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Vigilance benefits and competition costs in groups: do individual redshanks gain an overall foraging benefit?

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Animals gain antipredation benefits from being in larger groups through increased probability of predator detection, dilution of individual risk of being attacked and confusion of predators during attack. A further benefit is that individuals in larger groups can decrease the amount of time they spend being vigilant, while maintaining a high probability of predator detection. They may then gain extra time to forage, so increasing overall intake rate. Increasing group size, however, can also increase competition so that intake rates decrease. We investigated whether there was a foraging benefit in redshanks, *Tringa totanus*, that show the group size decrease in individual vigilance. Intake rates did not change with group size, despite an increase in time spent foraging. Interference competition increased with group size because individuals travelled more to find prey. Redshanks used the extra time available to forage to maintain intake rates under increased competition. Although the group size effect on vigilance did not accrue direct foraging benefits, larger groups formed, conferring other antipredation benefits. Intake rates were maintained because the interference competition was compensated by the benefits of reduced individual vigilance.

Keywords: antipredation; group size effect; interference competition; predator detection; redshank; *Tringa totanus*

Individual animals commonly decrease their vigilance in larger groups (see Elgar 1989; Lima & Dill 1990; Quenette 1990 for reviews). This inverse relationship between group size and time spent scanning the environment is often attributed to the antipredator function of vigilance. Individuals may decrease their investment in vigilance in larger groups due to decreased risk of predation caused by dilution, increased predator detection effects or greater confusion of a predator during attack (Lima 1995; Roberts 1996). Even if risk does not change with group size, each individual can contribute less as more members join the group because probability of detection is maintained by the 'many eyes' effect (Pulliam 1973). This means that being in a larger group has the potential to increase time for other activities. It has been suggested that this time can be allocated to foraging and therefore another benefit of feeding in groups could be increased food intake (Beauchamp 1998). Thus individuals could maximize their foraging efficiency by choosing to feed in larger groups. However, that in larger groups the extra time available results in an individual foraging benefit has not often been demonstrated empirically (Krause & Ruxton 2002).

Competition is also affected by group size with animals in larger groups often being subject to higher levels of competition (Clark & Mangel 1986). If individuals in larger groups are foraging in a more competitive environment where food becomes scarce or aggressive interactions increase, then more attention and time will be focused on interactions with and avoiding others, searching for prey and moving to find new food sources (e.g. Cresswell 1997). As a result any extra time gained through decreased vigilance may be allocated to these activities rather than to maximizing intake rates. For example,

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when oystercatchers, *Haematopus ostralegus*, feed in larger groups, aggressive interactions increase, causing a loss of foraging time to individuals and lowered intake (Stillman et al. 1997); even if individuals do not lose foraging time they still may not be able to increase their intake, for example, if prey become depleted as group size increases (Selman & Goss-Custard 1988). When competition increases with group size then individuals may not necessarily accrue feeding benefits in larger flocks and may even have lower intakes in larger groups.

Here we investigated the effects of flock size on individual foraging behaviour in a natural system where individuals forage in flocks of varying size and where both vigilance and competition are likely to vary with flock size. We examined the effects of flock size on vigilance behaviour and competition to determine whether birds gain any foraging benefit in larger flocks. We studied redshanks, *Tringa totanus*, wintering at the Tyninghame estuary in Scotland. This system has been extensively studied and it has been shown that redshanks in larger flocks suffer lower predation risk (through increased detection and dilution; Cresswell 1994b; Cresswell & Quinn 2004). Redshank flocks on the salt marsh area of the estuary forage mainly on *Orchestia* sp. (Yasué et al. 2003; Minderman et al. 2006). These mobile prey items use refuges in response to redshank activity and become temporarily unavailable as more birds pass through an area, causing interference competition among flock mates, which is reflected in lower intake rates (Minderman et al. 2006). As prey become unavailable and redshanks move to new areas where *Orchestia* have not yet been disturbed, a clear negative relationship between stepping rate and intake rate arises, suggesting that stepping rate is a good indicator of competition (Minderman et al. 2006). The redshank system is therefore ideal to investigate the effects of flock size on both time available for foraging and levels of competition. We tested whether redshanks accumulate multiple gains as flock size increases through decreased predation risk and increased foraging time or whether increased competition produces a decreased risk of predation but fewer feeding benefits.

Initially we confirmed that (1) individual vigilance declines with group size. Then we predicted that, with increasing group size, (2) time available for foraging would increase and (3) interference competition would increase (as indicated by stepping rate). We then predicted that (4) if individuals gain foraging time their overall intake rates would increase unless interference competition has a stronger negative effect on foraging success.

METHODS

Study Site

Observations were made at the Tyninghame estuary, Scotland, from December 2004 to February 2005 and from November 2005 to February 2006. The estuary consisted of a salt marsh (ca. 15 ha), bordered by woodland and mudflats. The salt marsh provides a feeding habitat for wintering redshanks, in particular for juveniles (Cresswell 1994a). Observations of foraging redshanks were conducted on birds feeding on a well-vegetated higher marsh area (ca. 10 ha) (Minderman et al. 2006). This area was delimited by the edge of the salt marsh on one side and by creeks in the middle of the marsh on the other side. Flocks of redshanks foraging in this area were very active, with foraging birds moving constantly, and earlier observations in this area suggested that prey availability and the diet of redshanks consisted mostly of *Orchestia* (Cresswell 1994a; Yasué et al. 2003; Minderman et al. 2006). Furthermore birds feeding in this area on the mobile *Orchestia* are affected by interference competition through temporary depression of prey availability (Minderman et al. 2006).

Ringing

Redshanks were caught at the start of each winter using a 5 × 15 m whoosh net. Individuals foraging in flocks on the salt marsh were targeted (birds feeding in other habitats tend to hold territories and feed alone; Cresswell 1994a). All birds were ringed with a unique combination of four coloured rings above the knee (see Cresswell et al. 2007). Birds were caught and ringed under British trust for Ornithology licence (permit number 4486). In the winter of 2004/2005 32 redshank were ringed, in 2005/2006 39 were ringed and the ringed population included three birds surviving from the previous year.

Focal Observations

Observations of foraging colour-ringed birds were made in the winter of 2004/2005 on 23 days between 6 December and 8 February and in the winter of 2005/2006 on 16 days between 16 November and 9 February. Individuals were identified using a telescope and then videorecorded using a Sony digital 8 video camera (×25 zoom); in 2005/2006 a Sony digital video camera was used in combination with a telescope (×30 zoom) for some focals. Information on the birds' identity, time of day, flock size, distance of the bird from predator-concealing cover and position in the flock was dictated directly onto the videorecord at the time of the observation. Flock spacing was obtained later from the video recordings. All focals lasted for 1 min. An individual would not be recorded more than three or four times during a single day and focals of the same individual were never conducted consecutively while the bird fed in the same flock. All birds recorded were within 150 m of the observer because behavioural information could not be obtained from videorecords of birds farther away. In total we recorded 159 observations of 21 individuals in the first winter and 160 observations of 25 individuals in the second winter.

Behavioural data were extracted from the videorecords using JWatcher behavioural recording software (version 0.9; Blumstein et al. 2000). Videorecords were played back in slow motion (at a third or a fifth of the original speed depending on the camera used) and the number of pecks, swallows and steps were recorded. Vigilance behaviour was scored as head up (above the horizontal body line),