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Males and females differentially adjust vigilance levels as group size increases: effect on optimal group size

Mark A. Whiteside [a, b, *], Ellis J. G. Langley [a], Joah R. Madden [a]

[a] *Centre for Research in Animal Behaviour, Psychology, University of Exeter, Exeter, U.K.*
[b] *Game and Wildlife Conservation Trust, Burgate Manor, Fordingbridge, U.K.*

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A strong motivation for one individual to aggregate with others is to reduce their vigilance because other group members provide coverage and warning of approaching predators. This collective vigilance means that a focal individual is usually less susceptible to predation than when alone. However, individuals differ in their vigilance levels depending on status and context. They may also differ in how they adjust their vigilance levels as group size changes. This flexibility in response means that the collective vigilance of a group, and hence its optimal size, is not intuitive. We demonstrate, in both natural and experimental systems, that male and female pheasants, *Phasianus colchicus*, in harems differentially adjusted their vigilance levels as harem size changed. Females became less vigilant as harems became larger, and benefited by increasing their foraging time. Conversely, males became more vigilant as harems became larger. We calculated the collective probability that a harem would detect a predator. Within natural harem sizes, a male and two females exhibited the highest probability of collective detection, with decreases as more females joined. This optimal harem size matched the average harem size observed at our study site. Females may join harems for benefits of collective vigilance. Despite both sexes having a shared interest in larger harems for mating benefits, optimal harem size is influenced by trade-offs in a nonsexual behaviour, vigilance. This results in males with relatively small harems, females associating with less preferred males and each male being surrounded by fewer females than he could mate with.

Vigilance provides individuals with early warning of potential threats, typically serving to reduce their chance of being predated (Elgar, 1989). However, vigilance is costly to an individual when it is exclusive to other activities such as foraging (Fortin, Boyce, Merrill, & Fryxell, 2004; Illius & Fitzgibbon, 1994). One way to ameliorate such costs is for individuals to aggregate and couple vigilance with alarm calling or other alerting mechanisms (Chivers & Smith, 1998; Hingee & Magrath, 2009; Pays, Beauchamp, Carter, & Goldizen, 2013) such that the group as a whole exhibits a level of collective vigilance when at least one individual is alert while others forage, rest or otherwise benefit. But what is the optimal group size for an individual based on its own vigilance levels?

Collective detection models are an efficient way to determine which group size provides the greatest benefit for an individual (Pulliam, 1973). These models can allow for the incorporation of complex variables such as delays in information transfer (Bednekoff & Lima, 1998), asynchrony (Pays, Jarman, Loisel, & Gerard, 2007; Pays, Renaud, et al., 2007) and spatial effects (Lima & Zollner, 1996). In most cases these models show that as group size increases, the proportion of time an individual spends being vigilant decreases (Elgar, 1989; Roberts, 1995; but see; Beauchamp, 2008). In collective detection models one of the key assumptions is that individuals are motivated to be vigilant to maximize safety in order to forage, rest or perform other important behaviours (Beauchamp, 1998) and these models seldom account for the possibility that individuals may differ in how they contribute to collective vigilance. However, body size, nutritional state (Bachman, 1993; Clutton-Brock et al., 1999) and reproductive state (Burger & Gochfeld, 1994) have caused individuals within groups to differ in their propensity to be vigilant. One model that does incorporate individual differences in vigilance is the security model (Dehn, 1990) based on observations of female pronghorn, *Antilocapra americana*, with and without the presence of dependent young (Lipetz & Bekoff, 1982). Aside from propensity to be vigilant, individuals may differ in how they adjust their vigilance depending on external factors such as their position within a group (Underwood, 1982) or the social composition of the group

* Correspondence: M. A. Whiteside, Centre for Research in Animal Behaviour, Psychology, University of Exeter, Exeter EX4 4QG, U.K.
E-mail address: M.Whiteside@exeter.ac.uk (M. A. Whiteside).

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(Cameron & du Toit, 2005). How individuals adjust their vigilance levels in response to different group sizes and what happens when individuals are dissimilar in their motivation is an area of research that has received little attention.

Harems, collections of females about a single male during the breeding season (Emlen & Oring, 1977), provide a case in which individuals, particularly the sexes, differ in their motivations to be vigilant. Clearly, both sexes benefit from increased vigilance offering early warning of predators, although because of crypsis, size, speed or armaments, one sex may be more likely to survive a predatory strike on the group than the other (Baker & Parker, 1979; Götmark, 1992; Slagsvold, Dale, & Kruszewicz, 1995). For males, vigilance offers benefits beyond simply reducing risk of predation. Males offering high levels of vigilance may be more attractive to choosy females (Dahlgren, 1990; Ridley & Hill, 1987). They may also be alert to the behaviour of sexual competitors and so reduce opportunities for their females to engage in extrapair copulations (Cameron & du Toit, 2005; Cowlishaw, 1997). Therefore, for a male, the value of being vigilant increases as harem size increases because the male's heightened vigilance protects the female with whom he has or will mate against both predators and harassment by other males. Predator threat and harassment from other males can disrupt all individuals directly or indirectly by interrupting foraging opportunities. Furthermore, vigilance by a male allows females in a harem to lower their own vigilance and hence increase nutrient intake prior to breeding, increasing their investment in his offspring. Conversely, the value of vigilance to a female is likely to decrease as harem size increases because she can rely on other harem members to provide collective coverage and so invest more time in foraging rather than being vigilant. For females there may be a greater incentive to forage over being vigilant: by preparing for an energetically costly breeding period they may derive disproportionate benefits from increased foraging opportunity (Artiss & Martin, 1995; Hannon & Martin, 1992; Portugal & Guillemain, 2011). With differing motivations to engage in vigilance mediated both by sex and by harem size, calculating the collective vigilance exhibited by a harem, and consequently understanding an optimal harem size, is not intuitive.

Pheasants, *Phasianus colchicus*, operate harem polygyny in a nonresource-based mating system (Ridley & Hill, 1987; Taber, 1949). The harems form at the end of winter and persist through spring during which time females must forage extensively to build energy reserves prior to breeding. Foraging typically occurs in open landscapes (Bertram, 1978) where pheasants face high levels of predation from terrestrial and aerial predators, including foxes, *Vulpes vulpes*, and goshawks, *Accipiter gentilis* (Brittas, Marcström, Kenward, & Karlbom, 1992; Kenward, Marcstrom, & Karlbom, 1981) with around 25% of birds being predated in their first year (Turner, 2004). Pheasants give vocal alarm calls (Heinz & Gysel, 1970) and thus can benefit from collective vigilance. It is suggested that females join harems to reduce their risk of being predated, and indeed there is speculation that females may select males because they provide high levels of vigilance (Ridley & Hill, 1987).

A male acquires mates through a complex process of territory acquisition through agonistic male–male interactions, followed by courtship displays to attract hens (Mateos & Carranza, 1997; Ridley, 1983). The acquired territory size and quality do not seem to affect female recruitment, with secondary sexual traits such as the wattle, spur length, body size and courtship behaviours (e.g. lateral struts) being better predictors of female choice (Göransson, von Schantz, Fröberg, Helgee, & Wittzell, 1990; Grahn, Göransson, & von Schantz, 1993; Ridley & Hill, 1987; von Schantz et al., 1989a; von Schantz et al., 1989b). Males offer no parental care (Taber, 1949), and females do not necessarily nest on the male's territory (Hill & Robertson, 1988), so males are not limited by provision of care or resources in their number of mates.

Therefore, on initial inspection, with no resource to protect or compete for, it appears that both sexes would benefit from increased harem size. Harems provide an opportunity for collective vigilance, such that all individuals could reduce their vigilance behaviour and so spend longer foraging or engaging in sexual display. Simple models of collective vigilance suggest that larger harems, where more females join a particular male, would result in both higher collective vigilance and lower individual contributions to vigilance for both sexes. Males further benefit directly by increasing their reproductive opportunities (Holm, 1973) and indirectly through mate choice copying such that large harems lead to ever greater recruitment of undecided females (Gibson, Bradbury, & Vehrencamp, 1991). Despite these apparent benefits to increasing harem size to both sexes, observed pheasant harems are not large. Most harem-holding males having two mates or fewer (Ridley & Hill, 1987), although on some sites, average harem size may be larger (e.g. 4.9 females; Robertson, 1986). One explanation is that if the sexes differ in the way they adjust their vigilance behaviour as group size changes, large harems do not provide the expected antipredator benefits. Indeed, it is possible that groups larger than the optimal size actually increase an individual's risk of predation, either because the group becomes more susceptible to detection (Cresswell & Quinn, 2011) or because the likelihood of collectively detecting a predator decreases.

We observed natural harems of pheasants prior to the start of the nesting period, and measured foraging and vigilance times in harems of different sizes. We expect that in larger harems, individual females could reduce their own vigilance levels, perhaps benefiting from collective vigilance by correspondingly increasing their foraging levels. Alternatively, additional females might not lead to more per capita foraging, perhaps due to interference or competition. With increased harem sizes a male may benefit from increased collective vigilance and hence be able to reduce his own vigilance for predators. If this occurs, male vigilance would decrease as harem size increases. Conversely, a male may pay a cost in terms of increased vigilance against competing males as his harem size increases and he invests more in mate guarding. If this occurs, then we expect that male vigilance would increase as harem size increases and there would be a corresponding cost in time spent foraging.

In wild populations, it is hard to discriminate whether females are joining harems of males that exhibit high levels of vigilance or whether males adjust vigilance levels according to harem size, and whether females operate fixed vigilance levels, choosing harems where they complement the vigilance efforts of others, or whether they too adjust their vigilance according to harem size. To explore this, we manipulated harem size in captive settings and observed whether males and females adjusted their vigilance levels or maintained fixed strategies. From observed vigilance levels in the wild we determined probabilities that a harem would detect a predator and from this calculated the harem size that produces the maximum likelihood of detecting a predator. We compared the sizes of harems observed in the population with the harem sizes predicted as providing the best probability of detecting a predator.

METHODS

Study Sites

This study comprised two parts. The first involved observing natural behaviour in the wild, conducted on the Middleton Estate, Hampshire, U.K. (51°18′N, 1°4′W), between 19 March and 11 April 2014. The estate hosts a game shoot and employs gamekeepers to