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**VIGILANCE PATTERNS OF WINTERING WIGEON: FEMALE
BENEFITS FROM MALE LOW-COST BEHAVIOUR**

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Keywords

female benefit; mate guarding; male constraint; male investment; vigilance; *Anas penelope*

Short title

Female benefits from male vigilance

Word Count: 4, 667

26 **Abstract**

27 Increased vigilance in male animals has been attributed to mate guarding (male investment
28 hypothesis), secondary sexual characteristics increasing predation risk (male constraint
29 hypothesis) or for benefit to the female (female benefits hypothesis). We studied Eurasian
30 wigeon *Anas penelope* while they grazed on dry land, a ‘risky’ foraging situation, at two
31 points during the winter period (pre and post pair formation) to assess if their behaviour
32 was more consistent with one of these three hypotheses. Males were always highly
33 vigilant, and vigilance increased markedly in more risky situations (smaller groups, higher
34 distance from water). Mean male vigilance only changed to a minor extent from the pre- to
35 the post-mating periods. Conversely, female vigilance significantly decreased after pairing,
36 and was then significantly lower than that of males. Prior to pairing, males and females had
37 similar rates of vigilance bouts. Overall, our findings suggest that higher vigilance in male
38 wigeons in this instance is best explained by the female benefits hypothesis. Because the
39 wigeons were foraging on land and were highly vigilant, even when unpaired, the females
40 could actually benefit from the males vigilance without males investing more time in
41 vigilance. In such a situation, paired males rely on ‘low-cost vigilance’ whereby vigilance
42 serves as a safety mechanism while simultaneously benefiting the female.

43

44

45 **Zusammenfassung**

46

47 **Wachsamkeitsmuster bei überwinternden Pfeifenten: Weibchen profitieren von**
48 **„Kosten-effizientem“ Verhalten der Männchen**

49

50 Besonders hohe Wachsamkeit männlicher Tiere wird in der Regel mit einer von drei
51 Hypothesen erklärt: dem Bewachen ihrer Weibchen (male investment hypothesis), als
52 sekundäres Geschlechtsmerkmal verbunden mit erhöhtem Risiko, erbeutet zu werden

53 (male constraint hypothesis), oder zum Nutzen der Weibchen (female benefits
54 hypothesis). Wir untersuchten eurasische Pfeifenten (*Anas penelope*) beim Grasensuchen auf
55 trockenem Land, einer risikoreichen Art der Nahrungssuche. Die Beobachtungen
56 fanden zu zwei Zeitpunkten während der Winterperiode (vor und nach der
57 Paarbildung) statt, um zu prüfen, ob ihr Verhalten eine der drei Hypothesen speziell
58 unterstützte. Die Männchen waren die ganze Zeit über sehr wachsam, und ihre
59 Wachsamkeit stieg in risikoreichen Situationen (in kleineren Gruppen, oder weiter
60 entfernt von Wasser) noch spürbar an. In der Zeit vor der Balz bis zu der Zeit danach
61 stieg die mittlere Wachsamkeit der Männchen kaum an, während im Unterschied dazu
62 die Wachsamkeit der Weibchen nach der Paarung deutlich nachließ und dann
63 signifikant niedriger als die der Männchen war. Vor der Paarbildung zeigten
64 Weibchen und Männchen ähnlich häufige Kurzphasen der Wachsamkeit. Unsere
65 Untersuchungen legen nahe, dass im vorliegenden Fall die erhöhte Wachsamkeit
66 männlicher Pfeifenten am besten von der „female benefits hypothesis“ erklärt wird.
67 Weil die Pfeifenten an Land auf Nahrungssuche gehen und dabei besonders im
68 unverpaarten Stadium außerordentlich wachsam sind, konnten die Weibchen von der
69 Wachsamkeit der Männchen profitieren, ohne dass diese Extra-Zeit dafür aufwenden
70 mußten. Die verpaarten Männchen begnügen sich mit dieser Kosten-effizienten
71 Wachsamkeit (low-cost vigilance), wobei diese als ein Sicherheitssystem dient, das
72 gleichzeitig den Weibchen nutzt.

73

74 **Introduction**

75 The role of vigilance and the factors affecting vigilance levels are among the central
76 questions of behavioural ecology (e.g. Krebs and Davies 1993). While vigilance in
77 animals can typically have an anti-predator role, it may also be directed towards
78 conspecifics, for example to avoid kleptoparasitism or to copy the behaviour of others
79 (reviewed in Elgar 1989; Lima 2009). In paired males, vigilance may additionally be
80 used to monitor the behaviour of competing other males (e.g., Dahlgren 1990). In
81 many species, especially birds, males show distinct and conspicuous secondary sexual
82 characters. While these may have a crucial role in sexual selection processes, such
83 characters may also make males more visible to predators than females of the same
84 species. Paired males may then be more vigilant than females because they face a
85 greater predation risk when in breeding plumage, not just because they guard their
86 mate (e.g., Lendrem 1983; Hart and Freed 2004). Lastly, males may use vigilance
87 behaviours to enhance female survival and to allow females more foraging and resting
88 time to enhance nutritional status and fecundity (e.g. Thompson and Popko 1981;
89 Lamprecht 1989; Artis and Martin 1995; Weibe and Martin 1988; Rodway 2007a),
90 with many studies reporting increased foraging times for the female when
91 accompanied by a mate (e.g. Gauthier 1987). Furthermore, evidence suggests that
92 male vigilance is important to females in mate selection, as females will preferentially
93 select vigilant males (Dahlgren 1990; Choudhury and Black 1993; Pizzari 2003).

94 These possible causes of paired male vigilance have been commonly termed
95 the “male investment”, “male constraint” and “female benefits” hypotheses,
96 respectively (e.g., Guillemain *et al.* 2003; Squires *et al.* 2007). The extent to which
97 vigilance of males and females in a given species is more consistent with one or the
98 other hypothesis may theoretically depend upon environmental conditions, though this

99 has never been properly tested. Ducks are good model organisms to study vigilance
100 behaviour patterns, because they are subject to frequent attacks by predators
101 (including during daylight hours, Guillemain *et al.* 2007a), they are highly gregarious
102 and form pair-bonds anew during each winter period that are maintained for a long
103 time before the breeding season itself, during spring (Mayhew and Houston 1989; see
104 however Mitchell 1997 for evidence of occasional re-mating over successive years in
105 this species). In waterfowl, such pairing in late autumn or early winter is considered to
106 be adaptive: paired birds indeed get dominant status within the flock which provides
107 better access to food (e.g. Johnson and Rohwer 1988; Black 2005), and for the male a
108 early pairing should translate into higher eventual breeding probability if sexual
109 competition for mates exists among individuals (e.g. Rohwer and Anderson 1988;
110 Oring and Saylor 1992; Bowler 2005). This in turn may allow paired females to
111 improve body condition, *sensu* the female benefits hypothesis, which is likely to
112 translate into higher breeding success (Guillemain *et al.* 2008). For example, Lercel *et*
113 *al.* (1999) demonstrated that female ducks that lose their mate after pairing during
114 winter experienced lower subsequent breeding success, hence demonstrating the
115 fitness benefit of early pairing in such species. Squires *et al.* (2007) determined for
116 harlequin ducks (*Histrionicus histrionicus*) that male vigilance could be explained by
117 the female benefits hypothesis, because unpaired males were less vigilant than paired
118 males despite having the same plumage, although this does not rule out the male
119 investment hypothesis. This is the opposite to what would be expected if the vigilance
120 was a result of male constraint. In common eiders (*Somateria mollisoma*), conversely,
121 it was concluded that male vigilance was primarily for paternity assurance, because
122 widowed females foraged at the same rate as prior to the loss of their mate, and
123 maintained body mass and clutch size which was comparable with previous breeding

124 seasons when paired (Hario and Hollmén 2004): females eiders had not been
125 benefiting nutritionally from having a mate.

126 During winter, previous studies of Eurasian wigeon *Anas penelope* have
127 demonstrated a significant difference in the length of time and frequency of vigilance
128 behaviour between the sexes during winter (Mayhew 1987). At this time males are
129 generally more vigilant than females (see also Goodburn 1984; Baldassarre and Bolen
130 2006). An earlier study in an acknowledged safe environment (mixed feeding flocks with
131 Brent Geese *Branta bernicla* L on large and open *Zoostera* sp. beds of the Exe Estuary,
132 UK, where predators were few) suggested that vigilance of male wigeons could be best
133 explained by the male investment hypothesis (Guillemain *et al.* 2003). This is because
134 males showed an increase in vigilance behaviour after pairing, not when they acquired
135 their brighter breeding plumage, and female vigilance rate did not differ between pre- and
136 post-pairing. In the present study, we also aimed to compare the vigilance levels of male
137 and female wigeons before and after the main period of pair formation, but in a less safe
138 environment in which birds were grazing on dry land, away from water. In such situation,
139 foraging wigeon use open water as a refuge in case of disturbance or predation event
140 (Mayhew and Houston 1989) and consequently their feeding is restricted to strips of
141 vegetation near to the water. Distance from water and flock size were measured as
142 covariates indicating varying levels of risk (e.g. Mayhew 1987; Elgar 1989). Vigilance in
143 wigeons typically increases with distance foraging from water, and decreases with
144 increasing flock size (Mayhew and Houston 1989). Such a situation may alter the relative
145 importance of the male investment, male constraint and female benefits hypotheses
146 compared to other safety contexts.

147 We predicted that if increased vigilance in males is primarily related to predator
148 detection (the male constraint hypothesis), then (1) the amount of vigilance behaviour

149 exhibited by both sexes should be similar before and after pairing, (2) vigilance should
150 decrease with increasing flock size at the same rate for both males and females, or at a
151 higher rate in the more conspicuous males, and (3) vigilance should increase with
152 increasing distance from water, again, at the same rate in males and females, or at a higher
153 rate in the more conspicuous males.

154 If mate guarding and paternity assurance plays a significant additional role in
155 vigilance (the male investment hypothesis), it was then predicted that (1) males should
156 become more vigilant than females in late winter, or the difference between males and
157 females should increase in late winter compared to early winter, (2) female vigilance
158 should remain constant or decrease in late winter (because they are being guarded by their
159 mate), and (3) male vigilance should increase with increasing flock size (because there are
160 more competing males), or remain similar if the benefits in terms of safety from predators
161 are counterbalanced by the costs in terms of sexual competition.

162 If the benefit to the female was the primary driving force of male vigilance (female
163 benefits hypothesis), it was predicted that (1) females should become less vigilant in late
164 winter compared to early winter as they are utilising their partners vigilance (2) male
165 vigilance should remain the same or increase in late winter compared to early winter, and
166 (3) vigilance should not be affected by group size or distance from water in either males or
167 females.

168

169 **Methods**

170 *Study site*

171 Traeth Lafan (Lavan Sands) is a large intertidal area of sand and mud flats lying on
172 the eastern edge of the Menai Straits, in Conwy Bay, North Wales, UK (53°17' N, 4°16'
173 W). The area as a whole has a range of exposures and a diversity of conditions enhanced

174 by freshwater streams that flow across the flats, and covers a total area of 2,643 ha. The
175 area is well used by members of the public, and is bordered by a railway line and a series
176 of public footpaths. The majority of the wigeon flock frequents a small intertidal area
177 comprising *Juncetum gerardii* and *Puccinellietum* salt-marsh, approximately 1.5 km west
178 of the village of Llanfairfechan (53°15' N, 4°1' W). The total number of wigeons present
179 each day varied between 180 – 440. Northern pintails *Anas acuta* regularly joined the
180 wigeon flock during grazing periods, along with lesser numbers of redshanks *Tringa*
181 *totanus*, Eurasian teals *Anas crecca* and mallards *Anas platyrhynchos*. There were no geese
182 or swans present. The main footpath that runs along the edge of the marsh and shoreline
183 experienced, on average, 37 human walkers along it per hour. Raptor flyovers were 2.9 and
184 2.1 per hour, for the November and March sampling sessions respectively. The main raptor
185 species involved in this were peregrine falcons (*Falco peregrinus*) and common buzzards
186 (*Buteo buteo*), and less frequently, merlins (*Falco columbarius*), common kestrels (*Falco*
187 *tinnunculus*) and on one occasion, hen harriers (*Circus cyaneus*).

188

189 *Vigilance recording*

190 Wigeon were counted and observed using an Opticron telescope (30x) and Opticron
191 binoculars (10 x 50). Observations were conducted from the 12th – 25th November, 2003,
192 and from the 4th – 16th March, 2004. The individual pairing status of each bird could not be
193 recorded (see below), so it is possible that some individuals from the November sample
194 were already paired, and some late individuals from the March sample (especially
195 juveniles) were still unpaired. However, November is when wigeons start to pair in
196 significant numbers (Guillemain *et al.* 2003) and most of these are generally paired by the
197 end of winter (Mayhew and Houston 1989), so that the two study periods were assumed to
198 adequately represent the pre- and post-pairing periods. A total of 562 focal observations

199 (*sensu* Altmann 1974) were used in the analyses, 244 in November and 318 in March.
200 Ducks were not individually marked, and it is therefore possible that some of them may
201 occasionally have been sampled twice. However, the incidence of double sampling during
202 the same day is likely to be low (see below), and thus should not cause an important
203 problem for statistical analyses. The traditionally high turnover of individuals among
204 wintering duck populations (Pradel *et al.* 1997, Guillemain *et al.*, 2010) also made the
205 double sampling of the same birds over different days unlikely. Counts were made during
206 daylight within 1.5 hours of low tide, for a total period of three hours – typically 1.5 hours
207 either side of low tide. Observations were made from a bench overlooking the tidal salt
208 marsh area, approximately 100 metres away from the region the wigeon most frequently
209 grazed. Because the birds formed many small groups, it was possible to get a large sample
210 number of many different flock sizes, and also limited the risk of sampling the same
211 individual more than once.

212 Sampling protocol followed that of Mayhew (1987) and Guillemain *et al.* (2002).
213 One focal bird was randomly selected from the approximate centre of the flock, sexed and
214 observed for 300 seconds. So as to provide an approximate equal number of each sex,
215 different sexes were observed alternatively, i.e. if the randomly selected individual was of
216 the ‘wrong’ sex, then the nearest bird of correct sex to this random one was observed
217 (Mayhew 1987).

218 Vigilance was measured as % time with head up in a grazing bird (i.e. grazing was
219 its predominant activity). At the start and end of each 300 s observation period, the flock
220 size was recorded and for each observation, a mean flock size allocated. The same
221 principle was applied to flock distance from water. The distances were estimated by eye, in
222 metres, but were considered to be reasonably accurate since the length of the area between
223 the footpath where the observations took place and the low tide of the water was known

224 (Mayhew and Houston 1989). The wigeon typically fed in compact, closely-knit groups in
225 the winter. However, at times there were a few individuals more widely dispersed. In order
226 to restrict the observations to birds feeding in clearly defined groups, birds further than 20
227 metres from the centre of the flock were not included in the estimation of flock size, or
228 selected for any vigilance recordings (Mayhew and Houston 1989). As the focus was on
229 one bird at a time (i.e. one bird typically filled the eyepiece of the telescope), it was not
230 possible to accurately determine whether each bird was paired or not. The maximum flock
231 size recorded during the sampling session was 350, and the maximum distance the wigeons
232 foraged from the waters edge was 35 metres.

233

234 *Statistical Analysis*

235 We used General Linear Models (GLM) to test for differences in proportion of time
236 spent vigilant by focal birds (arcsin-transformed during the statistical analyses, but
237 presented as percentages in the figures to ease reading) between sexes and periods of the
238 winter, taking into account the potential effects of distance from water and flock size.
239 Preliminary analyses suggested a non-linear relationship between vigilance rate and flock
240 size, so the latter was log-transformed before inclusion in the models. Similarly, a
241 significant correlation was initially found between flock size (log-transformed) and
242 distance from water ($P < 0.0001$). However, the regression coefficient was relatively low
243 ($r^2 = 0.55$), so that there was some variability in flock size that was not explained by
244 variability in distance. In order to tease apart the relative role of each variable on wigeon
245 vigilance (i.e., flock size and distance from water), both were therefore included at the
246 beginning of the model selection procedure. The variables and factors initially entered into
247 the GLM were, therefore, Sex, Month, Distance from water (hereafter “Distance”),
248 Log(FlockSize), and all possible interactions with up to three terms (the biological

249 meaning of more complicated models being difficult to interpret). A stepwise backwards
250 model selection procedure was then used, where non significant terms at $P = 0.05$ were
251 gradually removed, starting with the most complex interactions.

252 All values are presented as means \pm SE. All tests are considered significant if $P <$
253 0.05.

254

255 **Results**

256 The final model of the stepwise procedure provided an excellent fit to the data ($r^2 =$
257 0.91; Table 1). It first highlighted the major role of danger in itself on individual vigilance
258 rate, Log(FlockSize) alone being responsible of 75% of the explained variance (see ratio of
259 partial F-values from Table 1). Males were generally more vigilant than females, and
260 increased their vigilance rate from November to March, though to a limited extent (11.82%
261 ± 0.54 , $n = 149$ and $13.25\% \pm 0.58$, $n = 131$), while that of females decreased twice as
262 much ($10.58\% \pm 0.41$, $n = 138$ and $7.62\% \pm 0.42$, $n = 135$; Fig. 1).

263 The two sexes fed in flocks of similar size both in November (ANOVA: $F_{1,285} =$
264 0.02, $r^2 = 0.00$, $P = 0.8848$) and in March (ANOVA: $F_{1,264} = 0.77$, $r^2 = 0.00$, $P = 0.3819$).
265 The differences in vigilance rates between the two time periods could not be explained by
266 average flock size being different between November and March in either of the two sexes
267 (ANOVA on average Log(FlockSize): Males: $F_{1,278} = 0.58$, $r^2 < 0.01$, $P = 0.4485$; Females
268 $F_{1,271} = 3.03$, $r^2 = 0.01$, $P = 0.0830$). However, there was a significant effect of the
269 Sex*Log(FlockSize), the Month*Log(FlockSize) and the Sex*Month*Log(FlockSize)
270 interactions (Table 1) indicating that, despite average flock sizes being similar in all cases,
271 i) vigilance decreased at a higher rate with increasing flock size in males than in females,
272 ii) vigilance decreased at different rates in November and in March, and iii) the later
273 difference was of different magnitude between males and females. In the later case, the

274 negative slope of vigilance rate against flock size actually increased in magnitude from
275 November to March in males, and decreased in females (Fig. 2).

276 Males increased their foraging distance from water between the two time periods
277 (10.84m \pm 0.54 and 13.79m \pm 0.57 in November and March, respectively; ANOVA: $F_{1,278}$
278 = 13.99, $r^2 = 0.05$, $P = 0.0002$), while females showed an opposite trend (11.34m \pm 0.58
279 and 7.93m \pm 0.58, respectively; ANOVA: $F_{1,271} = 17.39$, $r^2 = 0.06$, $P < 0.0001$). While
280 males and females fed at a similar distance from water in November (ANOVA: $F_{1,285} =$
281 0.45, $r^2 = 0.00$, $P = 0.5043$), females thus fed at a shorter distance from water than males in
282 March (7.93 m \pm 0.60 and 13.79 m \pm 0.61, respectively; ANOVA: $F_{1,264} = 46.70$, $r^2 = 0.15$,
283 $P < 0.0001$). In March, males spent, on average, 25% of their time being vigilant when
284 foraging in small flocks (Fig. 2) compared to 15% of their time in November. Comparably,
285 time spent being vigilant by females in November when foraging in small flocks, as with
286 the males, was approximately 15%, reducing to 10% in March.

287 That no interaction with Distance was retained in the final model indicated that the
288 benefit birds gained from foraging closer to the water in terms of decreased vigilance was
289 similar in males and females, and did not differ between the two time periods, that is, the
290 slopes remained similar.

291

292 **Discussion**

293 Our data provides little support for the male investment hypothesis (Guillemain *et*
294 *al.* 2003), that males increase their vigilance to guard their mate when they become paired.
295 Even the slight increase in male mean vigilance from November to March could be simply
296 explained by non-mating reasons since males, on average, fed at a greater distance from
297 water in March. In both sexes, vigilance increased with foraging distance from water and
298 decreased with increasing flock size. We have shown that wigeons on our wetland study

299 site spent a *c.* 10% of their potential feeding time scanning their environment. This is
300 similar to what wigeons have been recorded to do when foraging on dry land previously
301 (Guillemain *et al.*, 2002 or Mayhew 1987). For comparison, female and unpaired male
302 wigeons on average spent less than 5% of their time vigilant while foraging on the Exe
303 Estuary, where males were apparently essentially vigilant to ensure paternity with their
304 mate and for pair bond protection (Guillemain *et al.* 2003). Compared to Mayhew and
305 Houston (1989), the wigeons in the current study foraged, on average, in larger flocks and
306 closer to the water. For example, at Caerlaverock, Solway Firth (Mayhew and Houston,
307 1989), the wigeons maximum foraging distance from the water was 60 metres, compared
308 to just 35 metres in the present study. This can be attributed to the smaller site in the
309 present study when compared to Caerlaverock. The total distance from the high tide line of
310 the sea to the footpath at the rear of the marsh was only approximately 80 metres.
311 Therefore, the wigeons were foraging at smaller distances from a water body, whether that
312 is the sea or one of the many small pools that were present within the marsh.

313 Male vigilance increased markedly in more risky situations (smaller groups, longer
314 distance from water), and only changed to a minor extent from the pre- to the post-mating
315 periods. Moreover, male and female vigilance was similar in the November period. This
316 suggests that the slightly higher vigilance rate of males during March compared to that of
317 females is not a result of the male constraint hypothesis (it is not related to the male's
318 plumage). The vigilance patterns are consistent with the predicted commonly observed
319 relationship between vigilance and distance from water or group size in wigeons (Mayhew
320 1987; Mayhew and Houston 1989). The increase in foraging distance during late winter in
321 the males supports the hypothesis that anti-predator vigilance plays a major role in the
322 behaviour of wigeons when in foraging flocks. It is highly likely that males are forced to
323 use these distant and more risky areas in late winter, when safer feeding patches closer to

324 water have been depleted (following general central-place foraging theory, e.g. Stephens
325 and Krebs 1986). The significant decrease in female vigilance between the two periods and
326 the lack of a similar increase in male mean vigilance (the difference in vigilance rates was
327 twice larger in females than in males) lends support to the female benefits hypothesis.
328 Females fed closer to the water in March than in November, i.e. were less at risk when they
329 were paired. Examination of Figure 2 shows that females decreased their vigilance from
330 November to March when they were foraging in the most risky situations, i.e. when in
331 smaller flocks. Male vigilance was maximum in such situations, and almost twice that of
332 females: in flocks of 3-5 birds males spent 20.4% of their time vigilant (± 0.5 , $n = 53$),
333 while females spent 11.7 % ± 0.5 ($n = 51$). Paired females in March will thus benefit from
334 the presence of their mate in such most risky situations, enabling them to continue foraging
335 and build body stores.

336 The female benefits hypothesis provides a satisfactory evolutionary
337 framework for vigilance patterns in paired birds, as the effectiveness of mate guarding
338 has been called into question (Struchbury and Neudorf 1998), mainly because of time
339 constraints on the male, and the tactics that females can adopt to circumvent male
340 guarding efforts. However, it has been shown that mate guarding can be effective in
341 partially assuring paternity, particularly when males are extremely attentive (Chuang-
342 Dobbs *et al.* 2001). For example, male common eiders spend 99% of their time mate-
343 guarding when the females are most fertile (Christensen 2000; Hario and Hollmén
344 2004). However, male birds of other species continue to follow females after the
345 fertile period has ended, suggesting that paternity assurance is not the primary reason
346 for general mate-guarding, and increased vigilance (Squires *et al.* 2007; Rodway
347 2007a). Martin *et al.* (2003) proposed that predation risk was more important than
348 partial loss of paternity, as a fatal attack on a female will result in a total loss of

349 offspring. It is, therefore, better for the male to invest in the female through allowing
350 her to feed at a higher rate than she would otherwise, and thus allowing the male to
351 potentially increase his own fitness. Quan et al (2003) suggested that male birds could
352 also achieve this through maintenance of the pair bond and female preference. The
353 question still remains, however, of whether females simply capitalise on male
354 vigilance or stimulate it (Artiss *et al.* 1999). A recent theory encompasses benefits for
355 both males and females. Rodway (2007a, 2007b) studied the time unpaired male
356 harlequin ducks spent engaged in display behaviour, which was mutually exclusive to
357 foraging. When the males became paired, they significantly reduced displaying
358 behaviour and increased foraging, thus increasing their energy intake. Simultaneously,
359 the females also increased foraging (Rodway 2007a; Rodway 2007b). Therefore, both
360 the male and female mutually benefit from pairing in terms of time-budget. However,
361 it has been proposed that the female should only pair early if the bond is beneficial for
362 her (Artis and Martin 1995). If food is plentiful and predation risk low, the female
363 should actually avoid the more conspicuous males (Artis and Martin 1995; Rodway
364 2007b). In wigeons, it is likely that as the wintering season progresses, food and
365 resources will be further from the water (see above) and thus involves riskier
366 foraging. Therefore, pairing up at this stage would be a good strategy for the female.
367 Both the male and female benefit from the female being in the best possible
368 physiological condition.

369 That males responded to group size more than females (they decreased their
370 vigilance to a greater extent with increasing group size), and did so to a higher extent in
371 March than in November (while the reverse would have been expected if there was a fierce
372 competition for females between males) suggests that the increase in male vigilance,
373 particularly in small flocks, is for the benefit of the female. If this increase vigilance was

374 anti-predator related, the relationships between male vigilance and flock size would be
375 expected to remain unchanged between November and March. Because the present
376 terrestrial feeding location is intrinsically dangerous (Mayhew 1988; Mayhew and Houston
377 1989; Larsen 1996), vigilance levels in male wigeon are particularly high in Traeth Lafan,
378 even in November. Once mated, the paired females are benefiting from this genuine high
379 level of vigilance by their mate to decrease their own vigilance and dedicate more time to
380 foraging (see also Jacobsen and Ugelvik 1994).

381 What is unusual is the lack of a large increase in male vigilance when paired (e.g.,
382 Martin 1984, Guillemain *et al.* 2003). From our data set, it is not possible to determine
383 whether males could increase their vigilance further at Traeth Lafan. It is likely male
384 wigeons at Traeth Lafan are already close to the maximum vigilance level they can afford
385 to be without compromising their daily energy intake. In this scenario, females are able to
386 benefit from the males vigilance at now extra cost to the male, and the males only need
387 provide minimal supplementary vigilance in late winter. This, coupled with already high
388 levels of vigilant behaviour in males means the females are able reduce their vigilance and
389 focus on foraging. This occurs with no detriment to the male's daily energy intake. The
390 only circumstance where this may alter is when foraging in small flocks, when males are
391 both significantly more vigilant than females and more vigilant than when foraging at the
392 same distance in early winter compared to late winter. If mate guarding and paternity
393 assurance can be ruled out as a function of vigilance in the present study, paired males and
394 females could potentially benefit from foraging in larger flocks to avoid the male having to
395 increase vigilance.

396 The present pattern would thus be similar to the situation recorded in Eurasian teal
397 foraging at deep depths, where males are already so vigilant because of their blind
398 exposure to predators when up-ending to forage that they do not increase vigilance after

399 acquiring a mate (Guillemain *et al.* 2007b). In both cases, this could explain how male
400 birds with high energy demands can afford the cost of maintaining a pair-bond during such
401 long periods in winter (see Rodway 2007b). Data are not available at present, but a
402 comparison of forced copulation attempts on female wigeons at Traeth Lafan and on the
403 Exe Estuary (where male wigeons are clearly vigilant for paternity assurance and/or pair-
404 bond protection) could allow testing the above hypothesis more specifically. This study,
405 therefore, suggests that whether male and female vigilance in a given species is more likely
406 to be driven by the male constraint, male investment or female benefits hypothesis may
407 depend very much upon the environmental safety conditions, and is not a fixed species-
408 specific life history trait. While they had long been considered as mutually exclusive
409 activities, the traditional distinction between non-vigilant feeding bouts and non-feeding
410 vigilance bouts in foragers was challenged a few years ago by Lima and Bednekoff (1999),
411 showing that some individuals were able to maintain anti-predator vigilance while foraging
412 with their head down. Similarly, the present study suggests that vigilance for several
413 purposes may be combined by paired males in some situations.

414

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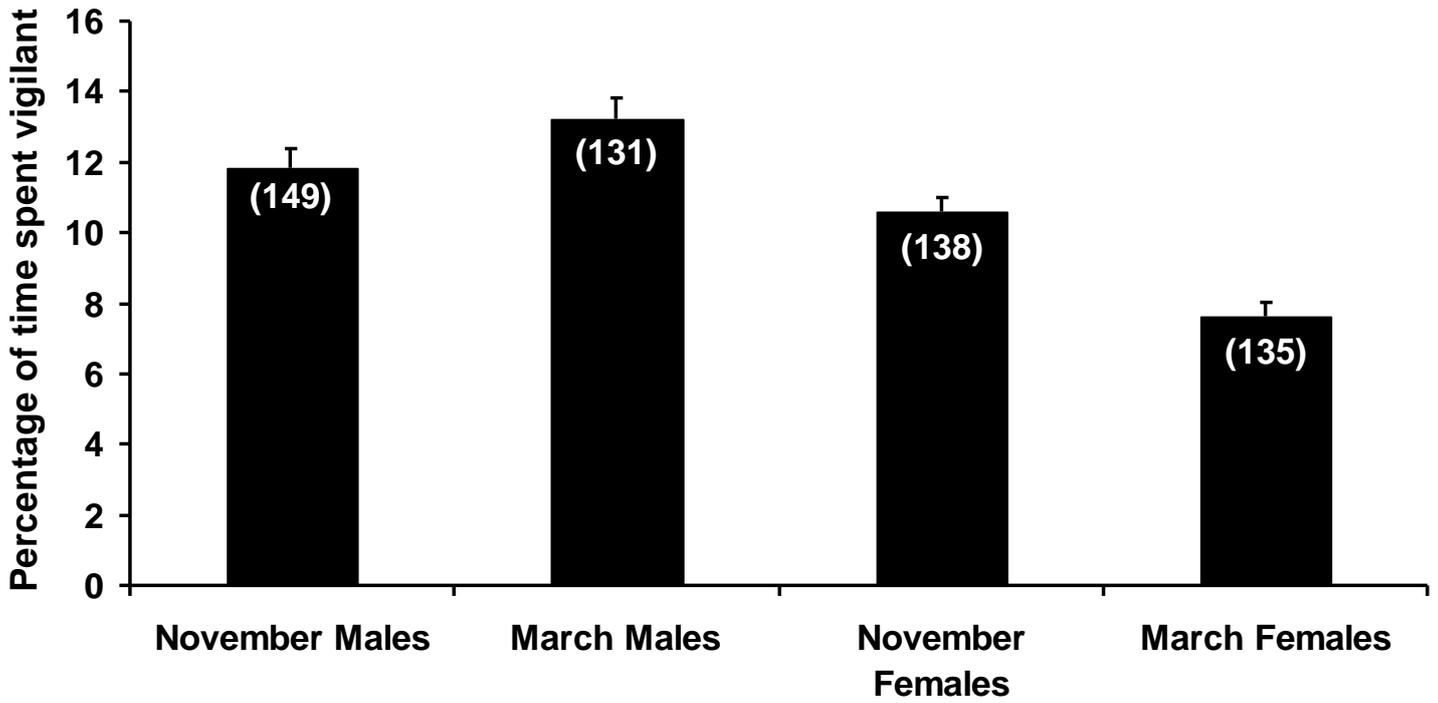
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550 **Fig. 1** Average percentage of time spent vigilant by male and female wigeon in November
551 and March. Vertical bars show standard errors, numbers in brackets are sample sizes. See
552 text for statistics.

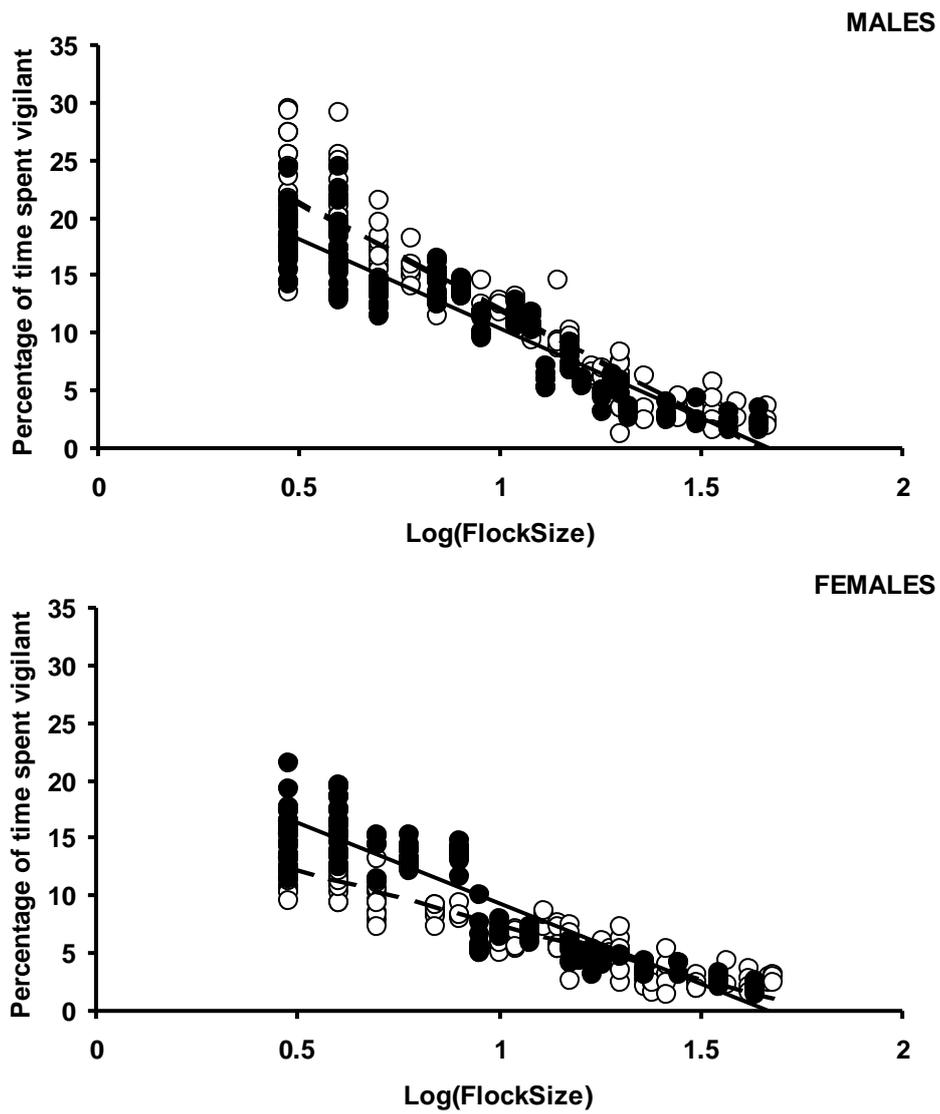
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555 **Fig. 2** Percentage of time spent vigilant by male (top) and female (bottom) wigeon as a
556 function of flock size (Log-transformed) during the two study periods. November data are
557 represented by black dots and plain lines, March data by white circles and dotted lines. See
558 text for statistics.

559



560

561 **Table 1** Best fitting models for the percentage of time spent vigilant by wigeon while
562 foraging, testing for differences between males and females (Sex), November and March
563 observation periods (“Month”), the effect of group size in which each focal bird foraged
564 (“Log(FlockSize)”) and the distance from water at which it did so (“Distance”), plus their
565 interactions. Only the final model of the backwards stepwise model selection procedure is
566 shown.

567

Variable	df	Estimate ± SE	Partial F	P-Value
<i>Complete model: $F_{8,544} = 710.24$, $r^2 = 0.91$, $P < 0.0001$</i>				
Sex (Males)	1	2.93 ± 0.21	194.02	<0.0001
Month (March)	1	-0.64 ± 0.21	9.35	0.0023
Log(FlockSize)	1	-12.00 ± 0.31	1471.82	< 0.0001
Distance	1	0.18 ± 0.02	114.63	< 0.0001
Sex*Month	1	1.68 ± 0.21	61.09	< 0.0001
Sex*Log(FlockSize)	1	-1.81 ± 0.21	75.66	< 0.0001
Month*Log(FlockSize)	1	0.59 ± 0.21	8.10	0.0046
Sex*Month*Log(FlockSize)	1	-1.15 ± 0.2112	30.55	< 0.0001

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