birds in a 0.5 Ha release

195 pen), after one month birds had dispersed across the study site. At this point the population density was

196 ~40 birds/km^2 which matched those of wild populations, falling within the density (16-54 birds/km^2) for

197 wild pheasants living in managed farmland in Austria and the density (0.6-64 birds/km^2) for pheasants in

198 their native range in China (Li 1996 in Johnsgard 1999). Crucially, within one month of release this

199 population showed clear sexual segregation which became pronounced as the year progressed

200 (see Whiteside et al. 2018). Releasing on sites without either predator control or recreational

201 hunting allowed us to measure natural predation rates. By using a system of motion sensitive

202 camera traps at feeding sites we were able to determine: 1) if pheasants avoid areas where foxes

203 had been present: and 2) if sexes differ in their willingness to enter an area where a fox had

204 previously been seen (essential for the PRH). The second population were birds that were reared

205 in captivity and released into the wild in large numbers (~ 350 birds in a 0.5 Ha release pen) as

206 part of a restocking programme. However, these birds were released on a much larger site and

207 within a few weeks of birds dispersing resulted in much lower density over the entire estate. On

208   this site there was managed predator control and the birds were subject to hunting. Birds released

209   using this method still show patterns of sexual segregation (Hill & Ridley 1987) similar to that

210   observed in pheasants released at lower density. Releasing onto a site that has recreational

211   hunting allows for us to conduct post mortem analysis that: 1) allows us to determine the extent

212   of sexual dimorphism in body size (essential for PRH, FSH and ABH) and in gut morphology

213   (essential for FSH); and 2) acts as a dietary snapshot, whereby crop sample analyses allows us to

214   determine diet (essential for FSH). Observing behaviour of pheasants during this period allows

215   us to determine activity budgets (essential for ABH).

216

217   **Material and methods**

218

219   *Rearing*

220

221   In May 2012 and 2013 we reared 1800 pheasants (900 / year) from one day old as part of

222   a long-term study to determine how early rearing conditions can influence development and post

223   release mortality. Chicks were placed in houses of 30 individuals with an equal sex ratio and

224   each house was randomly allocated a rearing treatment. While not relevant to this study, the

225   treatments included differences in supplemented diet in 2012 (see Table 1 and Whiteside et al.

226   2015) and access to perches in 2013 (see Table 1 and Whiteside et al. 2016b) as well as controls.

227   In 2014 and 2015 we reared a further 400 pheasants (200 / year) from one day old and housed

228   them in groups of 50 under identical conditions (see Table 1). Each year the birds were housed

229   for two weeks in heated sheds (2012/13: 1.3 m x 1.3 m; 2014/15: 2 m x 2 m) and were then

230   given access to an additional open grass run (2012/13 = 1.3 m x 6.8 m; 2014/15: 4 m x 12 m)

231   until release. All chicks were provided with age specific commercial chick crumbs (Sportsman

232   Game Feeds) *ad lib* and in excess. Water was provided *ad lib*. In all four years, birds were

233   marked with patagial wing tags (Roxan Ltd, Selkirk, UK) for identification with additional white

234   PVC wing tags (25mm x75 mm) with individually unique identifying numbers which could be

235   viewed from several tens of meters away.

236

237   *Release into the wild*

238

239   Following rearing, birds were randomly mixed from across different housing groups and
240   placed into open topped pens. Release pens typically consisted of wire mesh fences ~2 m high
241   enclosing an extensive area of woodland (GWCT 1991). In these pens birds were provided with
242   food and water *ad lib*. Birds could disperse from these pens and were free to roam and mix with
243   other released, as well as resident, pheasants. In 2012 and 2013 when birds were approximately
244   seven weeks old we released them onto the Middleton Estate, Hampshire, UK ($51^0$18'N, $1^0$4'W).
245   The estate, predominantly arable, hosts a game shoot and employs two game keepers to manage
246   the released pheasants through habitat management, providing supplementary food, and
247   controlling predator numbers. Between October and February birds were shot as part of a
248   recreational shoot. In 2014 and 2015 when birds were ten weeks old they were released at North
249   Wyke Farm, Devon ($50^0$77'N, $3^0$9'W). This site is grazed by cattle and sheep and no game
250   shooting or predator control occurred there. Forty feeders, filled with wheat, were placed within
251   the pen (n = 4) and in the surrounding countryside (n = 36) at a density of 0.16 per hectare. In
252   2014, each feeder was continuously monitored with Bushnell® Trophy motion activated
253   cameras. All animals that visited a feeder and its surrounding area were photographed and the
254   images were then viewed manually to record the time that pheasants and foxes visited the feeder
255   site. Individual pheasants could be identified from their wing tag numbers.

256

257   *Body size dimorphism*

258

259   We recorded the mass (Slater Super Samson spring balance – precision 5 g) and tarsus
260   length (precision 1 mm) of all birds upon release into the wild and for birds released in 2012 and
261   2013 we scored the same measures within four hours of them being shot.

262

263   For the released populations we used a General Linear Mixed Model (GLMM) to identify
264   whether males differed from females in their mass and tarsus length with rearing treatment and
265   sex as fixed factors and the rearing house as a random factor, with all two way interactions
266   included (Table 2). In 2014 and 2015 all birds were reared under identical conditions and
267   therefore rearing treatment was not included in the model. For birds shot in 2012 and 2013 a
268   General Linear Model (GLM) was used to ask if sexes differed in mass and tarsus length as

269   adults. The bird's age when shot, its rearing treatment and all two way interactions were included
270   in the GLM (Table 2).

271
272

273   *A test for the Predation Risk Hypothesis: First appearance at a feeder after the presence of a fox*

274

275   We recorded every sighting of a fox and pheasant at each of our feeder sites during
276   December 2014 and January 2015 using the motion camera traps. In order to test whether the
277   presence of foxes at feeders was an indicator of a risky environment that pheasants attended to,
278   we asked whether birds took longer to return to feeders after a fox had been there compared to
279   the time it took them to appear at a feeder after a time-matched control point the previous day.
280   We excluded instances where there were low visitation rates at a feeder, indicated by long
281   periods (>420 mins) between the time-matched control point and the first pheasant appearing.
282   This cut-off point was meaningful and discrete (Figure 1). This left a subset of the previous data
283   including 110 cases. We used a t-test to ask if pheasants took longer to approach a feeder if it had
284   been visited by a fox compared a time matched control point the previous day. We then looked at
285   each appearance of a fox and recorded the sex of the next pheasant to enter the same feeder
286   within a subsequent 30 minutes. We used a binomial test to determine if sexes differed in their
287   likelihood of approaching a feeder following a fox visit.

288

289   *A test for the Predation Risk Hypothesis: Do predation rates differ with sex*

290

291   In 2012 and 2013 we conducted searches of areas surrounding the release site to retrieve
292   birds that had been killed by predators. Searches were conducted daily from August-October and
293   then again in February. During the hunting season (late October to February) the area was visited
294   less frequently but more methodically by beaters who were engaged in driving the game to the
295   waiting hunters. They were informed of the project and searched for carcases and tags as they
296   walked through the site. In 2015 we collected birds that had been killed by a predator by
297   searching the release site and surrounding areas for carcases, locating these either directly or
298   guided by radio tags placed on 50 birds. In 2014 we did not conduct detailed searches for

299   carcases. A binomial test was used to test whether predation numbers differed between sexes

300   with the expected outcome based on the released sex ratio.

301

302

303   *A test for Forage Selection Hypothesis: Measuring gut morphology*

304

305   We collected linear gut measures (oesophagus, intestine, colon and ceca) and gut masses

306   (oesophagus, intestine, crop, gizzard and ceca; for methods see Leopold 1953) of 186 birds shot

307   in 2012. Ceca length and ceca mass were calculated as the average for both ceca. Gizzard

308   volume was measured as the height multiplied by width. We used a GLM to test whether gut

309   morphologies differed with sex. Since rearing treatment can influence gut morphology

310   (Whiteside et al. 2015) we included the rearing treatment and the age at which the bird was shot

311   as fixed factors (Table 2).

312

313   *A test for Forage Selection Hypothesis: Measuring crop contents in the wild*

314

315   In 2012, we removed the crops of 159 shot birds and measured the mass before and after

316   removal of its contents. Measures were transformed using the $\sqrt{x}$ transformation to meet

317   assumptions of normality and then a GLM was used to test if mass of crop content differed

318   between males and females. In 2013, we emptied the crops of 168 shot birds and quantified their

319   contents. We used a GLM to ask whether males differed from females in the number of different

320   food items discovered in their crops. Diet availability will change depending on when the bird is

321   shot and diet choice is influenced by rearing treatment (Whiteside et al. 2015) therefore in both

322   GLMs we included rearing treatment and the age of the bird when it was shot in the model

323   (Table 2). We separated all known items into common food categories (Wheat, Maize, Grass, Oil

324   Seed Rape, Insects, Seeds, Galls, Acorns) and used binomial tests to determine if sexes differed

325   in the likelihood of their crop containing food of each category.

326

327   *A test for Activity Budget Hypothesis: Measuring behaviour in the wild*

328

329   In 2012, we conducted continuous focal follows, for a maximum of 10 minutes,

330 observing 167 released pheasants between 18 September and 5 November. All observations were

331 conducted from inside a vehicle at a distance of > 10 m (e.g. Whiteside et al. 2016a) either

332 during the first 2 hours after first light or the final 2 hours before last light (Taber 1949). We

333 recorded the total time we observed the birds, the time spent foraging and the number of foraging

334 bouts they performed. A foraging bout began with the lowering of the head and neck towards the

335 ground and ended when the neck was raised. The proportion of time an animal spent foraging

336 was normalised using a logit transformation: log (y/1-y) (Warton & Hui 2010) and a GLM was

337 used to ask if the percentage of time spent foraging differed between the sexes.

338

339   In 2013, between 15 August and 16 September we conducted a series of 10 minute focal

340 follows with an instantaneous point sampling procedure at 30 second intervals on 214 pheasants.

341 This allowed us to collect state behaviours; in particular time spent performing resting, foraging

342 and locomotive behaviours and also aggressive interactions. All birds were identifiable from

343 their wing tags and were observed from a distance so as to not disturb their natural behaviours.

344 Vigilance was described as sitting or standing with neck extended and eyes open. Resting was

345 determined as either standing or lying with eyes closed. Aggressive interactions included threats,

346 run threats, lateral struts and fights (see Hill & Robertson 1988; Ridley 1983).We used a

347 Generalised Linear Model with a binomial distribution and a probit link function to ask if sexes

348 differed in their vigilance, walking and resting likelihoods. In all models early rearing

349 environment, time of day (AM or PM), and degree of aerial protection (open or closed) were

350 included as fixed factors, and all two-way interactions were assessed (Table 2).

351

Statistical Analyses

353   All GLM and GLMM analyses were conducted using SPSS v23. All models were

354 visually inspected for homogeneity of variance, normality of error and linearity.

355

Ethical Statement

357

358   All birds were reared using commercial procedures that adhere to the DEFRA Code of

359 Practice for the Welfare of Game Birds Reared for Sporting Purposes (DEFRA 2009). During

360   rearing, minimal handling was used for obtaining morphometrics and placing birds in testing

361   chambers. In 2012 and 2013, once birds dispersed from the release pen, gamekeepers supplied

362   supplementary feed and water, which was reduced after the shooting season (from 1st February).

363   The birds were shot as a part of a commercial shoot, and were not specifically shot for this study.

364   In 2014 and 2015 released birds were attended to by the authors and there was no shooting on the

365   study site. The work was approved by the University of Exeter Psychology Ethics Committee

366   and conducted under Home Office licences number PPL 30/3204 & PPL 30/2942

367

368   **RESULTS**

369

370   *Are birds sexually dimorphic during the period of the study?*

371

372   Males were significantly heavier (Table 3) and had longer tarsi (Table 4) compared to

373   females upon release into the wild and when they were shot as adults prior to their first breeding

374   season

375

376   *A test for the Predation Risk Hypothesis: Do sexes differ in their likelihood of being the first to*

377   *approach a feeder visited by a fox?*

378

379   Pheasants took significantly longer (approx. 2.5 times longer) to appear at a feeder after a

380   fox was present (193±35mins) than after a time-matched control point the previous day

381   (76±9mins) (t_{109} = 3.37, P = 0.001, Figure 2). There was no difference in the likelihood that a

382   male or female would be first to approach a feeding site in the following 30 minutes after the

383   sighting of a fox (female = 20; male = 30; Binomial test: P = 0.20).

384

385   *A test for Predation Risk Hypothesis: Do predation rates differ with sex?*

386

387   Predation did not differ with sex in the first 8 months after release in 2012 (Binomial

388   tests: 2012: female = 8; male = 5, P = 0.58); 2013 (Binomial test: female = 6; male = 12: P =

389   0.20); and 2015 (Binomial test: female = 15; male = 27: P = 0.12).

390

391   *A test for Forage Selection Hypothesis: Do sexes differ in their gut morphology?*

392

393   Males significantly differed from females in all aspects of measured gut morphologies

394   with larger and heavier gut regions, crops and gizzards (Table 5).

395

396   *A test for Forage Selection Hypothesis: Does diet composition differ between sexes?*

397

398   Males (17.38g ± 1.62) shot in 2012 had significantly more forage in their crops compared

399   to females (12.75g ± 1.08) ($F_{1,131} = 4.29$, $P = 0.040$, Figure 3). However, males (3.33 ± 0.16) did

400   not differ from females (3.52 ± 0.27) in the variety of food items found within their crop ($F_{1,147} =$

401   0.93, $P = 0.34$). The sexes appeared to utilise a similar diet with both sexes carrying similar

402   proportions of eight common food types in their crops. Males did not differ from females in the

403   likelihood that their crop would contain wheat, maize, grass, oil seed rape, insects, seeds, galls or

404   acorns (Table 6).

405

406   *A test for Activity Budget Hypothesis: Do other behaviour differ between sexes?*

407

408   Sexes did not differ in their percentage of time spent foraging; the length of each foraging

409   bout (Table 7); their likelihood of being vigilant ($F_{1,186} = 0.20$, $P = 0.66$) or their likelihood of

410   walking ($F_{1,186} = 2.54$, $P = 0.13$). There was only one incidence of resting behaviour during the

411   focal watches which was demonstrated by a male and there were no aggressive interactions

412   performed hence sex differences in these behaviours could not be compared.

413

414   **DISCUSSION**

415

416   During the late autumn and winter, when pheasants show an increased tendency to

417   sexually segregate (Whiteside et al. 2018), pheasants exhibited strong sexual size dimorphism.

418   Adult males were significantly heavier than females and had larger gut dynamics and heavier

419   gizzards, however, we found little evidence that sexes differed in behavioural and dietary

420   measures that are predicted to explain sexual segregation according to the three existing

421   hypotheses purporting to explain segregation due to size dimorphism (Bleich et al. 1997;

422   Bonenfant et al. 2007; Conradt 1998; Ruckstuhl 1998).

423

424   Males pheasants were 1.3x heavier than females which is similar to levels of dimorphism

425   seen in Northern giant petrel (*Macronectes halli*) (1.25: González-Solís 2004) but less than the

426   great bustard (*Otis tarda*) (2.48: Alonso et al. 2009), two avian species that are known to

427   sexually segregate. The extent of pheasant size dimorphism also closely matched that observed

428   in mammals exhibiting sexual segregation (red deer, *Cervus elephus*, (1.33: Clutton-Brock et al.

429   1982; Weckerly 1998), merino sheep, *Ovis aries*, (1.50: Michelena et al. 2004), bighorn sheep,

430   *Ovis canadensis*, (1.43: Blood et al. 1970). Pheasants share similarities with such ungulates

431   being highly terrestrial and sedentary, in contrast to the wide ranging and migratory petrel and

432   bustard.

433

434   Pheasants may reduce their risk of predation by increasing the lag between feeder

435   visitations after a fox visit compared to a time-matched control point the previous day,

436   suggesting that time taken to visit a feeder after a fox has been there provided a good assay of

437   risk sensitivity. However, we found that sexes did not differ in their exposure to fox predation

438   risk, at least at feeders, indicated by their likelihood of being the first bird to visit a feeding site

439   after a fox had been present. Such patterns of risk sensitivity may differ at non-feeding sites.

440   Better integrating our understanding of predator and pheasant movement would also help clarify

441   how predator risk might influence segregation. This similarity between the sexes in their

442   willingness to enter an area previously visited by a fox, the most common predator of pheasants

443   in the UK, may explain why we also found no differences in predation rates between sexes

444   across all three years in which we monitored predation. This may appear somewhat surprising,

445   particularly if the size and colouration of males makes them more conspicuous and indeed we

446   tended to find more males predated than females, perhaps because we used visual searches

447   favouring detection of the larger and more visible males. However, other studies using radio

448   collared release populations, also revealed no differences in predation rates between sexes (Musil

449   & Connelly 2009; Turner 2007). In contrast to the breeding season when nesting females are

450   more exposed to foxes either while sitting on the nest or attending dependent young, pheasants of

451   both sexes faced similar predation risks and rates during autumn/winter prior to the breeding

452   season. Therefore during this period they may not discriminate against high predation risk

453   habitats because they do not have to protect their young. In contrast, immediately after the

454   breeding season, precocial pheasant chicks frequently stay with their mother for over 28 days

455   (Riley et al. 1998) and during this time (June-August) females with young may occupy low risk

456   habitats. However, our recording periods did not encompass this time and our females were all

457   birds hatched in the spring and therefore had not yet bred. The similarity between the sexes in

458   predation risk and consequent predation rates suggests that the Predation Risk Hypothesis may

459   not adequately account for sexual segregation in pheasants.

460

461   During the period that pheasants sexually segregate, females were smaller in both body

462   size and in all aspects of their gut morphology. The longer intestinal system in male pheasants

463   suggests a better ability to efficiently digest a lower quality diet (Moss 1983). Larger gizzards in

464   the males also suggest a more effective grinding mechanism, perhaps allowing the digestion of

465   harder food items (Putaala & Hissa 1995). Such gastro-intestinal dimorphism is common in

466   sexually segregating ungulates, often with males having a larger rumen, small intestine and

467   colon, allowing for them to forage on much less digestible forage (Barboza & Bowyer 2000).

468   Such differences in morphologies could cause sexes to differ in their diet, perhaps with female

469   pheasants choosing higher quality foods which are easy to grind in the gizzard. However, we did

470   not observe differences in crop content when considering a suite of common food items.

471   Similarity in dietary preference was also observed in pheasants when tested as chicks in captivity

472   and presented with a choice of a variety of natural and man-made food items (Whiteside et al.

473   2017). Dietary difference between sexes often occurs, or become more pronounced, in periods

474   leading up to nesting and incubation (Lewis et al. 2002; Nisbet 1997). During the same period

475   that data from this study was collected, the degree of sexual segregation becomes stronger as the

476   pheasants get older (Whiteside et al. 2018), which may indicate that females begin to

477   differentiate their foraging behaviours more in the run up to the start of the breeding season in

478   March. Our sampling of crop contents finished at the start of February corresponding with the

479   end of the shooting season, so we may have missed this dietary switch at the advent of the

480   breeding season. Although dimorphic in gastro-intestinal morphology, our findings that sexes do

481   not differ in dietary breadth or composition suggest that the Forage Selection Hypothesis may

482   not adequately explain pheasant sexual segregation witnessed during the pre-breeding period.

483

484   Nutrient intake requirements are proportional to body size for many species (Demment &

485   Van Soest 1985), yet we found the dietary breadth and composition was similar for both sexes of

486   pheasants (see above). Therefore, we predicted that males would forage more than females,

487   while exhibiting correspondingly lower levels of alternative behaviours such as walking or

488   vigilance, leading to segregation. However we found that males and female pheasants did not

489   differ in their proportion of time spent foraging. One explanation is that there is a sex difference

490   in foraging efficiency and that males can consume enough nutrients in a similar time period.

491   Such an explanation is supported by the observation that male pheasant chicks were twice as

492   quick as females when presented with a novel food handling challenge (Whiteside et al. 2017). A

493   lack of sex differences in foraging has also been observed in desert big horn sheep, *Ovis*

494   *canadensis mexicana,* (Mooring et al. 2003) and musk ox, *Ovibos moschatus* (Côté et al. 1997).

495   Where sex differences in time spent foraging are observed it is often attributed to their

496   investment in reproduction (Lewis et al. 2002) and differences in parental care roles (Gray &

497   Hamer 2001; Thaxter et al. 2009). Although female pheasants will forage more than males prior

498   to nesting (Ridley & Hill 1987; Whiteside et al. 2016a), this occurs in early spring after hens

499   have abandoned their segregated winter aggregations and joined harems.

500

501   Much of the post-ingestion processing of foods in pheasants is conducted in the gizzard

502   (Putaala & Hissa 1995), with coarse material being fermented in the ceca, both of which are

503   smaller in females. Given the consistency in diet between sexes (see above) we predict that

504   females spend longer processing food. However, unlike in some sexually dimorphic ruminants

505   (Ruckstuhl & Neuhaus 2002) we found that males did not differ from females in the likelihood

506   that they would be resting, hence suggesting that resting activity cannot explain patterns of

507   sexual segregation.

508

509   The Activity Budget Hypothesis is not restricted to behaviours related to food processing,

510   as synchrony of other behaviours can also result in aggregation of the same sex. For instance,

511   increased movement rates by females have been suggested as a reason for sexual segregation in

512   big horn sheep (Ruckstuhl 1998). However, we found that male pheasants did not differ from

513   females in their occurrence of walking. Similar movement patterns across the sexes were

514 observed in merino sheep (Michelena et al. 2004). All locomotor behaviours that we measured
515 were consistent across sexes, therefore we believe that the Activity Budget Hypothesis fails to
516 predict sexual segregation in pheasants.

517

518   Aggression in pheasants is rarely seen between the sexes and male-male aggression is
519 typically restricted to the breeding season, peaking at the end of March (Ridley 1983) and
520 therefore it is not surprising that we observed no aggressive interactions at any of our point
521 samples. Consequently, we can, tentatively, reject aggression as a potential behavioural
522 mechanism driving sexual segregation. This contrasts with what we observed in young pheasants
523 in captivity where high levels of aggression was observed in males (Whiteside et al. 2017), and
524 perhaps a memory of these effects can persist over the following months driving segregation
525 post-release. However, this does not explain why the level of segregation becomes stronger over
526 time. Our use of state behaviour recording in this study may have missed sporadic but important
527 aggressive interactions, so if we suspect that segregation is driven by one sex trying to avoid
528 aggression by the other a more detailed recording of aggression is required.

529

530   It is important to acknowledge the limitation of using captive-reared pheasants as a model
531 system to help understand sexual segregation. Firstly, they are reared in an unnatural
532 environment. Whilst an artificial rearing environment allows us to control for important factors
533 like experience (e.g. of diet, predators) it may also distort future social dynamics due to the lack
534 of adult role models and a relatively limited and barren physical environment. Secondly, the
535 pheasants are released at high densities, greater than that of natural populations, and this could
536 influence availability of habitat or forage. However, such populations still exhibit sexual
537 segregation post release (Hill & Ridley 1987; Ridley 1983; Whiteside et al. 2018), although we
538 cannot confirm that the drivers of segregation match those of truly wild birds. Confirmation
539 would require a similarly detailed study on a wild population study where predators could be
540 observed and gut morphology and contents recorded.

541

542   Sexual dimorphism is fundamental to a suite of hypotheses that predict why many
543 species, mainly ungulates, sexually segregate at a fine scale (Pérez-Barbería & Gordon 1999).
544 Sexual size (and plumage) dimorphism is also observed and pronounced in pheasants and we

545   expected that it may explain observed patterns of sexual segregation outside the breeding season.

546   However, we found that the sexes did not differ in their predation risk, diet or behaviour. We

547   therefore found no support that the Predation Risk, Forage Selection or Activity Budget

548   hypotheses adequately explain sexual segregation of pheasants. We can conceive of three

549   explanations for this. First, birds (including pheasants) exhibit highly plastic gastro-intestinal

550   systems in order to reduce excess mass which is costly to flight (Dudley & Vermeij 1992;

551   Gasaway 1976; Whiteside et al. 2015). This flexibility may mean that gut size, and hence the

552   efficiency of nutrient absorption which underpins the hypotheses we tested, is not as closely

553   linked to body size as in ungulates. Consequently, the differences we observe in body size in

554   pheasants do not match differences in dietary needs or foraging patterns and so do not lead to a

555   segregation of the sexes. Second, segregation may be driven by other, social, factors. Pheasants

556   younger than those tested in this paper prefer to associate with others of the same sex in binary

557   choice tests, perhaps because males are aggressive and so seek out same sex partners to spar

558   with, or because females actively avoid males that may injure them (Whiteside et al. 2017). Such

559   preferences developed early in life may persist into early adulthood, even though the adults look

560   markedly different from the appearance of the chicks that we tested. Female pheasants older than

561   those tested in this paper also prefer to associate other females in binary choice tests (Madden &

562   Whiteside 2013) . For example, subtle initial differences in diet preferences may initially lead to

563   same sex aggregations (Forage Selection Hypothesis) in which the sexes learn improved foraging

564   techniques from one another (Social Attraction Hypothesis), which leads to synchronised

565   exploitation of specific food types (Activity Budget Hypothesis). Understanding why the sexes

566   segregate may require a more nuanced and integrative consideration of the current hypotheses.

567

568

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729

Figure 1

Distributions of the times for pheasants to appear after a time-matched control period, showing a clear break after ~420mins.

![Scatter plot showing time for pheasant to appear after time-matched control period (mins) on the y-axis (0 to 1800) versus Time-ordered observations on the x-axis (0 to 160).]

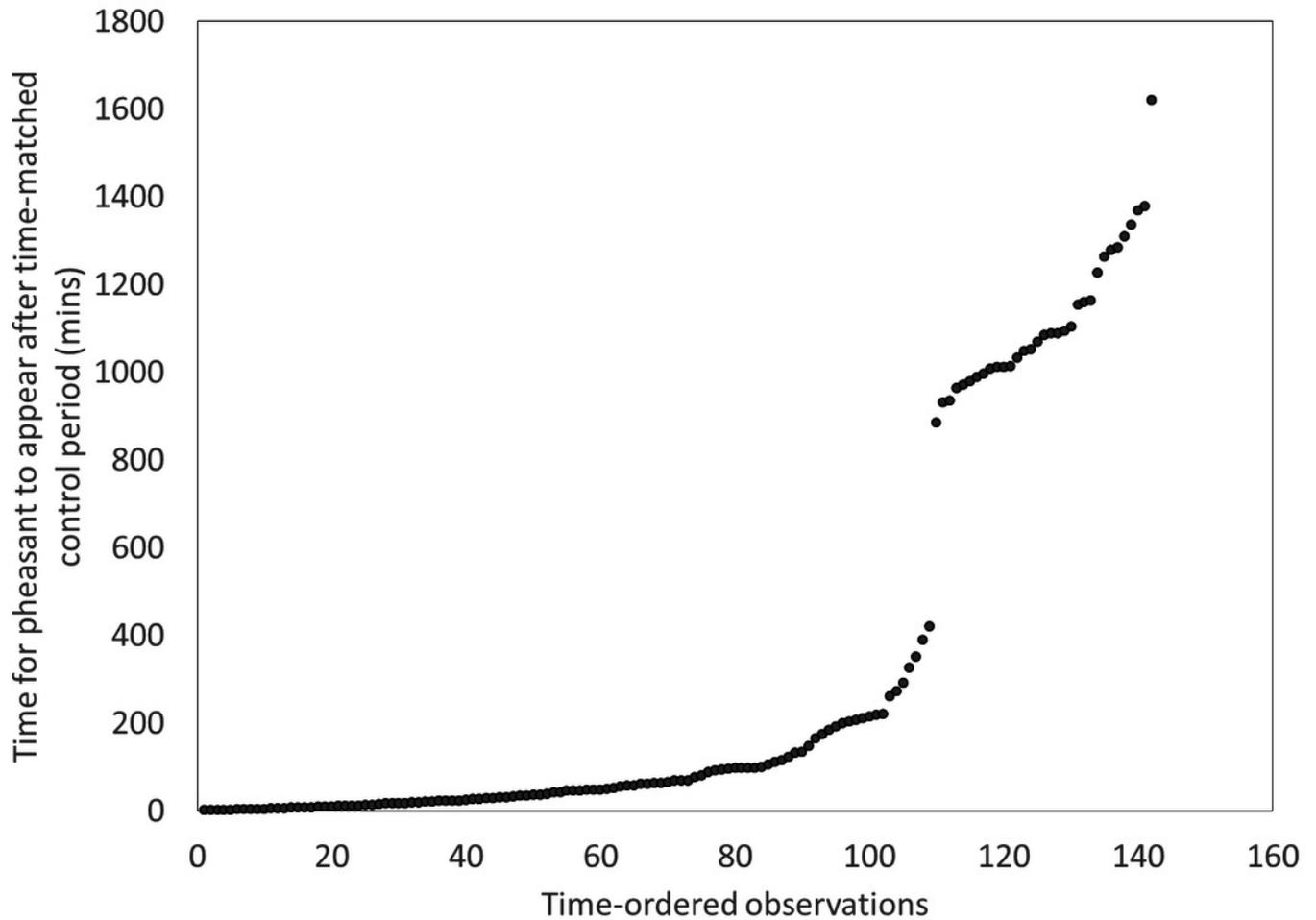



Figure 2

Time delay before a pheasant appears at a feeder after a fox has been present or a paired, time-matched control period 24hrs before the fox was sighted. Error bars = ±1SE.

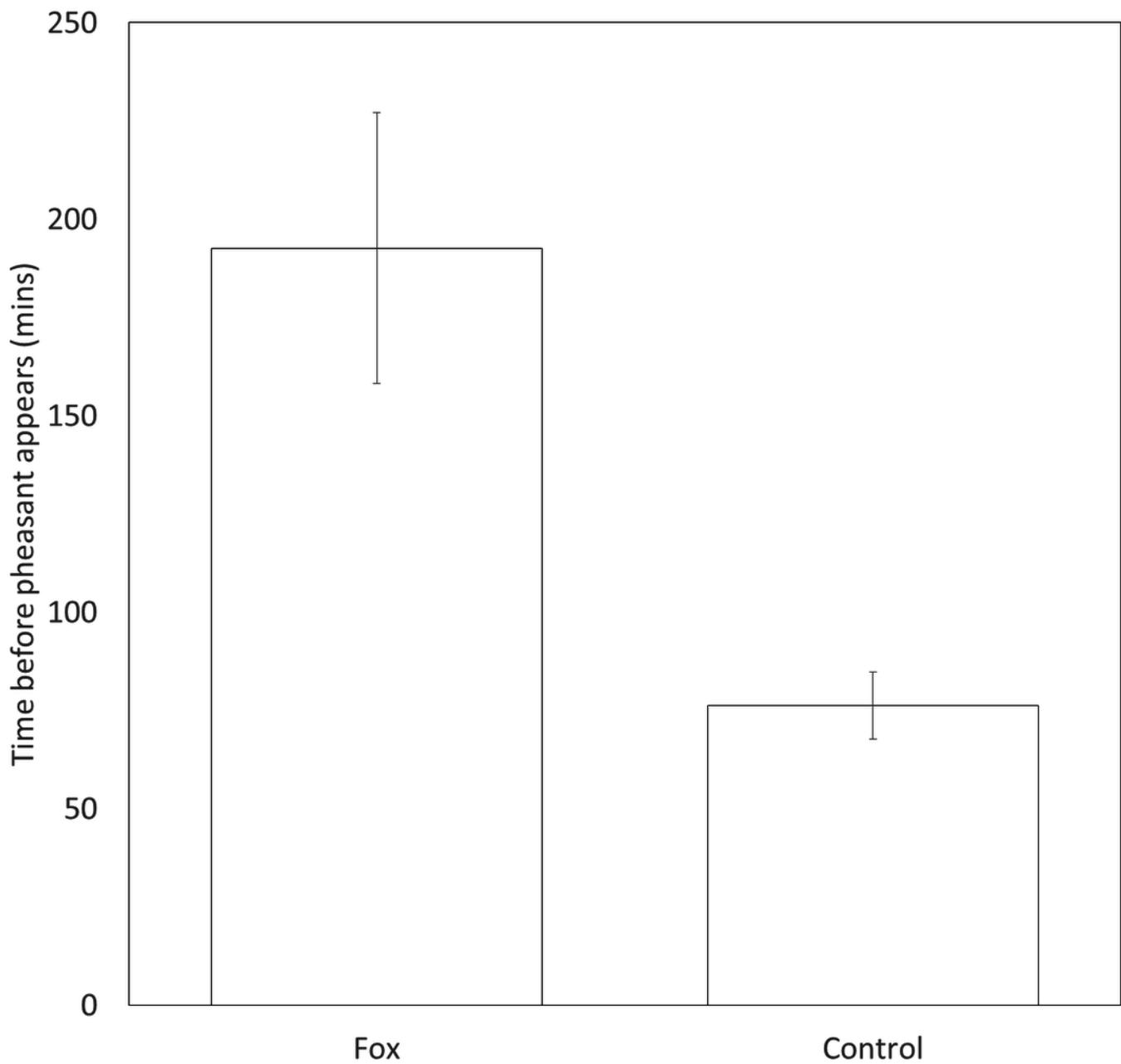
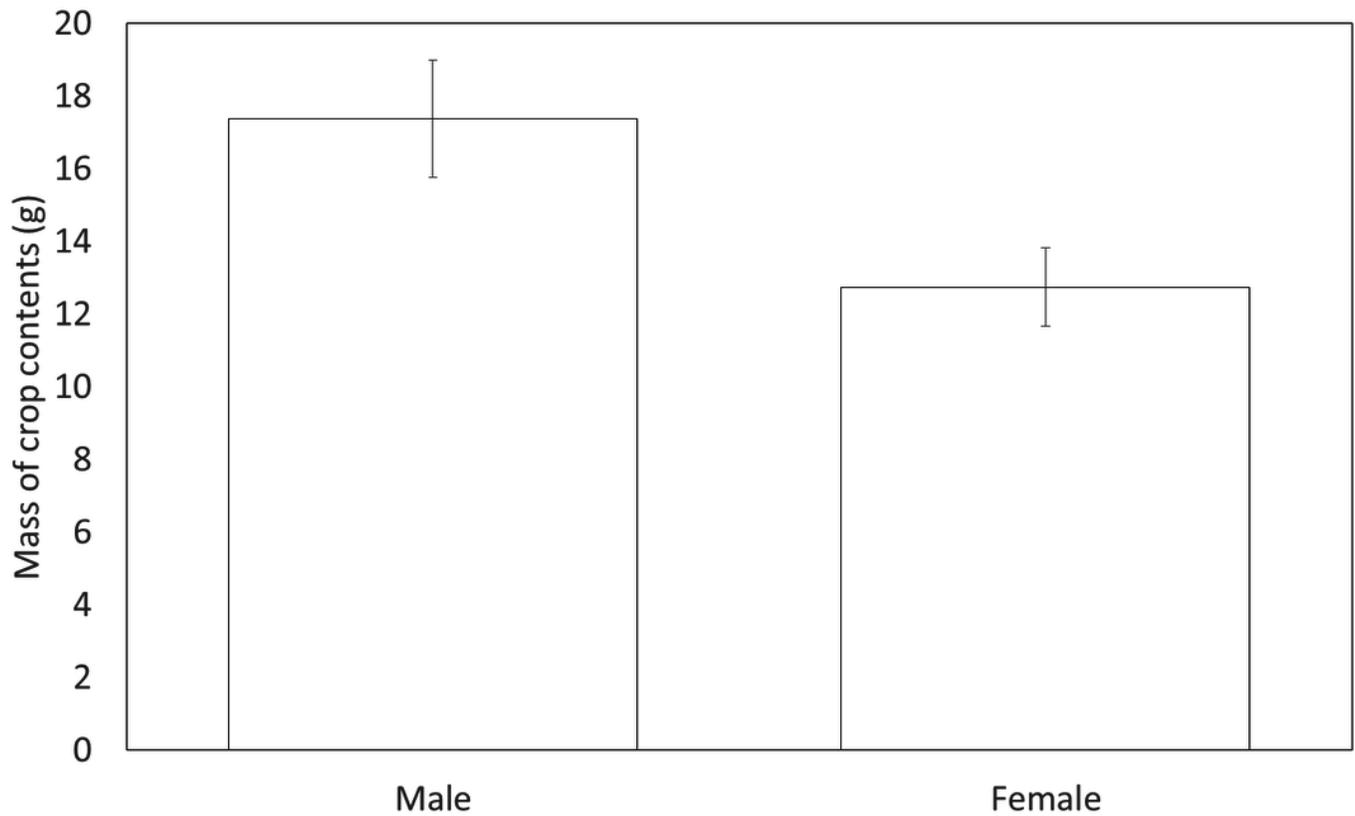



Figure 3

The mean mass of crop contents from birds shot in 2012. Error bars indicate +/- 1 SE

A description, for each year, of the conditions each bird was reared under, the numbers per house, the release sex ratio along with what data was collected.

Representing a description, for each year, of the conditions each bird was reared under, the numbers per house, the release sex ratio along with what data was collected. The default environment was analogous to current industrial rearing conditions and acted as our control; a barren, spatially simple environment that offered a monotonous chick crumb diet that as *ad lib* and in excess. Within the parenthesis next to the measures denotes the sample size and which hypotheses it was used to test: FSH = Forage Selection Hypothesis; PRH = Predation Risk Hypothesis; ABH = Activity Budget Hypothesis.

Year	Rearing (day 1 – release day)	Release day (day 43-62)	Post release (release day until 1 March)	Shooting season (1 October - 1 February)
2012	10 replicates of 3 dietary treatments 1) 1% mealworms; 2) 5% mixed seed; 3) Control Rearing numbers = 30 per house Release sex ratio(f:m) = 50:50 Large release number (game keeper)	Mass (871) Tarsus (871)	Foraging behaviour (167: ABH) Mortality (13: PRH)	Mass (233) Tarsus (233) Gut morphology (129: FSH) Crop mass (159: FSH)
2013	3x2 design. 10 replicates of 3 dietary treatments 1) 1% mealworms; 2) 5% mixed seed; 3) Control 15 replicates of 2 structural treatments 1) access to perches; and 2) control (no perches) Rearing numbers = 30 per house Release sex ratio(f:m) = 46:54 Large release number (game keeper)	Mass (901) Tarsus (901)	Foraging behaviour (214: ABH) Vigilance behaviour (214: ABH) Resting behaviour (214: ABH) Walking behaviour (214: ABH) Mortality (18: PRH)	Mass (202) Tarsus (202) Crop samples (147: FSH)
2014	No environmental treatments. All had control environment with the addition of Supplementary mealworms and mixed seed and had access to perches Rearing numbers = 50 per house Release sex ratio(f:m) = 46:54 Small release number (no game keeper)	None	Feeder use relative to possible predation events (50: PRH)	None
2015	No environmental treatments. All had control environment with the addition of Supplementary mealworms and mixed seed and had access to perches Rearing numbers = 50 per house	Mass (194) Tarsus (194)	Mortality (42: PRH)	None

Release sex ratio(f:m) = 46:54
Small release number (no game keeper)

2   Table 1: Representing a description, for each year, of the conditions each bird was reared under, the numbers per house, the release

3   sex ratio along with what data was collected. The default environment was analogous to current industrial rearing conditions and acted

4   as our control; a barren, spatially simple environment that offered a monotonous chick crumb diet that as *ad lib* and in excess. Within

5   the parenthesis next to the measures denotes the sample size and which hypotheses it was used to test: FSH = Forage Selection

6   Hypothesis; PRH = Predation Risk Hypothesis; ABH = Activity Budget Hypothesis.

The distribution, response variables, explanatory variables and random factors for all GLM and GLMMs used in the study

Question	Distribution	Response	Explanatory Factors	Random Factors
Do sexes differ in mass upon release into the wild?	Normal	Mass	Sex of focal Rearing treatment (2012 and 2013 only)	House
Do sexes differ in tarsus length upon release into the wild?	Normal	Tarsus length	Sex of focal Rearing treatment (2012 and 2013 only)	House
Do sexes differ in mass when shot as an adult?	Normal	Mass	Sex of focal Age when shot Rearing treatment	
Do sexes differ in tarsus length when shot as an adult?	Normal	Tarsus length	Sex of focal Age when shot Rearing treatment	
Do sexes differ in their gut morphology when shot as adults	Normal	Length/ Mass/ Volume	Sex of focal Age when shot Rearing treatment	
Do sexes differ in the mass of food found in their crop?	Normal	Mass	Sex of focal Age when shot	
Do sexes differ in the time spent foraging (2012)?	Normal	Percentage of time spent	Sex of focal Time of day	

		foraging (logit transformed)	(am/pm) Rearing treatment Degree of aerial protection (Open/Closed canopy)
Do sexes differ in foraging, walking and resting behaviours (2013)?	Binomial	Likelihood performing behaviour	Sex of focal Time of day (am/pm) Rearing treatment Degree of aerial protection (Open/Closed canopy)

Table 2 The distribution, response variables, explanatory variables and random factors for all
GLM and GLMMs used in the study

The mean mass in grams (range) of males and females released into the wild for three rearing seasons and the mass of adult birds shot in 2012 and 2013

Year (age)	Male mass (g)	Female mass (g)	df (df-error)	F	P
2012 (50 days)	643.69 (400-800)	536.32 (300-760)	1 (865)	688.29	< 0.001
2013 (43 days)	489.42 (350-630)	412.07 (220-540)	1 (889)	169.90	< 0.001
2015 (62 days)	738.31 (556-936)	607.82 (466-726)	1 (192)	233.37	< 0.001
2012 (Adult)	1577.18 (1140-2200)	1220.32 (1010-1510)	1 (124)	830.03	< 0.001
2013 (Adult)	1574.63 (1170-2000)	1223.66 (920-1500)	1 (223)	503.33	< 0.001

2 **Table 3** The mean mass in grams (range) of males and females released into the wild for three

3 rearing seasons and the mass of adult birds shot in 2012 and 2013

The mean tarsus length in mm (range) of males and females released into the wild for three rearing seasons and the tarsus length of adult birds shot in 2012 and 2013

Year (age)	Male tarsus (mm)	Female tarsus (mm)	df (df-error)	F	P
2012 (50 days)	69.01 (55-79.2)	63.28 (52.7-78)	1 (865)	144.09	< 0.001
2013 (43 days)	62.70 (51.2-69.9)	58.56 (45.7-65)	1 (873)	392.11	< 0.001
2015 (62 days)	72.57 (67.2-81.1)	65.48 (67.2-81.1)	1 (192)	312.50	< 0.001
2012 (Adult)	79.97 (72.95-88.2)	70.41 (63.2-76.15)	1 (221)	590.53	< 0.001
2013 (Adult)	80.79 (75.25-89.4)	71.34 (61.05-78.1)	1 (186)	547.3	< 0.001

2 **Table 4** The mean tarsus length in mm (range) of males and females released into the wild for

3 three rearing seasons and the tarsus length of adult birds shot in 2012 and 2013

Mass (g) and lengths (mm) of male and female gut morphologies (degrees of freedom = 1,128) for birds shot as adults in 2012

Dependent Variable	Sex	Mean	Std. Error	Relative difference	F	P
Oesophagus Length	Female	111.75	1.82	1.10	23.720	< 0.001
	Male	123.00	1.43			
Oesophagus Mass	Female	1.79	0.08	1.27	23.227	< 0.001
	Male	2.28	0.06			
Crop Mass	Female	3.67	0.16	1.22	16.318	< 0.001
	Male	4.48	0.12			
Gizzard Mass	Female	22.55	0.53	1.18	33.098	< 0.001
	Male	26.45	0.42			
Intestine Length	Female	1146.23	15.78	1.09	25.942	< 0.001
	Male	1248.35	12.37			
Intestines Mass	Female	15.73	0.41	1.17	25.475	< 0.001
	Male	18.34	0.32			
Colon Length	Female	100.31	2.02	1.08	11.128	< 0.001
	Male	108.88	1.58			
Colon Mass	Female	2.08	0.09	1.27	24.731	< 0.001
	Male	2.65	0.07			
Average Ceca Length	Female	214.67	3.90	1.12	26.408	< 0.001
	Male	240.13	3.06			
Average Ceca Mass	Female	3.33	0.11	1.21	26.301	< 0.001
	Male	4.04	0.09			
Gizzard Volume	Female	45070.23	1501.27	1.13	9.514	< 0.001
	Male	50955.55	1177.55			

2 **Table 5** Mass (g) and lengths (mm) of male and female gut morphologies (degrees of freedom =

3 1,128) for birds shot as adults in 2012

The percentage of males and females in the population with crop contents containing certain food for birds shot in 2013 with associated binomial statistics

Food item	Males (%)	Females (%)	P
Wheat	62.39	74.51	0.19
Maize	58.12	56.86	0.54
Grass	68.38	62.75	0.42
Oil Seed Rape	8.55	7.84	0.58
Insects	10.26	13.73	0.33
Seeds	47.86	56.86	0.24
Galls	7.69	7.84	0.58
Acorns	23.93	11.76	0.08

2 **Table 6** The percentage of males and females in the population with crop contents containing

3 certain food for birds shot in 2013 with associated binomial statistics

Table 7 The mean percentage of time spent foraging and the mean foraging bout length for males and females after release into the wild

Behaviour	Year	Male		Female		df (df-error)	F	P
		Mean	*SEM*	*Mean*	*SEM*			
Percentage Foraging	2012	32.41	2.24	35.23	3.2	1(139)	0.01	0.98
	2013	33.1	2.1	29.53	2.19	1(186)	1.84	0.18
Forage bout length	2012	14.63	1.29	16.09	1.49	1(139)	0.33	0.57
	2013	10.44	0.66	9.79	0.69	1(160)	0.46	0.5

2 **Table 7** The mean percentage of time spent foraging and the mean foraging bout length for

3 males and females after release into the wild