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Vigilance patterns of wintering Eurasian Wigeon: female benefits from male low-cost behaviour

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

Keywords Female benefit · Mate guarding · Male constraint · Male investment · Vigilance · *Anas penelope*

Zusammenfassung Besonders hohe Wachsamkeit männlicher Tiere wird in der Regel mit einer von drei Hypothesen erklärt: dem Bewachen ihrer Weibchen (male investment hypothesis), als sekundäres Geschlechtsmerkmal verbunden mit erhöhtem Risiko, erbeutet zu werden (male constraint hypothesis), oder zum Nutzen der Weibchen (female benefits hypothesis). Wir untersuchten eurasische Pfeifenten (*Anas penelope*) beim Grasen auf trockenem Land, einer risikoreichen Art der Nahrungssuche. Die Beobachtungen fanden zu zwei Zeitpunkten während der Winterperiode (vor und nach der Paarbildung) statt, um zu prüfen, ob ihr Verhalten eine der drei Hypothesen speziell unterstützte. Die Männchen waren die ganze Zeit über sehr wachsam, und ihre Wachsamkeit stieg in risikoreichen Situationen (in kleineren Gruppen, oder weiter entfernt von Wasser) noch spürbar an. In der Zeit vor der Balz bis zu der Zeit danach stieg die mittlere Wachsamkeit der Männchen kaum an, während im Unterschied dazu die Wachsamkeit der Weibchen nach der Paarung deutlich nachließ und dann signifikant niedriger als die der Männchen war. Vor der Paarbildung zeigten Weibchen und Männchen ähnlich häufige Kurzphasen der Wachsamkeit. Unsere Untersuchungen legen nahe, dass im vorliegenden Fall die erhöhte Wachsamkeit männlicher Pfeifenten am besten von der „female benefits hypothesis" erklärt wird. Weil die Pfeifenten an Land auf Nahrungssuche gehen und dabei besonders im unverpaarten Stadium außerordentlich wachsam sind, konnten die Weibchen von der Wachsamkeit der Männchen profitieren,

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ohne dass diese Extra-Zeit dafür aufwenden mußten. Die verpaarten Männchen begnügen sich mit dieser Kosten-effizienten Wachsamkeit (low-cost vigilance), wobei diese als ein Sicherheitssystem dient, das gleichzeitig den Weibchen nutzt.

Introduction

The role of vigilance and the factors affecting vigilance levels are among the central questions of behavioural ecology (e.g. Krebs and Davies 1993). While vigilance in animals can typically have an anti-predator role, it may also be directed towards conspecifics, for example to avoid kleptoparasitism or to copy the behaviour of others (reviewed in Elgar 1989; Lima 2009). In paired males, vigilance may additionally be used to monitor the behaviour of competing other males (e.g. Dahlgren 1990). In many species, especially birds, males show distinct and conspicuous secondary sexual characters. While these may have a crucial role in sexual selection processes, such characters may also make males more visible to predators than females of the same species. Paired males may then be more vigilant than females because they face a greater predation risk when in breeding plumage, not just because they guard their mate (e.g. Lendrem 1983; Hart and Freed 2004). Lastly, males may use vigilance behaviours to enhance female survival and to allow females more foraging and resting time to enhance nutritional status and fecundity (e.g. Thomas and Popko 1981; Lamprecht 1989; Artis and Martin 1995; Wiebe and Martin 1998; Rodway 2007a), with many studies reporting increased foraging times for the female when accompanied by a mate (e.g. Gauthier 1987). Furthermore, evidence suggests that male vigilance is important to females in mate selection, as females will preferentially select vigilant males (Dahlgren 1990; Choudhury and Black 1993; Pizzaro 2003).

These possible causes of paired male vigilance have been commonly termed the “male investment”, “male constraint” and “female benefits” hypotheses, respectively (e.g. Guillemain et al. 2003; Squires et al. 2007). The extent to which vigilance of males and females in a given species is more consistent with one or the other hypothesis may theoretically depend upon environmental conditions, though this has never been properly tested. Ducks are good model organisms to study vigilance behaviour patterns, because they are subject to frequent attacks by predators (including during daylight hours; Guillemain et al. 2007a), they are highly gregarious and form pair-bonds anew during each winter period that are maintained for a long time before the breeding season itself, during spring (Mayhew and Houston 1989; see, however, Mitchell 1997 for evidence of occasional re-mating over successive years in this species). In waterfowl, such pairing in late autumn or early winter is considered to be adaptive: paired birds indeed get dominant status within the flock which provides better access to food (e.g. Johnson and Rohwer 1998; Black 2005), and for the male, an early pairing should translate into higher eventual breeding probability if sexual competition for mates exists among individuals (e.g. Rohwer and Anderson 1988; Oring and Sayler 1992; Bowler 2005). This in turn may allow paired females to improve body condition, sensu the female benefits hypothesis, which is likely to translate into higher breeding success (Guillemain et al. 2008). For example, Lercel et al. (1999) demonstrated that female ducks that lose their mate after pairing during winter experienced lower subsequent breeding success, hence demonstrating the fitness benefit of early pairing in such species. Squires et al. (2007) determined for Harlequin Ducks (*Histrionicus histrionicus*) that male vigilance could be explained by the female benefits hypothesis, because unpaired males were less vigilant than paired males despite having the same plumage, although this does not rule out the male investment hypothesis. This is the opposite to what would be expected if the vigilance was a result of male constraint. In Common Eiders (*Somateria mollisoma*), conversely, it was concluded that male vigilance was primarily for paternity assurance, because widowed females foraged at the same rate as prior to the loss of their mate, and maintained body mass and clutch size which was comparable with previous breeding seasons when paired (Hario and Hollmén 2004); female eiders had not been benefitting nutritionally from having a mate.

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

We predicted that, if increased vigilance in males is primarily related to predator detection (the male constraint hypothesis), then (1) the amount of vigilance behaviour exhibited by both sexes should be similar before and after pairing, (2) vigilance should decrease with increasing flock size at the same rate for both males and females, or at a higher rate in the more conspicuous males, and (3) vigilance should increase with increasing distance from water, again at the same rate in males and females, or at a higher rate in the more conspicuous males.

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

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

Methods

Study site

Traeth Lafan (Lavan Sands) is a large intertidal area of sand and mud flats lying on the eastern edge of the Menai Straits, in Conwy Bay, North Wales, UK (53°17′N, 4°16′W). The area as a whole has a range of exposures and a diversity of conditions enhanced by freshwater streams that flow across the flats, and covers a total area of 2,643 ha. The area is well used by members of the public, and is bordered by a railway line and a series of public footpaths. The majority of the wintering Wigeon flock frequents a small intertidal area comprising *Juncetum gerardii* and *Puccinellietum* salt-marsh, approximately 1.5 km west of the village of Llanfairfechan (53°15′N, 4°1′W). The total number of Wigeon present each day varied between 180 and 440. Northern Pintail (*Anas acuta*) regularly joined the Wigeon flock during grazing periods, along with lesser numbers of Common Redshank (*Tringa totanus*), Eurasian Teal (*Anas crecca*) and Mallard (*Anas platyrhynchos*). There were no geese or swans present. The main footpath that runs along the edge of the marsh and shoreline experienced, on average, 37 human walkers along it per hour. Raptor flyovers were 2.9 and 2.1 per hour, for the November and March sampling sessions, respectively. The main raptor species involved in this were Peregrine Falcon (*Falco peregrinus*) and Common Buzzard (*Buteo buteo*), and, less frequently, Merlin (*Falco columbarius*), Common Kestrel (*Falco tinnunculus*) and, on one occasion, Hen Harrier (*Circus cyaneus*).

Vigilance recording

Wigeon were counted and observed using an Opticron telescope (×30) and Opticron binoculars (10 × 50). Observations were conducted from 12–25 November 2003 and from 4–16 March 2004. The individual pairing status of each bird could not be recorded (see below), so it is possible that some individuals from the November sample were already paired, and some late individuals from the March sample (especially juveniles) were still unpaired. However, November is when Wigeon start to pair in significant numbers (Guillemain et al. 2003) and most of these are generally paired by the end of winter (Mayhew and Houston 1989), so that the two study periods were assumed to adequately represent the pre- and post-pairing periods. A total of 562 focal observations (*sensu* Altmann 1974) were used in the analyses, 244 in November and 318 in March. Ducks were not individually marked, and it is therefore possible that some of them may occasionally have been sampled twice. However, the incidence of double sampling during the same day is likely to be low (see below), and thus should not cause an important problem for statistical analyses. The traditionally high turnover of individuals among wintering duck populations (Pradel 1997; Guillemain et al. 2010) also made the double sampling of the same birds over different days unlikely. Counts were made during daylight within 1.5 h of low tide, for a total period of 3 h—typically 1.5 h either side of low tide. Observations were made from a bench overlooking the tidal salt marsh area, approximately 100 m away from the region the Wigeon most frequently grazed. Because the birds formed many small groups, it was possible to get a large sample number of many different flock sizes, which also limited the risk of sampling the same individual more than once.

Sampling protocol followed that of Mayhew (1987) and Guillemain. (2002). One focal bird was randomly selected from the approximate centre of the flock, sexed and observed for 300 s. So as to provide an approximate equal number of each sex, different sexes were observed alternatively, i.e. if the randomly selected individual was of the 'wrong' sex, then the nearest bird of correct sex to this random one was observed (Mayhew 1987).

Vigilance was measured as % time with head up in a grazing bird (i.e. grazing was its predominant activity). At the start and end of each 300-s observation period, the flock size was recorded and, for each observation, a mean flock size allocated. The same principle was applied to flock distance from water. The distances were estimated by eye, in metres, but were considered to be reasonably accurate since the length of the area between the footpath where the observations took place and the low tide of the water was known (Mayhew and Houston 1989). The Wigeon typically fed in compact, closely-knit groups in the winter. However, at times, there were a few individuals more widely dispersed. In order to restrict the observations to birds feeding in clearly defined groups, birds further than 20 m from the centre of the flock were not included in the estimation of flock size, or selected for any vigilance recordings (Mayhew and Houston 1989). As the focus was on one bird at a time (i.e. one bird typically filled the viewing area of the telescope), it was not possible to accurately determine whether each bird was paired or not. The maximum flock size recorded during the sampling session was 350, and the maximum distance the Wigeon foraged from the waters edge was 35 m.

Statistical analysis

We used general linear models (GLM) to test for differences in proportion of time spent vigilant by focal birds (arcsin-transformed during the statistical analyses, but presented as percentages in the figures to ease reading) between sexes and periods of the winter, taking into account the potential effects of distance from water and flock size. Preliminary analyses suggested a non-linear relationship between vigilance rate and flock size, so the latter was log-transformed before inclusion in the models. Similarly, a significant correlation was initially found between flock size (log-transformed) and distance from water ($P < 0.0001$). However, the regression coefficient was relatively low ($r^2 = 0.55$), so that there was some variability in flock size that was not explained by variability in distance. In order to tease apart the relative role of each variable on Wigeon vigilance (i.e. flock size and distance from water), both were therefore included at the beginning of the model selection procedure. The variables and factors initially entered into the GLM were, therefore, Sex, Month, Distance from water (hereafter "Distance"), Log(FlockSize), and all possible interactions with up to three terms (the biological meaning of more complicated models being difficult to interpret). A stepwise backwards model selection procedure was then used, where non-significant terms at $P = 0.05$ were gradually removed, starting with the most complex interactions.

All values are presented as means ± SE. All tests are considered significant if $P < 0.05$.

Results

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

The two sexes fed in flocks of similar size both in November (ANOVA: $F_{1,285} = 0.02$, $r^2 = 0.00$, $P = 0.8848$) and in March (ANOVA: $F_{1,264} = 0.77$, $r^2 = 0.00$, $P = 0.3819$). The differences in vigilance rates between the two time periods could not be explained by average flock size being different between November and March in either of the two sexes (ANOVA on average Log(FlockSize): males: $F_{1,278} = 0.58$, $r^2 < 0.01$, $P = 0.4485$; females $F_{1,271} = 3.03$, $r^2 = 0.01$, $P = 0.0830$). However, there was a significant effect of the Sex × Log(FlockSize), the Month × Log(FlockSize) and the Sex × Month × Log(FlockSize) interactions (Table 1) indicating that, despite average flock sizes being similar in all cases, (1) vigilance decreased at a higher rate with increasing flock size in males than in females, (2) vigilance decreased at different rates in November and in March, and (3) the later difference was of different magnitude between males and females. In the later case, the negative slope of vigilance rate against flock size actually increased in magnitude from November to March in males, and decreased in females (Fig. 2).

Males increased their foraging distance from water between the two time periods (10.84 ± 0.54 and 13.79 ± 0.57 m in November and March, respectively; ANOVA: $F_{1,278} = 13.99$, $r^2 = 0.05$, $P = 0.0002$), while females showed an opposite trend (11.34 ± 0.58 and 7.93 ± 0.58 m, respectively; ANOVA: $F_{1,271} = 17.39$, $r^2 = 0.06$, $P < 0.0001$). While males and females fed at a similar

Table 1 Best fitting models for the percentage of time spent vigilant by Eurasian Wigeon (*Anas penelope*) while foraging, testing for differences between males and females (*Sex*), November and March observation periods (*Month*), the effect of group size in which each focal bird foraged [*Log*(*FlockSize*)] and the distance from water at which it did so (*Distance*), plus their interactions

Variable	*df*	Estimate ± SE	Partial *F*	*P* value
Complete model: $F_{8,544} = 710.24$, $r^2 = 0.91$, $P < 0.0001$				
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

Only the final model of the backwards stepwise model selection procedure is shown

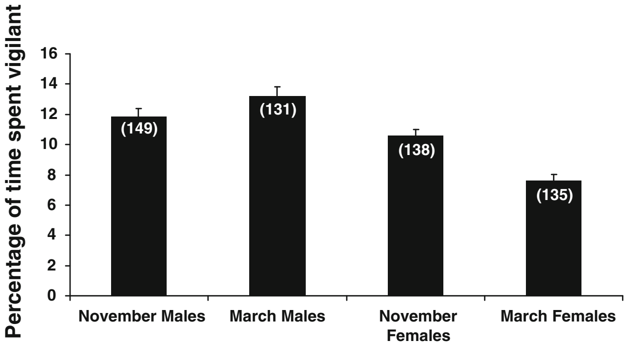

Fig. 1 Average percentage of time spent vigilant by male and female Eurasian Wigeon (*Anas penelope*) in November and March. *Vertical bars* show standard errors, *numbers in parentheses* are sample sizes. See text for statistics

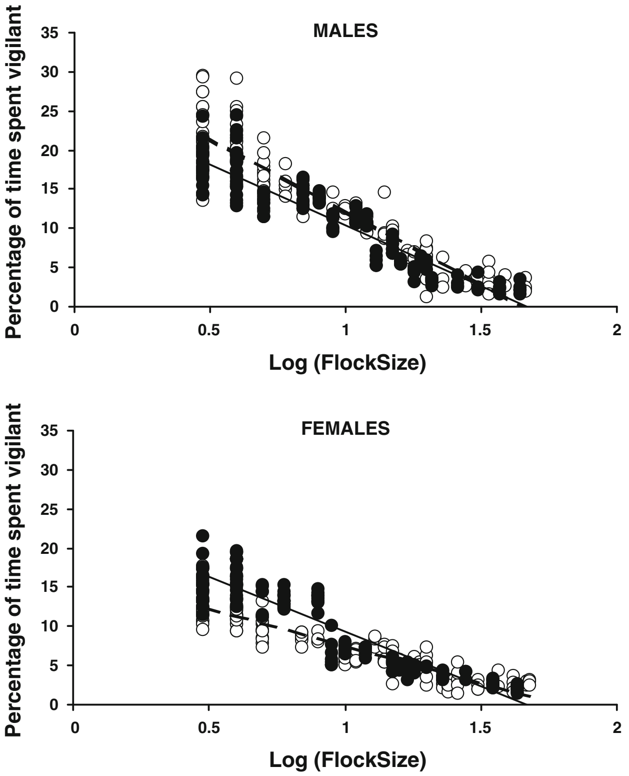

Fig. 2 Percentage of time spent vigilant by male (*top*) and female (*bottom*) Wigeon as a function of flock size (log-transformed) during the two study periods. November data are represented by *black dots* and *plain lines*, March data by *white circles* and *dotted lines*. See text for statistics

distance from water in November (ANOVA: $F_{1,285} = 0.45$, $r^2 = 0.00$, $P = 0.5043$), females thus fed at a shorter distance from water than males in March (7.93 ± 0.60 and 13.79 ± 0.61 m, respectively; ANOVA: $F_{1,264} = 46.70$, $r^2 = 0.15$, $P < 0.0001$). In March, males spent, on average, 25% of their time being vigilant when foraging in small flocks (Fig. 2) compared to 15% of their time in November. Comparably, time spent being vigilant by females in November when foraging in small flocks, as with the males, was approximately 15%, reducing to 10% in March.

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

Discussion

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

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

Male vigilance increased markedly in more risky situations (smaller groups, longer distance from water), and only changed to a minor extent from the pre- to the post-mating periods. Moreover, male and female vigilance was similar in the November period. This suggests that the slightly higher vigilance rate of males during March compared to that of females is not a result of the male constraint hypothesis (it is not related to the male's plumage). The vigilance patterns are consistent with the predicted commonly observed relationship between vigilance and distance from water or group size in Wigeon (Mayhew 1987; Mayhew and Houston 1989). The increase in foraging distance during late winter in the males supports the hypothesis that anti-predator vigilance plays a major role in the behaviour of Wigeon when in foraging flocks. It is highly likely that males are forced to use these distant and more risky areas in late winter, when safer feeding patches closer to water have been depleted (following general central-place foraging theory; e.g. Stephens and Krebs 1986). The significant decrease in female vigilance between the two periods and the lack of a similar increase in male mean vigilance (the difference in vigilance rates was twice as large in females than in males) lends support to the female benefits hypothesis. Females fed closer to the water in March than in November, i.e. were less at risk when they were paired. Examination of Fig. 2 shows that females decreased their vigilance from November to March when they were foraging in the most risky situations, i.e. when in smaller flocks. Male vigilance was maximum in such situations, and almost twice that of females: in flocks of 3–5 birds, males spent 20.4 ± 0.5% of their time vigilant ($n = 53$), while females spent 11.7 ± 0.5% ($n = 51$). Paired females in March will thus benefit from the presence of their mate in such most risky situations, enabling them to continue foraging and build body stores.

The female benefits hypothesis provides a satisfactory evolutionary framework for vigilance patterns in paired birds, as the effectiveness of mate guarding has been called into question (Struchbury and Neudorf 1998), mainly because of time constraints on the male, and the tactics that females can adopt to circumvent male guarding efforts. However, it has been shown that mate guarding can be effective in partially assuring paternity, particularly when males are extremely attentive (Chuang-Dobbs et al. 2001). For example, male Common Eiders spend 99% of their time mate guarding when the females are most fertile (Christensen 2000; Hario and Hollmén 2004). However, male birds of other species continue to follow females after the fertile period has ended, suggesting that paternity assurance is not the primary reason for general mate guarding, and increased vigilance (Squires et al. 2007; Rodway 2007a). Martin et al. (1993) proposed that predation risk was more important than partial loss of paternity, as a fatal attack on a female will result in a total loss of offspring. It is, therefore, better for the male to invest in the female through allowing her to feed at a higher rate than she would otherwise, and thus allowing the male to potentially increase his own fitness. Quan et al. (2003) suggested that male birds could also achieve this through maintenance of the pair bond and female preference. The question still remains, however, as to whether females simply capitalise on male vigilance or stimulate it (Artiss et al. 1999). A recent theory encompasses benefits for both males and females. Rodway (2007a, b) studied the time unpaired male Harlequin Ducks spent engaged in display behaviour, which was mutually exclusive to foraging. When the males became paired, they significantly reduced displaying behaviour and increased foraging, thus increasing their energy intake. Simultaneously, the females also increased foraging (Rodway 2007a, b). Therefore, both the male and female mutually benefit from pairing in terms of time budgets. However, it has been proposed that the female should only pair early if the bond is beneficial for her (Artis and Martin 1995). If food is plentiful and predation risk low, the female should actually avoid the more conspicuous males (Artis and Martin 1995; Rodway 2007b). In Wigeon, it is likely that, as the wintering season progresses, food and resources will be further from the water (see above) and thus involve riskier foraging. Therefore, pairing up at this stage would be a good strategy for the female. Both the male and female benefit from the female being in the best possible physiological condition.

That males responded to group size more than females (they decreased their vigilance to a greater extent with increasing group size), and did so to a greater extent in March than in November (while the reverse would have been expected if there was a fierce competition for females between males) suggests that the increase in male vigilance, particularly in small flocks, is for the benefit of the female. If this increased vigilance was anti-predator-related, the relationships between male vigilance and flock size would be expected to remain unchanged between November and March. Because the present terrestrial feeding location is intrinsically dangerous (Mayhew 1988; Mayhew and Houston 1989; Larsen 1996), vigilance levels in male Wigeon are particularly high in Traeth Lafan, even in November. Once mated, the paired females are benefitting from this genuine high level of vigilance by their mate to decrease their own vigilance and dedicate more time to foraging (see also Jacobsen and Ugelvik 1994).

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

The present pattern would thus be similar to the situation recorded in Eurasian Teal foraging at deep depths, where males are already so vigilant because of their blind exposure to predators when up-ending to forage that they do not increase vigilance after acquiring a mate (Guillemain et al. 2007b). In both cases, this could explain how male birds with high energy demands can afford the cost of maintaining a pair bond during such long periods in winter (see Rodway 2007b). Data are not available at present, but a comparison of forced copulation attempts on female Wigeon at Traeth Lafan and on the Exe Estuary (where male Wigeon are clearly vigilant for paternity assurance and/or pair-bond protection) could allow testing the above hypothesis more specifically. This study, therefore, suggests that whether male and female vigilance in a given species are more likely to be driven by the male constraint, male investment or female benefits hypothesis may depend very much upon the environmental safety conditions, and therefore is not a fixed species-specific life history trait. While they had long been considered as mutually exclusive activities, the traditional distinction between non-vigilant feeding bouts and non-feeding vigilance bouts in foragers was challenged a few years ago by Lima and Bednekoff (1999), showing that some individuals were able to maintain anti-predator vigilance while foraging with their head down. Similarly, the present study suggests that vigilance for several purposes may be combined by paired males in some situations.

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