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

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Sexual segregation outside of the mating season is common in sexually dimorphic and polygamous species. 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; the Predation Risk Hypothesis, the Forage Selection Hypothesis, and the Activity Budget Hypothesis, in a single system the pheasant, *Phasianus colchicus*. 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. We suspect that constraints imposed on birds by flight does not allow for sufficient sexual dimorphism to prompt behavioural differences that drive sexual segregation. Instead, we consider that segregation may be mediated by a fourth hypothesis, the Social Preference Hypothesis, whereby social preferences acquired during ontogeny may have the greatest influence on sexual segregation of pheasants, as adults, in the wild.

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

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Abstract

Sexual segregation outside of the mating season is common in sexually dimorphic and polygamous species. 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; the Predation Risk Hypothesis, the Forage Selection Hypothesis, and the Activity Budget Hypothesis, in a single system the pheasant, *Phasianus colchicus*.

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. We suspect that constraints imposed on birds by flight does not allow for sufficient sexual dimorphism to prompt behavioural differences that drive sexual segregation. Instead, we consider that segregation may be mediated by a fourth hypothesis, the Social Preference Hypothesis, whereby social preferences acquired during ontogeny may have the greatest influence on sexual segregation of pheasants, as adults, in the wild.

Key-words

Behavioural synchrony, Body size dimorphism, Diet, Group living, Gut morphology, Predation,

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Introduction

Sexual segregation, in which females and males experience separation in time and/or space outside of the mating season, is common in a variety of birds, mammals, fish and reptiles (Bleich et al. 1997; Ruckstuhl and Neuhaus 2005; Ruckstuhl and Neuhaus 2000). Sexual segregation is particularly prevalent in species with strong sexual dimorphism (Ruckstuhl and Neuhaus 2002) and those with polygynous mating systems (Clutton-Brock 1989). However, there is little consensus about the underlying factors driving sexual segregation (Alves et al. 2013; Bonenfant et al. 2007).

There are three main, but non-exclusive, hypotheses proposed to explain why sexual segregation occurs in polygynous populations that are commonly linked by a dependence on sexual dimorphism (Bon and Campan 1996; Bowyer 2004). The first, the Predation Risk Hypothesis (PRH), or Reproductive Strategy Hypothesis, postulates that sexual segregation results from differing strategies between sexes as they try to maximise their own reproductive success (Main and Coblentz 1996). Here, females, perhaps accompanied by dependent and vulnerable young, trade-off habitat quality and nutrient intake with predation risk (Corti and Shackleton 2002; Main and Coblentz 1996). In contrast, males may opt to maximize their competitive advantage by investing in growth and therefore exploit nutrient rich habitats despite the risk of increased predation (Clutton-Brock et al. 1982; Prins 1989). The second, the Forage Selection Hypothesis (FSH), or Sexual Dimorphism Body-size Hypothesis (Main 1996), predicts that allometric differences in body size, bite size, energy requirements and/or fibre digestion between the sexes can lead to differences in diet selection and habitat choice (Barboza and Bowyer 2000; Demment 1982; Main and Coblentz 1996). Individuals, typically females, with a smaller gut system are less able to digest lower quality food items and are predicted to feed on higher quality diets than larger (typically male) conspecifics (Barboza and Bowyer 2001; Demment and Van Soest 1985). The third, the Activity Budget Hypothesis states that body size dimorphism promotes differences in activity budgets and synchrony of these behaviours results in aggregation of the sexes (Conradt 1998; Ruckstuhl and Neuhaus 2002; Ruckstuhl and Neuhaus 2000). Here, energetic requirements and digestive abilities predict that the smaller sex will spend more time foraging and less time resting and digesting than the larger sex (Ruckstuhl

91   1999; Ruckstuhl 1998), such that females will congregate to engage in foraging together while

92   males rest in areas with low risk of predation.

93

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

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

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

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

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

99   Bon and Campan 1996; Bowyer and Kie 2004), in particular ruminants (Bowyer and Kie 2004)

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

101   always feasible in such free-ranging mammalian systems to collect the physiological and

102   behavioural data necessary to explicitly separate and test these competing hypotheses.

103   Furthermore, in some study locations, their natural predators have disappeared, rendering it

104   difficult to explore the effects of predation risk. Finally, many species that have been studied are

105   dietary specialists, meaning that variations in diet quality may chiefly depend on differences

106   between particular plants, even those of the same species, and thus dietary intake is difficult to

107   determine accurately without measuring the nutrient quality of each mouthful (Dove and Mayes

108   1996).

109

110   The pheasant, *Phasianus colchicus,* provides an alternative system to ungulates to try to

111   tease apart hypotheses of segregation based on sexual size dimorphism. Pheasants become

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

113   weeks old) exhibit preference for their own sex (Whiteside et al. 2017). As adults, males have

114   highly conspicuous plumage and are 40% larger than the cryptic females (Wittzell 1991) and

115   exhibit sexual segregation outside of the mating season (Hill and Ridley 1987). Specifically,

116   during the late autumn and winter, females aggregate in same sex groups whereas males avoid

117   both males and females (Whiteside et al 2018 submitted). Such segregation persists until early

118   March (Hill and Ridley 1987; Hill and Robertson 1988) when harems of females visit and

119   eventually join territory-holding males, which likely reduces their harassment by other males

120   (Ridley and Hill 1987) and allows females to decrease their vigilance levels and so increase time

121 spent foraging (Whiteside et al. 2016a), until they independently start to nest and incubate their

122 eggs (Taber 1949).

123

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

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

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

127 study and reliance on data from feeder use meant that fine scale differences in habitat structure

128 may have not been captured (Whiteside et al 2018 submitted). During early life when reared in

129 captivity it appeared that social preferences were driving segregation (Whiteside et al. 2017).

130 However, under wild conditions, and as adults, when body-size dimorphism is more pronounced,

131 we may find other hypotheses better explain sexual segregation.

132 Therefore, we tested three main hypotheses for sexual segregation in free-living, size dimorphic

133 adult pheasants in this study (see Table 1 for summary of predictions).

134

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

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

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

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

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

140 (Whiteside 2018 submitted) (Hill and Ridley 1987), and this therefore removes the influence that

141 caring for young could have on assortment. However, males may still opt for a riskier foraging

142 and movement strategy if there is a benefit for their growth. Therefore, if the Predation Risk

143 Hypothesis influences segregation then we expect that predation risk (in terms of willingness to

144 approach an area where predators have recently visited) and consequently predation rates will

145 differ between sexes.

146

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

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

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

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

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

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

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

154 absorbers of low quality diet (Barboza and Bowyer 2000). In addition, body size dimorphisms

155 may correspond to differences in food processing efficiency via bite size (Illius and Gordon

156 1987) or grinding capacity in the gizzard (Putaala and Hissa 1995). If the Forage Selection

157 Hypothesis influences segregation then we expect that the sexes will differ in their gut

158 morphology matching a corresponding difference in diet.

159

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

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

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

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

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

165 operates then we expect that during the periods of sexual segregation the behaviour, in particular

166 foraging, locomotion or resting time, will differ between the sexes.

167

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

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

170 wild. The first population was released in lower numbers in an environment that did not have

171 predator control or shooting. Although initial release density was unnaturally high, after one

172 month birds had dispersed across the study site. At this point the population density ~40 birds/km^2

173 matched those of wild populations, falling within the density (16-54 birds/km^2) for wild pheasants living

174 in managed farmland in Austria and the density (0.6-64 birds/km^2) for pheasants in their native range in

175 China (Li 1996 in Johnsgard 1999). Crucially, this population showed clear patterns of sexual

176 segregation (see Whiteside et al. submitted). Releasing on sites without both predator control and

177 anthropogenic hunting allowed us to measure natural predation rates. By using a system of

178 motion sensitive camera traps at feeding sites we were able to determine: 1) if pheasants avoid

179 areas where foxes had been present: and 2) if sexes differ in their willingness to enter an area

180 where a fox had previously been seen (essential for the PRH). The second population were birds

181 that were reared in captivity and released into the wild in large numbers as part of a restocking

182 programme (Whiteside et al. 2015; Whiteside et al. 2016b). On this site there was managed

183 predator control and the birds were subject to hunting. Birds released using this method still

184 show patterns of sexual segregation (Hill and Ridley 1987) similar to that observed in pheasants

185 released at lower density. Releasing onto a site that has hunting of pheasants allows for us to

186 conduct post mortem analysis that: 1) allows us to determine the extent of sexual dimorphism in

187 body size (essential for PRH, FSH and ABH) and in gut morphology (essential for FSH); and 2)

188 acts as a dietary snapshot, whereby crop sample analyses allows us to determine diet (essential

189 for FSH). Observing behaviour of pheasants during this period allows us to determine activity

190 budgets (essential for ABH).

191

192

193 **Material and methods**

194

195 *Rearing*

196

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

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

199 release mortality. Chicks were placed in houses of 30 individuals and each house was randomly

200 allocated a rearing treatment. While not relevant to this study, the treatments included

201 differences in supplemented diet in 2012 (see Whiteside et al. 2015) and access to perches in

202 2013 (see Whiteside et al. 2016b) as well as controls. In 2014 and 2015 we reared a further 400

203 pheasants (200 / year) from one day old and housed them in groups of 50 under identical

204 conditions. Each year the birds were housed for two weeks in heated sheds (2012/13: 1.3 m x 1.3

205 m; 2014/15: 2 m x 2 m) and were then given access to an additional open grass run (2012/13 =

206 1.3 m x 6.8 m; 2014/15: 4 m x 12 m) until release. All chicks were provided with age specific

207 commercial chick crumbs (Sportsman Game Feeds) *ad lib* and in excess. Water was provided *ad*

208 *lib*. In all four years, birds were marked with patagial wing tags (Roxan Ltd, Selkirk, UK) for

209 identification with additional white PVC wing tags (25mm x75 mm) with individually unique

210 identifying numbers which could be viewed from several tens of meters away.

211

212 *Release into the wild*

213

214   Following rearing, birds were randomly mixed from across different housing groups and
215 placed into open topped pens. Release pens typically consisted of wire mesh fences ~2 m high
216 enclosing an extensive area of woodland (GWCT 1991). In these pens birds were provided with
217 food and water *ad lib*. Birds could disperse from these pens and were free to roam and mix with
218 other released, as well as resident, pheasants. In 2012 and 2013 when birds were approximately
219 seven weeks old we released them onto the Middleton Estate, Hampshire, UK ($51^0$18'N, $1^0$4'W).
220 The estate, predominantly arable, hosts a game shoot and employs two game keepers to manage
221 the released pheasants through habitat management, providing supplementary food, and
222 controlling predator numbers. Between October and February birds were shot as part of a
223 recreational shoot. In 2014 and 2015 when birds were ten weeks old they were released at North
224 Wyke Farm, Devon ($50^0$77'N, $3^0$9'W). This site is grazed by cattle and sheep and no game
225 shooting or predator control occurred there. Forty feeders, filled with wheat, were placed within
226 the pen (n = 4) and in the surrounding countryside (n = 36) at a density of 0.16 per hectare. In
227 2014, each feeder was continuously monitored with Bushnell® Trophy motion activated
228 cameras. All animals that visited a feeder and its surrounding area were photographed and the
229 images were then viewed manually to record the time that pheasants and foxes visited the feeder
230 site. Individual pheasants could be identified from their wing tag numbers.

231

232 *Body size dimorphism*
233   We recorded the mass (Slater Super Samson spring balance – precision 5 g) and tarsus
234 length (precision 1 mm) of all birds upon release into the wild and for birds released in 2012 and
235 2013 we scored the same measures within four hours of them being shot.

236

237   For the released populations we used a General Linear Mixed Model (GLMM) to identify
238 whether males differed from females in their mass and tarsus length with rearing treatment and
239 sex as fixed factors and the rearing house as a random factor, with all two way interactions
240 included (Table 2). In 2014 and 2015 all birds were reared under identical conditions and
241 therefore rearing treatment was not included in the model. For birds shot in 2012 and 2013 a
242 General Linear Model (GLM) was used to ask if sexes differed in mass and tarsus length as
243 adults. The bird's age when shot, its rearing treatment and all two way interactions were included
244 in the GLM (Table 2).

245

246

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

248

249   We recorded every sighting of a fox and pheasant at each of our feeder sites during

250 December 2014 and January 2015 using the motion camera traps. In order to test whether the

251 presence of foxes at feeders was an indicator of a risky environment that pheasants attended to,

252 we asked whether birds took longer to return to feeders after a fox had been there compared to

253 the time it took them to appear at a feeder after a time-matched control point the previous day.

254 We excluded instances where there were low visitation rates at a feeder, indicated by long

255 periods (>420 mins) between the time-matched control point and the first pheasant appearing.

256 This cut-off point was meaningful and discrete (Figure 1). This left a subset of the previous data

257 including 110 cases. We used a t-test to ask if pheasants took longer to approach a feeder if it had

258 been visited by a fox compared a time matched control point the previous day. We then looked at

259 each appearance of a fox and recorded the sex of the next pheasant to enter the same feeder

260 within a subsequent 30 minutes. We used a binomial test to determine if sexes differed in their

261 likelihood of approaching a feeder following a fox visit.

262

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

264

265   In 2012 and 2013 between August and October and during February the following year

266 we conducted daily searches of areas surrounding the release site to retrieve birds that had been

267 killed by predators. During the hunting season (late October to February) the area was visited

268 less frequently but more methodically by beaters who were engaged in driving the game to the

269 waiting hunters. They were informed of the project and searched for carcases and tags as they

270 walked the site. In 2015 we collected birds that has been killed by a predator by searching the

271 release site and surrounding areas for carcases, locating these either directly or guided by radio

272 tags placed on 50 birds. In 2014 we did not conduct detailed searches for carcases. A binomial

273 test was used to test whether predation numbers differed between sexes with the expected

274 outcome based on the released sex ratio.

275

276

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

278

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

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

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

282 volume was measured as the height multiplied by width. A GLM was used to ask if these gut

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

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

285 as fixed factors (Table 2).

286

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

288

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

290 removal of its contents. Measures were transformed using the SQRT(x) transformation to meet

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

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

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

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

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

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

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

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

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

300

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

302

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

304 observing 167 released pheasants between 18 September and 5 November. We recorded the total

305 time we observed the birds, the time spent foraging and the number of foraging bouts they

306 performed. A foraging bout began with the lowering of the head and neck towards the ground

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

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

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

310

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

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

313   This allowed us to collect state behaviours; in particular time spent performing resting, vigilance

314   and locomotive behaviours. All birds were identifiable from their wing tags and were observed

315   from a distance so as to not disturb their natural behaviours. Vigilance was described as sitting or

316   standing with neck extended and eyes open. Resting was determined as either standing or lying

317   with eyes closed. We used a Generalised Linear Model with a binomial distribution and a probit

318   link function to ask if sexes differed in their vigilance, walking and resting likelihoods. In all

319   models early rearing environment, time of day (AM or PM), and degree of aerial protection

320   (open or closed) were included as fixed factors, and all two-way interactions were assessed

321   (Table 2).

322

323   *Statistical Analyses*

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

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

326

327   *Ethical Statement*

328

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

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

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

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

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

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

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

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

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

338

339   **RESULTS**

340

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

342

343   Upon release into the wild males were on average 1.2 times heavier (Table 3) and had

344   1.09 times longer tarsi (Table 4) than females. Males were on average 1.29 times heavier (Table

345   3) and had 1.13 times longer tarsi (Table 4) than females when shot as adults.

346

347

348   *Testing the Predation Risk Hypothesis: Do sexes differ in their likelihood of being the first to*

349   *approach a feeder visited by a fox?*

350

351   Pheasants took about 2.5 times longer to appear at a feeder after a fox was present

352   (193±35mins) than after a time-matched control point the previous day (76±9mins) (t_{109} = 3.37,

353   P = 0.001, Figure 2). There was no difference in the likelihood that a male or female would be

354   first to approach a feeding site in the following 30 minutes after the sighting of a fox (Binomial

355   test: *P* = 0.20).

356

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

358

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

360   tests: 2012, *P* = 0.58); 2013 (Binomial test: *P* = 0.20); and 2015 (Binomial test: *P* = 0.12).

361

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

363

364   Males differed from females in all aspects of measured gut morphologies with larger and

365   heavier gut regions, crops and gizzards (Table 5).

366

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

368

369   Males (17.38g ± 1.62) shot in 2012 had a 1.4 times greater mass of forage in their crop

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

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

372 0.93, P = 0.34). The sexes appeared to utilise a similar diet with both sexes carrying similar

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

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

375 acorns (Table 6).

376

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

378

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

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

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

382 focal watches which was demonstrated by a male. Hence no statistical comparisons between

383 sexes could be conducted.

384

385 **DISCUSSION**

386

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

388 sexually segregate (Whiteside et al. 2018 submitted), pheasants exhibited strong sexual size

389 dimorphism. Adult males were 1.3 times heavier than females which is similar to, although

390 slightly less than, levels of dimorphism observed in other terrestrial species that exhibit sexual

391 segregation (red deer, *Cervus elephus*, (1.33: Clutton-Brock et al. 1982; Weckerly 1998), merino

392 sheep, *Ovis aries*, (1.50: Michelena et al. 2004), bighorn sheep, *Ovis canadensis*, (1.43: Blood et

393 al. 1970). Although males and females differed in size, we found little evidence that sexes

394 differed in behavioural and morphological measures that are predicted to explain sexual

395 segregation according to of the three existing hypotheses purporting to explain segregation due

396 to size dimorphism (Bleich et al. 1997; Bonenfant et al. 2007; Conradt 1998; Ruckstuhl 1998).

397

398   Pheasants may facultatively reduce their risk of predation by increasing the lag between

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

400 suggesting that time taken to visit a feeder after fox presence provided a good assay of risk

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

402 feeders, indicated by their likelihood of being the first bird to visit a feeding site after a fox had

403 been present. Such similarity between sexes in willingness to enter an area previously visited by

404 a fox, the most common predator of pheasants in the UK, may explain why we also found no

405 differences in predation rates between sexes across all three years in which we monitored

406 predation. Our technique of recovering carcasses could have been biased by our recovery

407 techniques favouring detection of the larger and more visible males, yet other studies using radio

408 collared release populations, revealed similar patterns with no differences in mortality between

409 sexes (Musil and Connelly 2009; Turner 2007). One reason for exposure to similar predation

410 risks and subsequent predation rates across sexes during autumn/winter is that pheasants do not

411 nest until the spring (Hill and Robertson 1988) and therefore females, the lone carer (Taber

412 1949), are without dependent young during the period of sexual segregation. Therefore they may

413 not discriminate against high predation risk habitats because they do not have to protect their

414 young. In contrast, immediately after the breeding season, precocial pheasant chicks frequently

415 stay with their mother for over 28 days (Riley et al. 1998) and during this time (June-August)

416 females with young may occupy low risk habitats. However, our recording periods did not

417 encompass this time and our females were all birds hatched in the spring and therefore had not

418 yet bred. The similarity between the sexes in predation risk and consequent predation rates

419 suggests that the Predation Risk Hypothesis may not adequately account for sexual segregation

420 in pheasants.

421

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

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

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

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

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

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

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

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

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

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

432   sexes exhibited similar dietary preference when tested as chicks in captivity and presented with a

433   diet choice test (Whiteside et al. 2017). Dietary difference between sexes often occurs, or

434   become more pronounced, in periods leading up to nesting and incubation (Lewis et al. 2002;

435   Nisbet 1997). Sexual segregation becomes stronger as the birds get older (Whiteside et al., 2018

436   submitted), which may indicate that females begin to differentiate their foraging behaviours

437   more in the run up to the start of the breeding season in March. Our sampling of crop contents

438   finished at the start of February corresponding with the end of the shooting season, so we may

439   have missed this dietary switch at the advent of the breeding season. Although dimorphic in

440   gastro-intestinal morphology, our findings that sexes do not differ in dietary breadth or

441   composition suggest that the Forage Selection Hypothesis may not adequately explain pheasant

442   sexual segregation witnessed during the pre-breeding period.

443

444   With body size being proportional to intake requirements in many species (Demment and

445   Van Soest 1985) and given the consistency between sexes in their dietary breadth observed in

446   our study (see above), we predicted that males would forage more than females, while exhibiting

447   correspondingly lower levels of alternative behaviours such as walking or vigilance. However

448   we found that males and female pheasants did not differ in their proportion of time spent

449   foraging. One explanation is that there is a sex difference in foraging efficiency and that males

450   can consume enough nutrients in a similar time period, such foraging efficiency was observed in

451   male pheasant chicks being twice as quick as females when presented with a forage handling

452   challenge (Whiteside et al. 2017). A lack of sex differences in foraging has also been observed in

453   desert big horn sheep, *Ovis canadensis mexicana,* (Mooring et al. 2003) and musk ox, *Ovibos*

454   *moschatus* (Côté et al. 1997). Differences in time spent foraging between sexes in ungulates is

455   often attributed to their investment in reproduction (Lewis et al. 2002) and differences in parental

456   care roles (Gray and Hamer 2001; Thaxter et al. 2009). Prior to nesting, female pheasants will

457   forage more than males (Ridley and Hill 1987; Whiteside et al. 2016a), but this occurs after hens

458   have abandoned their winter segregation patterns and joined harems so as to be continuously

459   associated with at least one harem-holding male. Harem formation occurs after our period of

460   observations of associations ceased.

461

462   Pheasants have a pair of ceca that are analogous to the ungulate hind gut, and which are

463   significantly larger in males. Similarly, much of the post-ingestion processing of foods in

464   pheasants is conducted in the gizzard (Putaala and Hissa 1995), which is smaller in females. As

465   such, given the consistency in diet between sexes (see above) we may predict that females spend

466   longer processing food. However, unlike in some sexually dimorphic ruminants (Ruckstuhl and

467   Neuhaus 2002) we found that males did not differ from females in the likelihood that they would

468   be resting, hence suggesting that resting activity cannot explain patterns of sexual segregation.

469

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

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

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

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

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

475   observed in merino sheep (Michelena et al. 2004). With all behaviours that were measured being

476   consistent across sexes we consider that the Activity Budget Hypothesis fails to predict sexual

477   segregation in pheasants.

478

479   *Conclusion*

480

481   Sexual dimorphism is fundamental to a suite of hypotheses that predict why many

482   species, mainly ungulates, sexually segregate (Pérez-Barbería and Gordon 1999). Sexual size and

483   plumage dimorphism is pronounced in pheasants and may therefore be associated with observed

484   patterns of sexual segregation outside the breeding season. However, we found that the sexes did

485   not differ in their predation risk, diet or behaviour. We therefore find no support that the

486   Predation Risk, Forage Selection or Activity Budget hypotheses adequately explain sexual

487   segregation of pheasants. We may find that sexual segregation is not a consequence of size

488   dimorphism but instead could be an artefact of early life preferences. The Social Preference

489   Hypothesis suggests that ontogenetic differences in behaviour result in males and females

490   differing in their motivation to interact (Bon and Campan 1996; Le Pendu et al. 2000). The

491   Social Preference Hypothesis provided the best support for why we see segregation of captive

492   pheasants during early development in conditions that controlled for habitat availability, diet and

493   predation, during a period where sexual size dimorphism would have less effect (Whiteside et al.
494   2017). However, after release into the wild and as sexual dimorphism became more pronounced,
495   we predicted that it would impact predation risk, diet choice and activity budgets, and therefore
496   three hypotheses that rely on size dimorphism could work in concert with early social preference
497   to drive sexual segregation. We did not test specifically for the Social Preference Hypothesis
498   amongst wild adults, due to the difficulty of administering preference tests to wild pheasants, our
499   previous work demonstrates that during the mating season, and outside of the period of sexual
500   segregation, females that were caught in the wild and faced with a social preference test still
501   preferred to spend time with their own sex (Madden and Whiteside 2013).

502

503

504   For sexual dimorphism to drive sexual segregation it has to be sufficient to cause
505   differences in behaviour, dietary choice or predation risk, with attendant differences in patterns
506   of movement, space use or temporal dynamics. Although pheasants are dimorphic in size to a
507   similar extent to ungulates, we may find that avian systems, exemplified by the pheasant, may
508   not have sufficiently large differences in morphology to force sexes to segregate. For instance,
509   the avian gastro-intestinal system may differ in size, processing and digestive power between
510   sexes. However, unlike the mammalian system, a bird's weight is constrained by capacities for
511   flight. The ceca can weigh up to 5 % of a bird's total body weight (Moss 1983). As such, this
512   mass may dramatically increase the energetic costs of flight (Dudley and Vermeij 1992). Cecal
513   fermentation may also contribute less than 5 % of the daily energy requirements (Gasaway et al.
514   1975). As a consequence, the ceca are highly plastic and lengths can change in response to the
515   season and diet to ensure they are most effective (Gasaway 1976; Whiteside et al. 2015). Where
516   terrestrial species are able to simply enlarge their gut system to hold more forage, the constraints
517   of flight may mean that birds cannot (Sedinger 1997). This could have consequences on how
518   much size dimorphism can influence sexual segregation in birds. Although males have larger
519   digestive systems, the differences in size between sexes may not be large enough to translate into
520   significant behavioural differences or dietary differences that provoke sexual segregation in
521   pheasants. Consequently, our work reveals that studies of sexual segregation should encompass a
522   wider range of taxa than are commonly considered and that existing hypotheses may not
523   adequately explain segregation in certain taxa, especially birds.

References

Alves J, da Silva AA, Soares AM, Fonseca C (2013) Sexual segregation in red deer: is social behaviour more important than habitat preferences? Anim Behav 85:501-509

Barboza PS, Bowyer RT (2000) Sexual segregation in dimorphic deer: a new gastrocentric hypothesis Journal of Mammalogy 81:473-489

Barboza PS, Bowyer RT (2001) Seasonality of sexual segregation in dimorphic deer: extending the gastrocentric model Alces 37:275-292

Bleich VC, Bowyer RT, Wehausen JD (1997) Sexual segregation in mountain sheep: resources or predation? Wildlife Monographs:3-50

Blood DA, Flook DR, Wishart WD (1970) Weights and growth of Rocky Mountain bighorn sheep in western Alberta The Journal of Wildlife Management:451-455

Bon R, Campan R (1996) Unexplained sexual segregation in polygamous ungulates: a defense of an ontogenetic approach Behav Process 38:131-154

Bonenfant C, Gaillard J-M, Dray S, Loison A, Royer M, Chessel D (2007) Testing sexual segregation and aggregation: old ways are best Ecology 88:3202-3208

Bowyer RT (2004) Sexual segregation in ruminants: definitions, hypotheses, and implications for conservation and management Journal of Mammalogy 85:1039-1052

Bowyer RT, Kie JG (2004) Effects of foraging activity on sexual segregation in mule deer Journal of Mammalogy 85:498-504

Clutton-Brock TH (1989) Review lecture: mammalian mating systems Proceedings of the Royal Society of London B: Biological Sciences 236:339-372

Clutton-Brock TH, Guinness FE, Albon S (1982) Red deer: behavior and ecology of two sexes. University of Chicago Press,

Conradt L (1998) Could asynchrony in activity between the sexes cause intersexual social segregation in ruminants? Proceedings of the Royal Society of London B: Biological Sciences 265:1359-1368

Conradt L, Roper T (2000) Activity synchrony and social cohesion: a fission-fusion model Proceedings of the Royal Society of London B: Biological Sciences 267:2213-2218

Corti P, Shackleton DM (2002) Relationship between predation-risk factors and sexual segregation in Dall's sheep (Ovis dalli dalli) Canadian Journal of Zoology 80:2108-2117

Côté SD, Schaefer JA, Messier F (1997) Time budgets and synchrony of activities in muskoxen: the influence of sex, age, and season Canadian Journal of Zoology 75:1628-1635

DEFRA (2009) Code of practice for the welfare of game birdsreared for sporting purposes. Department for Environment, Food and Rural Affairs,

Demment M (1982) The scaling of ruminoreticulum size with body weight in East African ungulates African Journal of Ecology 20:43-47

Demment MW, Van Soest PJ (1985) A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores Am Nat:641-672

Dove H, Mayes R (1996) Plant wax components: a new approach to estimating intake and diet composition in herbivores The journal of nutrition 126:13

Dudley R, Vermeij G (1992) Do the power requirements of flapping flight constrain folivory in flying animals? Functional Ecology 6:101-104

Gasaway WC (1976) Seasonal variation in diet, volatile fatty acid production and size of the cecum of rock ptarmigan Comparative Biochemistry and Physiology Part A: Physiology 53:109-114 doi:http://dx.doi.org/10.1016/S0300-9629(76)80021-7

Gasaway WC, Holleman DF, White RG (1975) Flow of digesta in the intestine and cecum of the rock ptarmigan Condor:467-474

571   Gray CM, Hamer KC (2001) Food-provisioning behaviour of male and female Manx shearwaters, Puffinus
572   puffinus Anim Behav 62:117-121
573   GWCT (1991) Gamebird releasing. Game and Wildlife Conservation Trust, Fordingbridge, Hampshire
574   Hessler E, Tester JR, Siniff DB, Nelson MM (1970) A biotelemetery study of survival of pen-reared
575   pheasants released in selected habitats The Journal of Wildlife Management 34:267-274
576   Hill DA, Ridley MW (1987) Sexual segregation in winter, spring dispersal and habitat use in the pheasant
577   (*Phasianus colchicus*) Journal of Zoology 212:657-668 doi:10.1111/j.1469-7998.1987.tb05962.x
578   Hill DA, Robertson PA (1988) The pheasant: ecology, management and conservation. Blackwell Scientific
579   Books, Oxford
580   Hoodless A, Draycott R, Ludiman M, Robertson P (2001) Spring foraging behaviour and diet of released
581   pheasants (Phasianus colchicus) in the United Kingdom Game & wildlife science 18:375-386
582   Illius AW, Gordon IJ (1987) The Allometry of Food Intake in Grazing Ruminants J Anim Ecol 56:989-999
583   doi:10.2307/4961
584   Johnsgard P (1999) The pheasant of the world: biology and natural history. Washington: Smithsonian
585   Institution Press,
586   Kenward R, Hall D, Walls S, Hodder K (2001) Factors affecting predation by buzzards *Buteo buteo* on
587   released pheasants *Phasianus colchicus* Journal of Applied Ecology 38:813-822
588   Kenward RE, Marcström V, Karlbom M (1981) Goshawk winter ecology in Swedish pheasant habitats The
589   Journal of Wildlife Management 45:397-408
590   Krauss G, Graves H, Zervanos S (1987) Survival of wild and game-farm cock pheasants released in
591   Pennsylvania The Journal of wildlife management 51:555-559
592   Le Pendu Y, Guilhem C, Briedermann L, Maublanc M-L, Gerard J-F (2000) Interactions and associations
593   between age and sex classes in mouflon sheep (Ovis gmelini) during winter Behav Process
594   52:97-107
595   Leopold AS (1953) Intestinal morphology of gallinaceous birds in relation to food habits The Journal of
596   Wildlife Management 17:197-203
597   Lewis S et al. (2002) Sex-specific foraging behaviour in a monomorphic seabird Proceedings of the Royal
598   Society of London B: Biological Sciences 269:1687-1693
599   Loe LE et al. (2006) Testing five hypotheses of sexual segregation in an arctic ungulate J Anim Ecol
600   75:485-496
601   Madden JR, Whiteside MA (2013) Variation in female mate choice and mating success is affected by sex
602   ratio experienced during early life Anim Behav 86:139-142
603   Main MB, Coblentz BE (1996) Sexual segregation in Rocky Mountain mule deer The Journal of Wildlife
604   Management:497-507
605   Michelena P, Bouquet PM, Dissac A, Fourcassie V, Lauga J, Gerard J-F, Bon R (2004) An experimental test
606   of hypotheses explaining social segregation in dimorphic ungulates Anim Behav 68:1371-1380
607   Mooring MS, Fitzpatrick TA, Benjamin JE, Fraser IC, Nishihira TT, Reisig DD, Rominger EM (2003) Sexual
608   segregation in desert bighorn sheep (Ovis canadensis mexicana) Behaviour 140:183-207
609   Moss R (1983) Gut size, body weight, and digestion of winter foods by grouse and ptarmigan Condor
610   85:185-193
611   Musil DD, Connelly JW (2009) Survival and reproduction of pen-reared vs translocated wild pheasants
612   Phasianus colchicus Wildlife Biology 15:80-88
613   Nisbet IC (1997) Female Common Terns Sterna hirundo eating mollusc shells: evidence for calcium
614   deficits during egg laying Ibis 139:400-401
615   Pérez-Barbería F, Gordon I (1999) Body size dimorphism and sexual segregation in polygynous
616   ungulates: an experimental test with Soay sheep Oecologia 120:258-267
617   Prins H (1989) Condition changes and choice of social environment in African buffalo bulls Behaviour
618   108:297-323

619   Putaala A, Hissa R (1995) Effects of hand-rearing on physiology and anatomy in the grey partridge
620   Wildlife Biology 1:27-31
621   Ridley M, Hill D (1987) Social organization in the pheasant (*Phasianus colchicus*): harem formation, mate
622   selection and the role of mate guarding Journal of Zoology 211:619-630
623   Riley TZ, Clark WR, Ewing E, Vohs PA (1998) Survival of Ring-Necked Pheasant Chicks during Brood
624   Rearing The Journal of Wildlife Management 62:36-44
625   Ruckstuhl K (1999) To synchronise or not to synchronise: a dilemma for young bighorn males? Behaviour
626   136:805-818
627   Ruckstuhl K, Manica A, MacColl A, Pilkington J, Clutton-Brock T (2006) The effects of castration, sex ratio
628   and population density on social segregation and habitat use in Soay sheep Behav Ecol Sociobiol
629   59:694-703
630   Ruckstuhl K, Neuhaus P (2002) Sexual segregation in ungulates: a comparative test of three hypotheses
631   Biological Reviews of the Cambridge Philosophical Society 77:77-96
632   Ruckstuhl K, Neuhaus P (2005) Sexual segregation in vertebrates. Cambridge University Press,
633   Ruckstuhl KE (1998) Foraging behaviour and sexual segregation in bighorn sheep Anim Behav 56:99-106
634   Ruckstuhl KE, Neuhaus P (2000) Sexual segregation in ungulates: a new approach Behaviour 137:361-
635   377
636   Sedinger JS (1997) Adaptations to and consequences of an herbivorous diet in grouse and waterfowl
637   Condor:314-326
638   Taber RD (1949) Observations on the breeding behavior of the ring-necked pheasant Condor 51:153-175
639   Thaxter CB et al. (2009) Sex-specific food provisioning in a monomorphic seabird, the common guillemot
640   Uria aalge: nest defence, foraging efficiency or parental effort? J Avian Biol 40:75-84
641   Turner C (2007) The fate and management of pheasants (*Phasianus colchicus*) released in the UK.
642   Imperial College
643   Warton DI, Hui FKC (2010) The arcsine is asinine: the analysis of proportions in ecology Ecology 92:3-10
644   doi:10.1890/10-0340.1
645   Weckerly FW (1998) Sexual-size dimorphism: influence of mass and mating systems in the most
646   dimorphic mammals Journal of Mammalogy 79:33-52
647   Whiteside MA, Langley EJG, Madden JR (2016a) Males and females differentially adjust vigilance levels
648   as group size increases: effect on optimal group size Anim Behav 118:11-18
649   Whiteside MA, Sage R, Madden JR (2015) Diet complexity in early life affects survival in released
650   pheasants by altering foraging efficiency, food choice, handling skills and gut morphology J Anim
651   Ecol 84:1480-1489 doi:10.1111/1365-2656.12401
652   Whiteside MA, Sage R, Madden JR (2016b) Multiple behavioural, morphological and cognitive
653   developmental changes arise from a single alteration to early life spatial environment, resulting
654   in fitness consequences for released pheasants Royal Society Open Science 3
655   doi:10.1098/rsos.160008
656   Whiteside MA, van Horik JO, Langley EJG, Beardworth CE, Laker PR, Madden JR (2017) Differences in
657   social preference between the sexes during ontogeny drive segregation in a precocial species
658   Behav Ecol Sociobiol 71:103 doi:10.1007/s00265-017-2332-2
659   Wittzell H (1991) Natural and sexual selection in the pheasant *Phasianus colchicus*. Lund University
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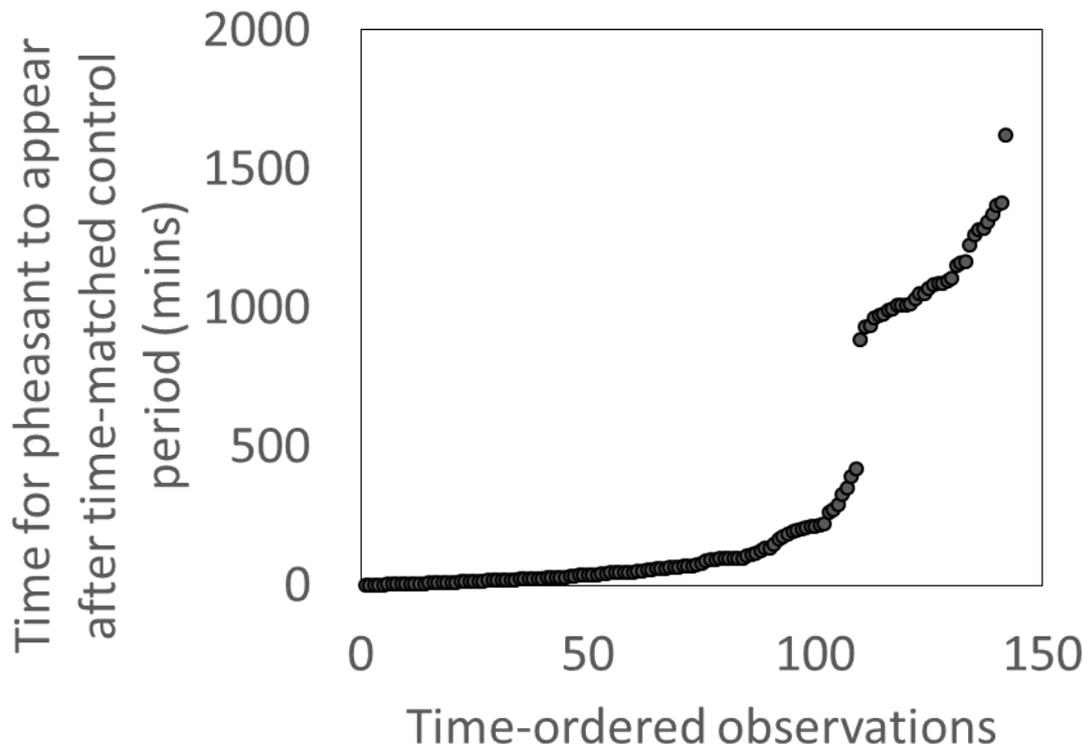
661

663

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

Figure 1 Distributions of the times for pheasants to appear after a time-matched control period, showing a clear break after ~420mins.

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.

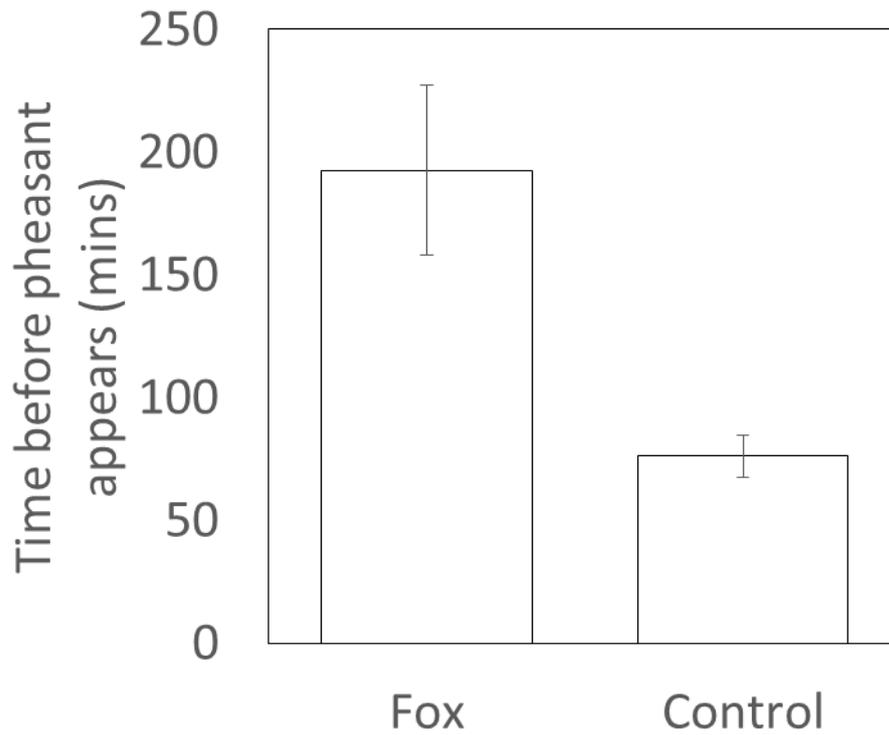



Figure 2 Time delay before a pheasant appears at a feeder after a fox has been present or a paired, time-matched control period 24hrs before the fox was sighted. Error bars = ±1SE.

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

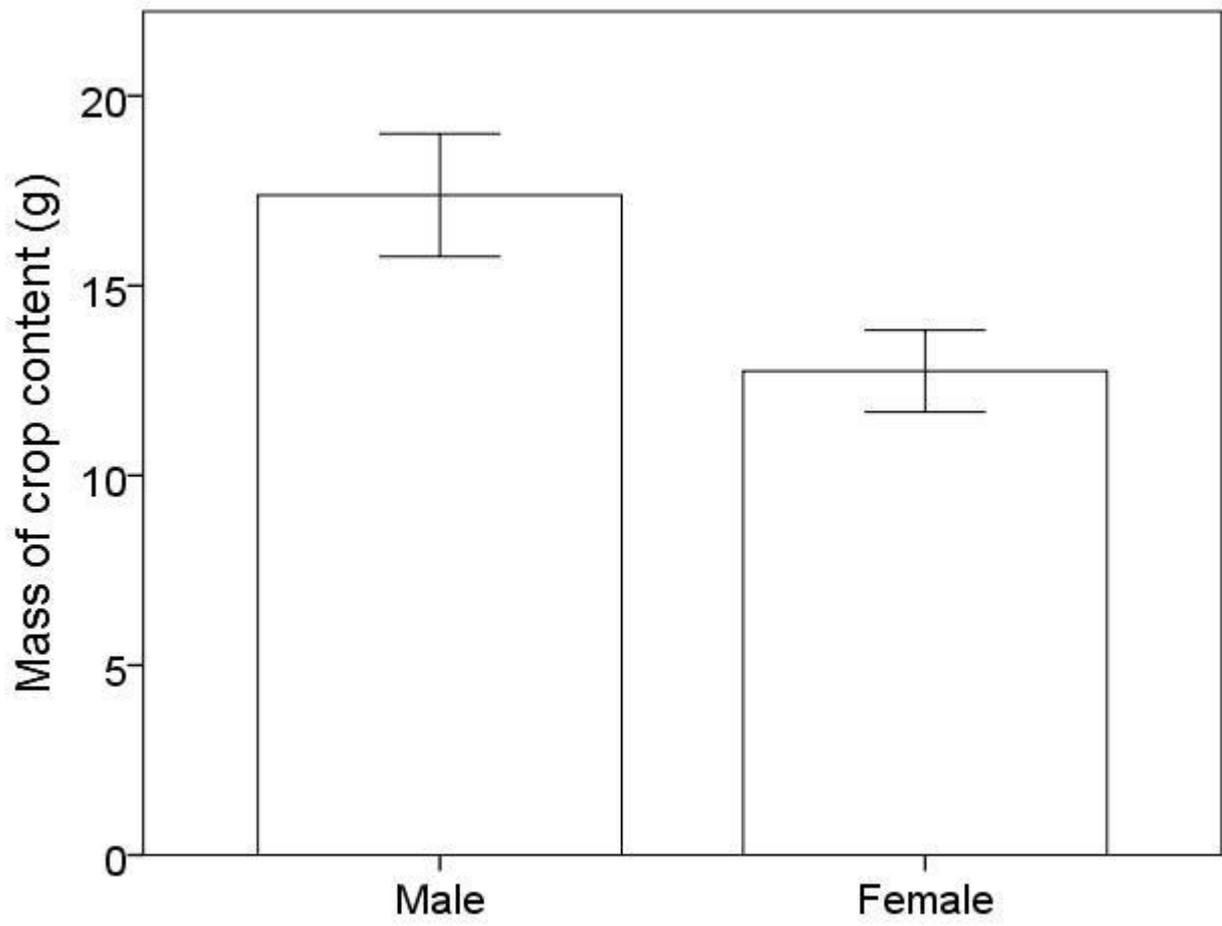



Figure 3 The mean mass of crop contents from birds shot in 2012. Error bars indicate +/- 1 SE

Hypotheses and predictions to explain sexual segregation in adult pheasants

Hypothesis	Size dimorphism	Predictions
Predation Risk Hypothesis	Yes	No segregation should occur when monomorphic in body size
		Sexually dimorphic males adopt a more risky foraging strategy and have higher predation rates
Forage Selection Hypothesis	Yes	No segregation should occur when monomorphic in body size.
		Sexes should differ in their crop contents
Activity Budget Hypothesis	Yes	No segregation should occur when monomorphic in body size.
		Foraging or resting behaviour should differ between the sexes during periods when they are dimorphic in body size only.

1   **Table 1** Hypotheses and predictions to explain sexual segregation in adult pheasants

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 foraging (logit transformed)	Sex of focal Time of day (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	Sig
2012 (50 days)	643.69 (400-800)	536.32 (300-760)	1 (865)	688.29	*P* < 0.001
2013 (43 days)	489.42 (350-630)	412.07 (220-540)	1 (889)	169.90	*P* < 0.001
2015 (62 days)	738.31 (556-936)	607.82 (466-726)	1 (192)	233.37	*P* < 0.001
2012 (Adult)	1577.18 (1140-2200)	1220.32 (1010-1510)	1 (124)	830.03	*P* < 0.001
2013 (Adult)	1574.63 (1170-2000)	1223.66 (920-1500)	1 (223)	503.33	*P* < 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	Sig
2012 (50 days)	69.01 (55-79.2)	63.28 (52.7-78)	1 (865)	144.09	P < 0.001
2013 (43 days)	62.70 (51.2-69.9)	58.56 (45.7-65)	1 (873)	392.11	P < 0.001
2015 (62 days)	72.57 (67.2-81.1)	65.48 (67.2-81.1)	1 (192)	312.50	P < 0.001
2012 (Adult)	79.97 (72.95-88.2)	70.41 (63.2-76.15)	1 (221)	590.53	P < 0.001
2013 (Adult)	80.79 (75.25-89.4)	71.34 (61.05-78.1)	1 (186)	547.3	P < 0.001

Table 4 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

Mass (g) and lengths (mm) of male and female gut morphologies (degrees of freedom = 1,128) for birds shot as adults in 2012 and 2013

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

Table 5 Mass (g) and lengths (mm) of male and female gut morphologies (degrees of freedom = 1,128) for birds shot as adults in 2012 and 2013

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

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

Table 6 The percentage of males and females in the population with crop contents containing certain food for birds shot in 2013 with associated binomial statistics

Manuscript to be reviewed

The mean percentage of time spent foraging and the mean foraging bout length (s) for males and females after release into the wild

Behaviour	Year	Male Mean	SE M	Female Mean	SE M	df (df-error)	F	Sig
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

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