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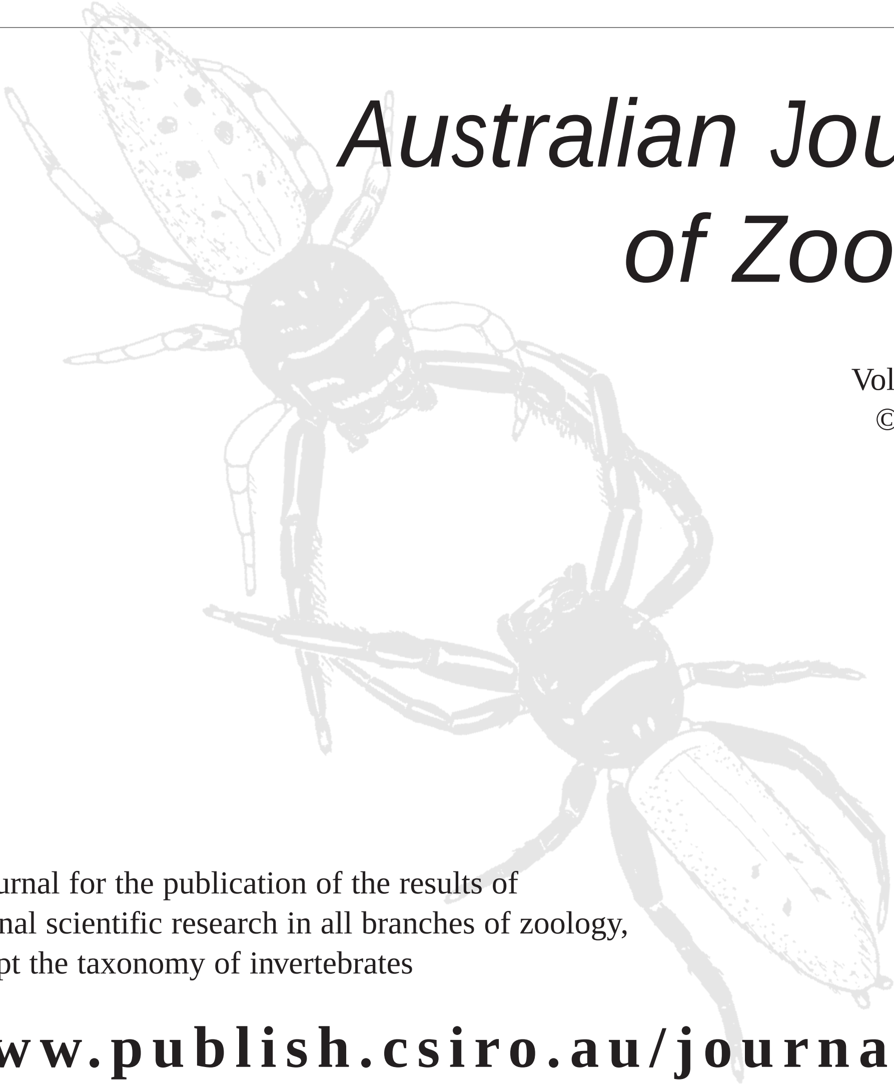

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The influence of visual obstructions on the vigilance and escape behaviour of house sparrows, *Passer domesticus*

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Abstract

The scanning and flight behaviour of birds that forage in flocks may be influenced by several variables, including the size of the flock and the presence of visual obstructions. Visual obstructions can conceal both potential predators and flock mates from a foraging bird, and individuals may increase their scanning rate accordingly, although concealing flock mates may result in more variable scanning rates as they come in and out of vision. We examined these ideas experimentally by observing house sparrows foraging at a feeder with and without visual obstructions. Birds foraging in the presence of visual obstructions had generally higher and more variable scanning rates. When the birds were approached by a human observer, they took flight earlier in larger flocks, although their reaction was generally delayed when there were obstructions. These data indicate that visual obstructions increase the probability of predation because individuals are less likely to detect a predator and/or the alarm flight of other individuals.

Introduction

Many animals that forage on the ground periodically raise their heads and visually scan the environment, presumably for conspecifics, predators and other threats (Lima 1990). For a wide range of species, the proportion of time that individuals spend scanning declines as group size increases (see Elgar 1989). The nature of this relationship may be affected by several factors (Elgar 1989), including the distance from cover (Lazarus and Symonds 1992; Pöysä 1994), the geometry of the foraging group (Bekoff 1995; Sadedin and Elgar 1998), and the presence of predators (see Elgar 1989) and visual obstructions (Elgar *et al.* 1984; Metcalfe 1984; Lima 1987; Lima and Zollner 1996).

Visual obstructions may influence the vigilance behaviour of animals in several ways. First, the obstructions may effectively conceal the predator, allowing it to initiate its final exposed attack closer to the victim (e.g. Metcalfe 1984). If a predator is closer when it is first detected, then selection favours more frequent vigilance to compensate for the greater risk. Second, visual obstructions may interfere with an individual's ability to monitor the behaviour of other group members, including their foraging success or alarm flights (Lima and Zollner 1996). Thus, an individual may adjust its scanning rate according to the number of visible birds, rather than to the actual flock size (Elgar *et al.* 1984). In this case, the scanning rate will not only be generally higher across different group sizes, but will also be more variable for each group size as individuals come in and out of vision.

Previous attempts to evaluate these ideas experimentally have simulated visual obstructions with a single barrier placed across a feeder (Elgar *et al.* 1984; Lima 1987; Lima and Zollner 1996). While this approach has clarified the importance of collective detection (Lima and Zollner 1996), it has several limitations because the barrier is a continuous visual obstruction that permanently 'splits' the flock. This not only prevents individuals from observing other 'flock mates', but may also be perceived as a structure that entirely conceals predators. Thus,

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individuals foraging near a barrier may increase their vigilance in order to compensate for this higher risk (Lazarus and Symonds 1992). A more common experience for individuals foraging in groups are those obstructions, such as plants and rocky outcrops, that briefly obstruct their view of other flock mates and the final approach of a potential predator.

Here, we investigate experimentally the influence of visual obstructions on the scanning and predator-avoidance behaviour of foraging house sparrows, *Passer domesticus*. In particular, we examine the nature of the relationship between scanning rate and flock size for birds foraging at a feeder with and without small obstructions that would impede visual detection of flock mates but not predators. This experimental design ensures that different individuals come into and out of view unpredictably, rather than being permanently obscured by a single wall. We also investigate the response by sparrows to a potential threat while foraging in each of the two experimental treatments.

Methods

House sparrows were observed in the Systems Garden, University of Melbourne (Parkville, Melbourne), during March and April 1998. A foraging plot of 1 m^2 was delimited over a grassy area, using pegs, and house sparrows were attracted to this feeder by placing large quantities of commercial 'budgie mix' within the plot for several days prior to data collection. Four handfuls of this seed were then evenly distributed within the plot every day throughout the period of the study. The plot was located in roughly the same place in the Systems Garden.

The influence of visual obstructions on the behaviour of the sparrows was assessed by placing eight upturned black planting pots (10 cm high and 10.5 cm diameter) in and around the feeder. Four planting pots were placed outside the feeder, approximately 10 cm from each corner; and four planting pots were placed approximately 10 cm inside the border of the feeder, midway along each length. The pots were placed on black discs of the same diameter. We compared the behaviour of sparrows foraging in the feeder among the pots on discs (experimental) with sparrows that were foraging in the feeder without pots but with discs (control). The choice of treatment varied randomly from day to day.

We observed the sparrows approximately 10 m from the feeder during the early morning and late afternoon. We did not record observations of mixed-species flocks (e.g. when in the presence of spotted turtle doves, *Streptopelia chinensis*). Once a flock of birds alighted in the feeder, a haphazardly selected individual was chosen, and the number of scans was recorded for around 60 s, or until the bird took flight (median = 60 s). A single scan was denoted when an individual lifted its head from feeding for more than 2 s. These data were used to derive scanning rates for birds foraging in flocks of known size. The reaction of sparrows to a potential threat was examined by recording the distance at which more than 50% of the flock took flight when an observer walked slowly toward the feeder. These disturbance trials took place at different times throughout the study period in order to control for temperature or daylight effects, and the choice of treatment (with and without pots) was randomised. The observer rarely wore the same combination of clothes.

Our analysis may include some repeated measures of the same individual. However, the sparrows observed in this study were drawn from a very large urban population comprising many hundreds of individuals. The size and membership of sparrow flocks in these populations typically changes frequently and rapidly (e.g. Elgar 1985). Thus, the frequency of repeated measures is negligible and unlikely to have systematically biased the data. In the unlikely event that our data were derived from only a few individuals, any observed patterns would demonstrate that individual sparrows adjust their behaviour according to their physical and social environment.

Results and Discussion

The scanning behaviour of house sparrows foraging at the feeder was influenced by the presence of obstructions and flock size (Fig. 1). Analysis of covariance revealed that the variation in scanning rates was significantly explained by flock size ($F_{1,81}$ = 64.5, P < 0.001) and the presence of obstructions ($F_{1,81}$ = 31.9, P < 0.001). The interaction term was not significant ($F_{1,80}$ = 0.91, P > 0.34). A comparison of the intercept of the two regression curves (no obstructions: $y = 14.71 - 1.71x$, n = 42, r^2 = 0.67; with obstructions: $y = 17.55 - 1.34x$, n = 2, r^2 = 0.29) indicated that sparrows foraging with obstructions increased their vigilance rate by almost three scans per min.

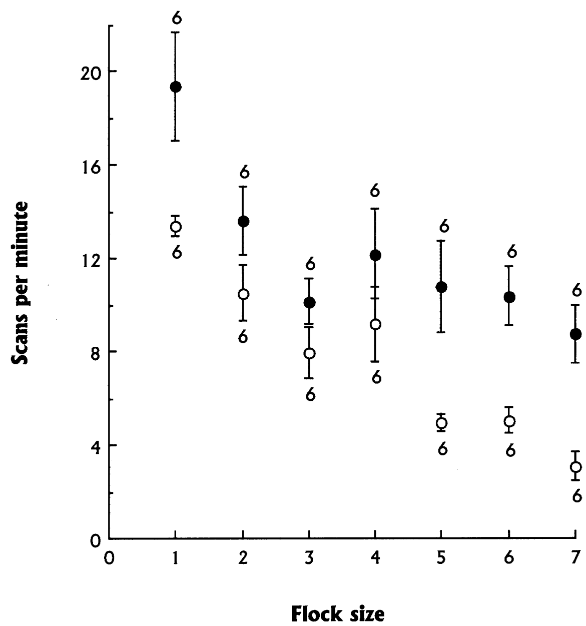

Fig. 1. The relationship between flock size and scanning behaviour of sparrows foraging in the feeder with (●) or without (○) visual obstructions. Values are means ± s.e., with sample sizes given above or below

The presence of obstructions also influenced the amount of variation in scanning rates that was explained by flock size: 67% of the variation in scanning rate was explained by flock size when there were no obstructions in the feeder, compared with 29% when there were visual obstructions. While it is not possible to attribute directly this two-fold difference to the presence of obstructions, there is a significant difference between the two treatments in the variance of the residuals from the regression curve of vigilance on flock size ($F_{40,40} = 3.00$, $P < 0.01$). In other words, there was much more scatter around the regression curve when the sparrows foraged in the presence of obstructions.

The negative correlation between scanning rates and flock size is consistent with previous studies of numerous species of mammals and birds (Elgar 1989; Quenette 1990; Roberts 1996). The consistently higher scanning rates of sparrows that are foraging among obstructions is also concordant with previous observational (Metcalfe 1984) and experimental (Elgar *et al.* 1984; Bekoff 1995; Lima and Zollner 1996) studies. The primary difference is in the experimental design: the previous studies used a single 'wall' obstruction that split the flock and effectively reduced the flock size. The experimental arrangement of the present study more closely matches the rocky environment of the shorebirds observed by Metcalf (1984). Additionally, the scans measured in this study were considerably longer than those measured by Elgar *et al.* (1984), since the data analysed in the latter study included scans of less than 2-s duration.

There are at least two explanations for the generally higher rates of scanning by sparrows foraging among visual obstructions. These explanations are not mutually exclusive. First, the sparrows may have perceived a higher risk of predation, as a result of their impaired ability to scan the environment thoroughly, and increase their scanning rates accordingly (see Lima 1987). The non-significant interaction term indicates that this risk of predation was constant across all flock sizes. While we cannot discount this explanation, it is not convincing because the dimensions of the pots ensure that there is no reduction in visibility of avian predators, and little obstruction of terrestrial predators like cats that are much taller than the pots. According to our rough calculations, the pots inside the feeder would conceal a stationary, 30-cm-high predator located further than 2.25 m from a sparrow located at the centre of the feeder. However, the sparrow would not have to move very far around the feeder to detect any predator exceeding 50 cm in length. The pots outside the feeder would conceal these predators at distances exceeding 15 m.

Second, the sparrows may scan more frequently when foraging among visual obstructions because other flock mates are not always visible. These individuals will tend to inaccurately gauge, usually by underestimating, the size of the flock. Consequently, scanning rates will be generally higher because the birds perceive a smaller flock. Additionally, the perceived flock size for birds among obstructions will vary from time to time, resulting in more variable scanning rates for particular flock sizes. The two-fold difference in the variation in scanning rates explained by flock size in the treatment with and without visual obstructions is consistent with this explanation, but is not expected if the birds were simply reacting to an increased risk of predation.

It is possible that the pots will interfere with the attack behaviour of the predator. For example, the pots might make it more difficult to keep the prey in view, interfer with the line of attack, or generally confuse the predator. While we have no data on these possible effects, the increased vigilance behaviour of sparrows in the presence of pots suggests that the pots increase, rather than decrease, the possibility of a successful attack by the predator.

The time when the sparrows take flight in the face of an approaching potential threat is expected to depend on when they are first aware of the threat, the speed of approach and the degree of safety provided by the immediately surrounding habitat. In our experiments, the speed of approach was kept constant, and there was no indication that the barriers provided any safety; alarmed sparrows never alighted on the pots and typically flew into the surrounding shrubs and trees. Therefore, it seems reasonable to assume that the relative distance at which the sparrows took flight reflects the relative time of detection.

The speed of reaction by a flock of foraging house sparrows to a potential threat was also influenced by flock size and the presence of obstructions (Fig. 2). Analysis of covariance revealed that the variation in reaction time was significantly explained by the flock size ($F_{1,85}$ = 70.3, $P < 0.001$) and the presence of obstructions ($F_{1,85} = 31.2$, $P < 0.001$), but not their interaction ($F_{1,84} = 0.001$, $P > 0.96$). A comparison of the intercept of the two regression curves (no obstructions: $y = 3.87 + 0.49x$, $r^2 = 0.41$; with obstructions: $y = 2.50 + 0.49x$, $r^2 = 0.49$) indicates that the sparrows reacted later if there were obstructions, and the threat could be closer to the flock by 1.4 m.

These data reveal that sparrows confronted with a threat take flight earlier when in larger flocks (see Elgar 1989). This arises because the threat is detected earlier, rather than because

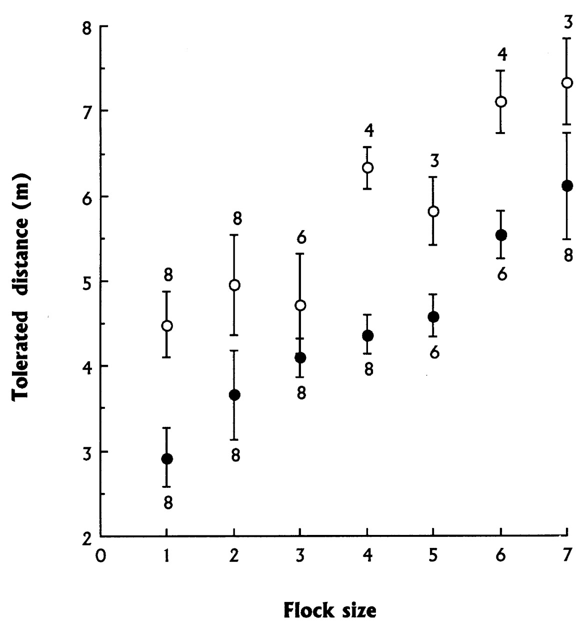

Fig. 2. The relationship between flock size and the minimum 'tolerated' distance between the feeder and an approaching human when most of the flock alighted, for sparrows foraging with (●) or without (○) visual obstructions. Values are means ± s.e., with sample sizes given above or below.

individuals in a group are somehow more vulnerable and hence take evasive action more quickly. The threat is detected earlier as a result of the effects of corporate vigilance; the probability that any individual detects a predator and takes flight can increase with group size, even though each individual may be less vigilant (Pulliam 1973; Lima 1995).

The presence of visual obstructions may increase the time it takes birds to react to a threat in two ways. First, the visual obstructions may prevent the birds from seeing the predator, and thus react later. Second, the obstructions may decrease the probability that an individual detects an alarm flight. Elgar *et al.* (1986) showed that sparrows that did not detect the alarm flights of flock mates were the last to take flight. Interestingly, the increase in vigilance rates of birds foraging among obstructions did not fully compensate for the lower probabilities of detecting a threat or the behaviour of other individuals.

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