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ORIGINAL ARTICLE

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Does vigilance always covary negatively with group size? Effects of foraging strategy

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Abstract The possible effects of foraging strategy on the relationship between vigilance and group size were studied in three species of waders with different foraging strategies. I predict that (1) pause–travel species should show no relationship between scanning and group size, because these species scan for prey as well as for predators; (2) continuous-tactile foraging species should show a positive relationship between flock size and vigilance level, because in their large groups vigilance towards other birds could be used to avoid interference and aggression; and (3) continuous-visual searching species should show the general pattern of decreasing vigilance when group size increases as predicted by both the ‘many eyes’ and the ‘predatory risk’ hypotheses. Results support the predictions for the influence of foraging strategy on the relationship between vigilance level and group size. The mutual exclusion of foraging and scanning can determine the importance of the ‘many eyes’ hypothesis. Such exclusion seems to be determined by foraging strategy. The influence of foraging on scanning must be taken into account in future studies on the group-size effect.

Keywords Flocking · Foraging strategy · Group size · Vigilance · Waders

Introduction

Most studies on the relationship between vigilance and group size have shown a decrease in individual vigilance when group size increases (for reviews on this topic see Barnard and Thompson 1985; Elgar 1989; Lima 1990; Lima and Dill 1990; Quenette 1990). Two hypotheses have been put forward to explain this negative relationship: the ‘many eyes hypothesis’ (Pulliam 1973; Lima 1990) states that as group size increases there are more eyes scanning for predators; hence an individual may reduce the time devoted to scanning without decreasing the group’s collective vigilance. The ‘predation risk hypothesis’ (Roberts 1996) holds that vigilance would be reduced with increasing group size because the individual risk of predation declines with increasing group size. The two hypotheses are not mutually exclusive (Roberts 1996) and the group-size effect remains unclear (Roberts 1996). However, one study has shown a positive correlation between vigilance and group size (McKinstry and Knight 1993) whilst some studies have shown no such relationship at all (Pöysä 1987; Keys and Dugatkin 1990; Caterall et al. 1992; Slotow and Rothstein 1995). Positive relationships have been explained by spatial constraints, which increase agonistic interactions and cause individuals to increase their vigilance of conspecifics (McKinstry and Knight 1993). The lack of a significant relationship has been explained by the confounding effects of other variables such as food density and quality, distance to cover, proximity of the observer, age, and sex (Elgar 1989). Another possible factor affecting the relationship between group size and vigilance is foraging strategy. Its effect on vigilance and flocking has been shown independently for each (Goss-Custard 1980; Pöysä 1987; Barbosa 1995, 1997a), but its effect on the covariation of both variables remains to be assessed.

Waders are a good group of birds with which to study such an effect because of the variety of foraging strategies they show (Barbosa and Moreno 1999). Foraging strategies in waders include

1. Pause–travel. Species using this strategy mainly forage by scanning the area ahead and pecking at the substrate surface in a stop-run-stop fashion when prey is detected (Metcalfe 1985).
2. Continuous-tactile searching. Species using this approach forage as they walk, probing continuously with the bill into the substrate (Gerritsen and Sevenster 1985).

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3. Continuous-visual searching. Species using this strategy forage in a continuous fashion pecking at items detected by sight.

These three strategies have been shown to influence scanning and flocking behaviour. Species with visual strategies, both pause–travel and continuous, tend to form smaller flocks than tactile-search species mainly because of mutual interference and disturbance (Barbosa 1995). On the other hand, pause–travel species scan less frequently than continuous-searching species, as they use the information obtained when searching for prey also for predator detection (Barbosa 1995).

I recorded scanning behaviour in three species of waders showing different foraging methods to test the hypothesis that the different foraging strategies will influence the relation between vigilance and group size in different ways. I predicted that (1) pause–travel species should show no relationship between scanning and group size since, although these species engage in antipredatory scanning behaviour, they can use the information gathered during scanning for prey also for predator avoidance; (2) continuous-tactile species should show a positive relationship between flock size and vigilance level, because in these species group size can be high, promoting vigilance towards other birds to avoid interference and aggression; and (3) continuous-visual species should show the general pattern of decreasing vigilance when group size increases as predicted both by the 'many eyes' and the 'predatory risk' hypotheses.

Methods

The study was conducted at Ebro Delta Natural Park (NE Spain, 40°43′N, 00°44′E), one of the most important areas for waders in the Mediterranean (Barbosa 1997b). The area consists of 32,000 ha in total, of which 15,000 are rice fields, 9,500 market garden, and 7,500 natural wetlands (beaches, salt-marshes, lagoons). The area potentially suitable for waders is 16,000 ha (Martinez-Vilalta 1985). There are five raptor species present in this area: marsh harrier (*Circus aeruginosus*, 3.21 individuals km^{-2}); hen harrier (*C. cyaneus*, 0.28); buzzard (*Buteo buteo*, 1.21); kestrel (*Falco tinnunculus*, 1.10), and merlin (*F. columbarius*, 0.07) (Tombal and Tombal 1988).

I recorded scanning and flocking behaviour of three species showing the main foraging strategies of waders (Table 1): pause–travel strategy, lapwing (*Vanellus vanellus*); continuous-visual strategy, black-winged stilt, (*Himantopus himantopus*); and continuous-tactile strategy, dunlin (*Calidris alpina*) (Barbosa and Moreno 1999). Observations were made between November and April in 1990–1991 and 1991–1992. Scanning and flocking behaviour were recorded using the focal observation method (Altmann 1974). Focal birds were arbitrarily chosen during regular surveys of the study area and their behaviour was tape-recorded for 2 min on average. All observations were made during daylight with 8×30 binoculars or a 40×60 spotting scope. To minimise pseudoreplication (Hurlbert 1984) small numbers of birds from different areas in the flock were sampled (see Barbosa 1995, 1996a, 1997a, c; Barbosa and Moreno 1999). Each bird sampled was at least 20 m from the previous bird sampled. Both the size of the study area (16,000 ha) and the population size of these species (18,000 individuals) made it highly unlikely that the same individual was sampled twice. Vigilance rate (number of scans per minute foraging) was recorded as a variable characterising scanning behaviour. A scan was defined as a single event of raising the head from the head-down foraging position to a position of bill line above the horizontal. This posture is generally considered to be related to antipredatory behaviour (see Lima and Dill 1990 and references therein). In pause–travel species, scanning for prey could be confused with scanning for predators. However, the following criteria make it easy to distinguish between the two types of behaviour. When the bird is scanning for prey it looks to the front and the bill is horizontal, but when it is scanning for predators, the bird looks upwards and the bill is clearly above the horizontal (see Fig. 1 in Barbosa 1995).

Table 1 Sample size of 2-min focal observations of single individuals (*n*), mean, and standard error (*SE*) of scan rates and flock sizes in the three species studied

	Scan rate (scan/min)			Flock size		
	n	Mean	SE	*n*	Mean	SE
Lapwing (pause–travel)	38	0.37	0.16	38	34.02	11.30
Black-winged stilt (continuous visual)	24	1.86	0.31	24	13.29	2.78
Dunlin (continuous tactile)	108	1.23	0.15	108	185.18	16.46

A flock is considered as all birds (con- and heterospecific) within 10 m of the nearest neighbour. Flock sizes ranged from 1 to 600 individuals. Flock size and flock density are strongly associated in waders as there are space constraints imposed by their foraging habitats in winter (Goss-Custard 1980) that prevent flock dispersal as more birds join. In Mediterranean estuaries larger flocks are denser than smaller ones (A.B., personal observation) and intake rates decrease with increasing flock size (Barbosa 1996b). Therefore, flock size is correlated with flock density, at least in this study area.

The three species used the three main habitats in the study area (rice fields, lagoons, and littoral areas) in different ways. Lapwings exclusively used rice fields; black-winged stilts mainly used lagoons but also rice fields and littoral areas; dunlins used littoral areas and rice fields (Barbosa 1994, 1996b). There were no differences in flock size or scanning behaviour between habitats in black-winged stilt (flock size $F_{2,21}$=1.25, P=0.30; scan rate $F_{1,21}$=1.36, P=0.27); therefore data from the different habitats were pooled for this species. However, as dunlin showed differences in flocking and scanning behaviour between habitats (Barbosa 1997c), data for this species were analysed separately for each habitat. Foraging strategy, not habitat, accounted for most of the differences in scanning and flocking behaviour among species (scanning, foraging strategy: $F_{2,173}$=11.97, P=0.000014, habitat: $F_{2,173}$=2.13, P=0.12; flocking, foraging strategy: $F_{2,173}$=40.14, P=0.00001, habitat: $F_{2,173}$=0.77, P=0.46). Rice fields did not show high vegetation, potentially affecting scanning during the sampling period. Moreover, the complexity was similar between habitats in the study area (Barbosa 1994, 1997c).

Relationship between scanning behaviour and flock size was also studied by categorising flock size into three groups, small (1–20 individuals), medium (21–100), and large (>100). Scanning rates and flock sizes were log transformed to achieve normal distribution of data. Statistical analysis included least-squares regression analysis and ANOVA. Probabilities smaller than 5% are termed significant.

Results

Differences among the three species in their relationship between scanning behaviour and flock size were found. The pause–travel species, lapwing, did not show any significant relationship between scanning behaviour and flock size (r=0.03, P=0.83, n=38). The continuous-visual species, the black-winged stilt, showed a significant neg-

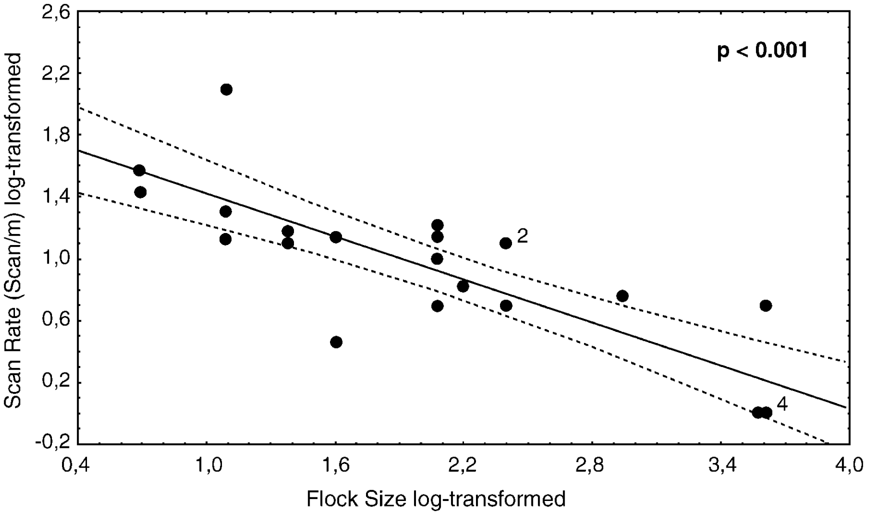

Fig. 1 Least squares regression between scan rate and group size in black-winged stilt (*Himantopus himantopus*). *Dotted lines* indicate 95% confidence limits. Points with more than one observation are *numbered*. Scatterplots of lapwing and dunlin were omitted because results were not significant

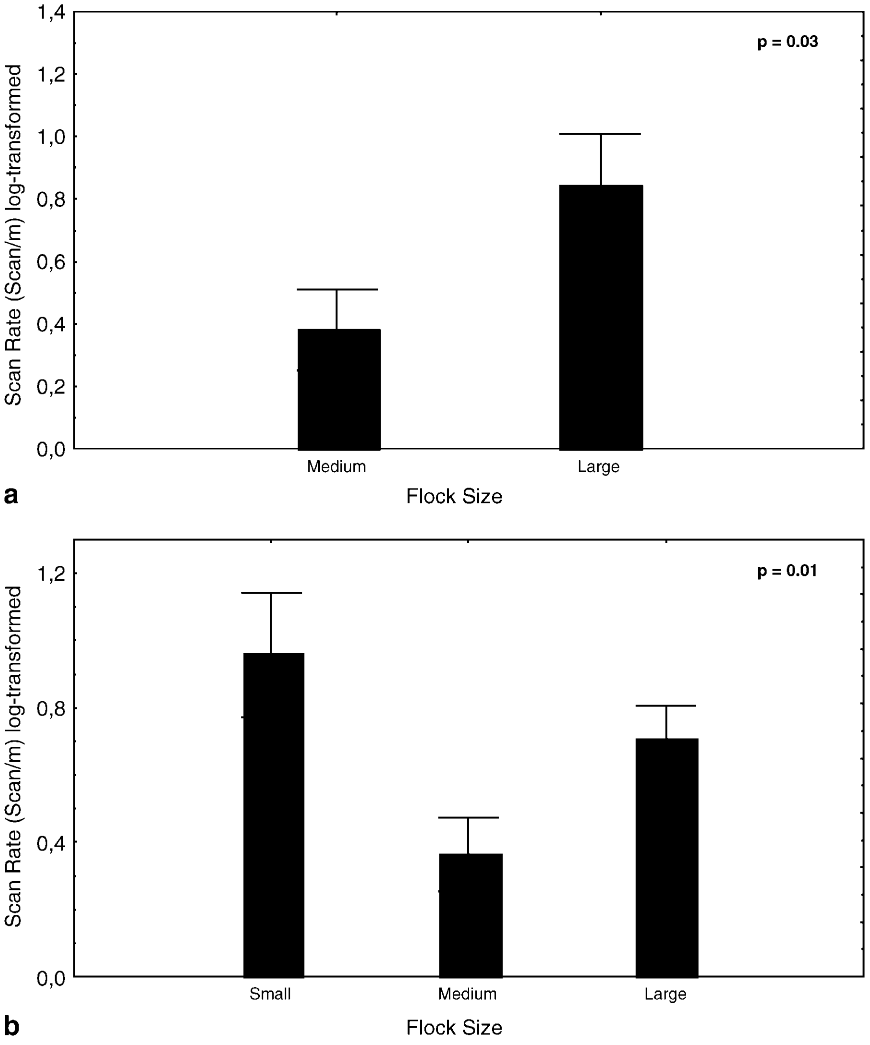

Fig. 2 **a** Differences in scan rates between medium and large flocks in dunlin foraging in rice fields (small-flock category not shown as they were not present in this habitat). Values are means±standard error. **b** Differences in scan rate between small, medium, and large flocks in dunlin in littoral habitats. Values are means±standard error

ative relationship between scan rate and flock size (r=–0.83, P<0.001, n=23; Fig. 1). The continuous-tactile species, dunlin, showed a positive and significant relationship between scan rate and flock size in rice fields (r=0.53, P=0.006, n=24) but not in littoral habitats (r=0.01, P=0.88, n=84). When analysed by flock-size categories in the species where no relationships had been found, scan rates did not differ among flock-size categories in lapwing ($F_{2,35}$=0.15, P=0.85). However, dunlin showed different scan rates among flock-size categories in both rice field ($F_{1,24}$=4.92, P=0.03; Fig. 2a) and littoral habitats ($F_{2,82}$=4.51, P=0.01; Fig. 2b).

Discussion

The results show that a decrease in vigilance level with increasing flock size is not a general rule and that foraging strategy affects the relationship between these two variables. Only the continuous-visual species, black-winged stilt, fits the expected general pattern found by most authors (see Roberts 1996 and Beauchamp 1998 for reviews). The visual pecking strategy is considered as the most primitive foraging strategy in birds (Zweers 1991; Zweers et al. 1994, 1997) and is certainly the most common. Beauchamp (1998) reviewed the relationship between flock size and vigilance level in 46 studies. He found that 40 studies (86.9%) showed a negative relationship between the variables. Of these 40 studies, most (32; 80%) dealt with birds using a visual foraging strategy and in the few cases (4; 10%) that birds used tactile strategies, flock sizes were very small, ranging between 1 and 28 individuals. The remaining 10% used specialised behaviour to forage.

My results show that in the pause–travel species there was no such significant relationship, showing that vigilance to detect predators was independent of flock size. This is probably because this species can also use the information obtained when scan searching for prey as antipredatory vigilance (Barbosa 1995). Therefore, as this species must scan to forage, an increase in flock size does not decrease individual scanning behaviour and the amount of information obtained to detect predators does not vary with flock size.

Increasing flock size could also increase interference and aggression between individuals (Goss-Custard 1980). The pause–travel strategy depends on a large search area and species using this strategy seemingly avoid forming very large flocks (Pienkowski 1983; Barbosa 1995), which can reduce the aggression level, thereby also reducing the need to scan for other flock mates. This precludes the possibility of a positive relationship between scanning and flock size. Nevertheless, this scenario is the most plausible explanation for the positive relationships found in the tactile-foraging species. Dunlin showed high vigilance levels in large flocks in both rice fields and littoral habitats. In small flocks (less than 20 individuals), however, vigilance levels seemed to be reduced, which agrees with the pattern found in Beauchamp (1998).

The functional mechanism explaining the group size effect remains unclear (Roberts 1996). The ‘many eyes’ hypothesis (Pulliam 1973; Lima 1990) and the ‘predation risk’ hypothesis (Roberts 1996) have been proposed to explain such an effect. A comparison of the pattern found in lapwing and black-winged stilt may be used to test these two hypotheses. The ‘predation risk’ hypothesis (Roberts 1996) predicts that vigilance should be reduced with increasing group size, if risk diminishes accordingly. Lapwing and black-winged stilt did not differ in mean flock size (t=1.41, P=0.16, n=62). Therefore the flock-size-dependent risk could be assumed to be the same and does not explain the differences in these species. The ‘many eyes’ hypothesis (Pulliam 1973; Lima 1990), however, predicts a reduction in vigilance level when flock size increases because there should be more eyes scanning for predators and therefore, individuals can reduce their vigilance time without decreasing the collective vigilance (Pulliam 1973; Lima 1990). In lapwing, scanning for predators and searching for prey are not mutually exclusive activities, due to their pause–travel foraging strategy. In this species collective vigilance is almost always assured due to the information obtained during the search for prey. Therefore, there is no reason to change vigilance levels in response to flock size. However, in black-winged stilt, as in most species of birds, vigilance and searching for prey are mutually exclusive activities that do not assure a minimum of collective vigilance. Therefore vigilance and flock size should be negatively related. This implies that the mutual exclusion of foraging and scanning can be used to test the effect of the ‘many eyes’ hypothesis and such exclusion seems to be determined by the foraging strategy used.

Foraging and scanning can be inversely related, although a decrease in scanning time appears sufficient but not always necessary to influence intake rate (Beauchamp 1998). The correlation between scanning and flock size could be causally related to food availability. However, the present results are probably not biased in that direction. Species that used several habitats showed their highest intake rates in their most preferred habitats: lagoons and littoral areas in the case of the black-winged stilt and littoral areas in the case of the dunlin (A.B., unpublished data). However, the results show no differences in scanning behaviour or flocking behaviour for black-winged stilt between habitats with higher and lower intake rates; hence, in this species, intake rates did not influence scanning behaviour. Dunlin showed higher vigilance levels in rice fields, the less preferred habitat (Barbosa 1997c). However, Fig. 2 shows that the relationship of flock size and scanning behaviour follows the same direction in both habitats, and therefore, the function between flock size and scanning did not differ between habitats.

The lack of a significant relationship between scan rate and flock size in the pause–travel species that exclusively used rice fields may have been the result of low predator risk in that habitat. However, predation risk was actually higher in rice fields (Tombal and Tombal 1988). Moreover, Barbosa (1995) did not find differences in scanning or flocking behaviour among species with the same foraging strategy using habitats with different predation risk. In conclusion, my present results support the initial predictions on how foraging strategy affects the covariation between vigilance level and flock size.

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