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In Focus

Featured Articles in This Month's *Animal Behaviour*

Harem Size: Safety over Sex

There are three key ingredients to reproductive success: food, sex and predation avoidance. The problem comes in allocating the right combination of time to each. This is particularly an issue when vigilance is used to decrease predation risk because, for many animals, looking out for predators means not foraging or having sex. An animal might solve this problem by joining a group, to share vigilance duties and so increase opportunities to spend time on other behaviours. There is a wealth of data on the individuals joining groups, the context in which they join groups, and the relative costs and benefits to joining a group. There is also a long history of work on estimating the group size for which it would be optimal for an animal to join, to stay or to leave.

One group of models that is especially concerned with the role that vigilance plays in determining optimal group sizes is that of collective detection. A typical outcome from such models is that as group size increases, the amount of time any individual in that group spends on vigilance decreases, time that individual can then allocate to other behaviours. Relatively little attention, however, has been directed to investigating how optimal group size might be affected if individuals vary in their contribution to the group's vigilance.

Mark Whiteside, Ellis Langley and Joah Madden (University of Exeter, U.K. and the Game and Wildlife Conservation Trust, U.K.) have taken harem size in pheasants, *Phasianus colchicus*, as a useful system in which to examine this question (pp. 11–18 in this issue; Fig. 1). Harem size in pheasants would seem, at least at first sight, to be the result of a shared interest: a male should gain more mates the larger his harem, and both he and his females should spend less time being vigilant, through collective vigilance, as the number of females in his harem increases. But pheasants in the wild would appear to disagree: most males manage harems of no more than two females. Indeed, one might argue that actually most male pheasants are not harem holders at all.

To determine whether an explanation could be found in the adjustments individuals made in their levels of vigilance, Whiteside and coauthors observed both the time spent by individuals foraging and the time spent being vigilant, for harems of varying size in the wild, and they also manipulated harem sizes of captive pheasants. To this they added data from the wild birds to determine the relationship between harem size and the probability that that harem would detect a predator.

They observed 81 male and 43 female pheasants living wild on an estate in the U.K., just before the breeding season began in earnest. The captive manipulations involved 10 males assigned to a harem of either two or four females. After 7 days of one harem size, males were assigned to the other harem size.

In line with predictions of collective detection models, Whiteside et al. found that the larger the harem, the less time both wild and captive females spent being vigilant and the more time they spent foraging. However, the reverse was true for wild males: the larger their harem, the more time males spent being vigilant and the less time they spent foraging. This latter effect was a little less marked for captive males, as although these males increased their vigilance when they had four females rather than two in their harem, they seemed to do so without a marked effect on the time they could spend foraging. Females, then, appear to gain from being in a larger harem whereas the males may be balancing the costs of decreased foraging with the benefits of increased vigilance (for predators, or perhaps for other males).

Modelling the probability of detecting a predator (based on the data from wild birds), however, showed that detection peaks in harems containing 2.7 females. A female joining a harem already containing two females actually decreases the probability that the group detects a predator. It appears that this may be due to females increasingly lowering their own levels of vigilance as more females join their harem. The male, however, needs to increase his levels to compensate.

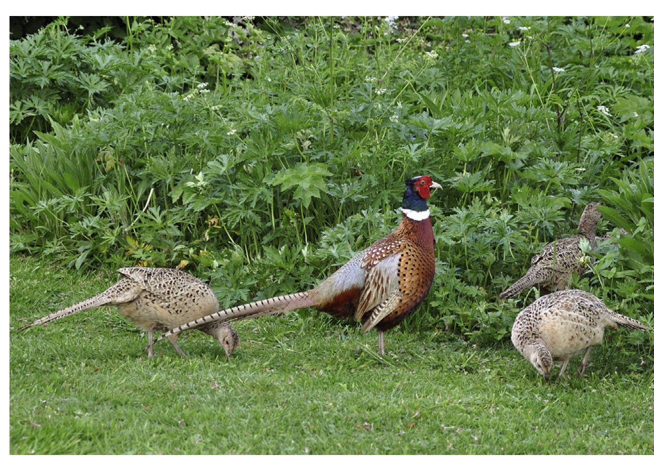

Figure 1. A vigilant male pheasant and his foraging females. Photo: Peter Thompson.

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Those male pheasants on this estate that held a harem had an average of two females in the harem (comparable to those of other pheasant populations). As this number is lower than would be advantageous to the females, but is beneficial to the males, one might speculate that the male is controlling the number of females in his harem, perhaps because of the cost entailed in shouldering an increasing burden of vigilance (looking out for other males as well as predators).

Although better quality males may be more able to afford the costs of a slightly larger harem, seemingly few manage to sustain a harem much larger than two. Pheasant harems make us think again about the relative costs and benefits to the individuals in a harem. Certainly in pheasants, harem size does not seem to be all about the sexual attractiveness of the harem holder but may have a lot more to do with the male sustaining the cost of watching out for predators.

Susan D. Healy
Executive Editor

Why Day-active Male Birds Croon at Night

In the north-temperate zone, nights tend to be quieter than days, or at least birdsong is less prominent and diverse than in the day. This is because most birds are active during the day (diurnal), although there are notable exceptions such as nightingales, *Luscinia megarhynchos*, corncrakes, *Crex crex*, and woodcocks (*Scolopax* spp.), which are active during the night (nocturnal) or most active at dawn or dusk (crepuscular). Nocturnal song has been studied in most detail in birds that are primarily night-active, and the available evidence suggests that, as in diurnal species, nocturnal song serves to attract mates and to repel competing males. However, one-fourth of passerine species that are primarily day-active also sing infrequently during the night. The function of nocturnal song in such species is poorly understood, although it occurs regularly in some species.

A paper in this issue (pp. 105–114) presents data that address the function of infrequent nocturnal song in the field sparrow, *Spizella pusilla*, a passerine that sings primarily during the day, and is typically inactive and sleeping at night (Fig. 2). This sparrow sings both simple and complex songs. Complex songs are performed most often at dawn and are thought to function in male–male interactions and to advertise territorial boundaries. In contrast, simple songs are sung throughout the day and appear to have the dual function of repelling males and attracting females. During the night, males infrequently sing both types of song, with simple songs being sung early in the season and complex songs more often when nest construction and laying occur. This difference suggests that the two kinds of song may have different functions, a possibility examined in this paper. As members of mated pairs (social mates) engage in extrapair matings, the songs could potentially serve either to inhibit territorial intrusions by males and/or to attract receptive, nearby females.

The authors, Antonio Celis-Murillo, Thomas J. Benson (both of the University of Illinois, Urbana-Champaign, IL, U.S.A.), J. Roberto Sosa-López (CONACYT-Instituto Politécnico Nacional, Oaxaca, México) and Michael P. Ward (University of Illinois, Urbana-Champaign, IL, U.S.A.) used a combination of descriptive and experimental approaches to evaluate the function of nocturnal song in the field sparrow. They used acoustic recording units (ARUs) in combination with an automated sound detection and classification system to ask whether female fertility stage, presence of a neighbour's song or presence of an intruder's song were reliable predictors of simple or complex nocturnal songs, observations that could offer insight into song function. Additionally, the authors used an automated radiotelemetry system (ARTS) in combination with ARUs and an automated song playback system to conduct experimental assessment of the responses of male and female field sparrows to nocturnal single songs during the period before females were fertile and during the peak fertility and postfertile stages. They reasoned that if song functions to repel intruders, males should respond to songs with countersinging and movement, whereas if the function is to locate mates for extrapair copulations, females should instead respond with movement and should do so most often during their fertile period.

Figure 2. Adult field sparrow, *Spizella pusilla*. Photo: Jen Mui.

This careful combination of observations and experiments demonstrated that males, including the focal, paired male, intruders and neighbours sang complex songs most often when females were fertile (building nests and laying eggs), strongly suggesting a reproductive function, but not discriminating between defence from intruders and attraction of mates for extrapair copulations. Neighbours and intruders also sang more when the focal male was singing, but these findings applied only to complex song. Performance of simple songs was not associated with any variables that were measured.

The playback experiments demonstrated that both males and females moved more in response to both short and long complex songs than to control songs (those of two other species). However, they also demonstrated that males did not perform countersinging in response to songs by simulated intruders at night, suggesting that the function of the song was not to repel intruders. The experiment further demonstrated that focal males were most responsive to playback of complex song during the fertile stages of their mates, but they showed similar singing behaviour during the pre- and postfertile stages of their mates, suggesting that the nocturnal singing behaviour of males was strongly driven by the fertility stage of their social mates. Females also responded to simulated complex songs at night, moving actively, and they did so most strongly during the prefertile and fertile stages, suggesting that these songs function primarily in the location of extrapair males by females and in the acquisition of extrapair matings.

Overall, these intriguing insights suggest that the purpose of nocturnal song in field sparrows and in other species that rarely sing at night may, like soft song in other species, be to coordinate nocturnal movements facilitating extrapair matings at night when intruders are less easily detected than is the case during the day. It will be fascinating to learn whether this is a typical function of rare nocturnal singing in other species of passerines.

Susan A. Foster
Executive Editor