



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.

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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 Tynninghame 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 Tynninghame 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).

Ringling

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),

head down (below the horizontal body line) or head horizontal (at the horizontal body line). During analysis, birds were considered to be vigilant only when in the head up posture and nonvigilant when the head was down or horizontal. Although some level of vigilance could be maintained when the head was not up (Lima & Bednekoff 1999) the quality of information birds gained would be difficult to quantify and is likely to vary with variation in height and density of the surrounding salt marsh grass and possible occlusion by flock mates. Also, searching and probing for *Orchestia*, an active and cryptic prey, is likely to be a very attention-demanding task which suggests that the probability of detecting predators is limited when redshanks have head down or horizontal body positions (Kaby & Lind 2003).

Analysis

Focal data from both winters were combined. All predictions were tested using generalized linear models (GLMs), which were conducted using SPSS version 12.0 (SPSS, Inc., Chicago, IL, U.S.A.). Models used one response variable and possible confounding factors. In all models bird (individual) was included as a random factor (to control for variable number of focals per individual); season (2004/2005 or 2005/2006) and position in the flock (edge or central) were fixed factors. Time of day, time of year and time of year squared (to control for possible nonlinear seasonal effects such as daylength), flock details (i.e. flock size, distance to cover, flock spacing) and, where relevant, behavioural variables (number of steps, pecks and swallows) were included as covariates (when not included as the response variable). In the model for stepping rate we tested for any possible nonlinear effects of flock size on vigilance and time spent foraging by including flock size squared in these models. No interactions between covariates were considered unless they directly related to the hypothesis being tested. The response variables that were not normally distributed were transformed to normality as follows: ln (interscan interval + 0.01), arsine (time spent foraging) and square-root (swallows per minute).

Birds that were not scanning were searching for food, so time not spent vigilant genuinely reflected time available to feed. Therefore time spent foraging was calculated as 1 minus the proportion of time spent vigilant in a focal. Swallow, pecking and stepping rates are all reported as a number per minute and distance to cover was estimated in metres but distances between birds within a flock (flock spacing) are reported as the estimated average number of bird lengths between individuals. These were determined from the video recordings and taken as the spacing at the start of the focal, although flocks are dynamic and spacing between individuals may change during a focal. Overall flock spacing was unlikely to change significantly during the 1 min period of observation.

RESULTS

In the GLMs, flock size was a significant predictor of transformed interscan interval (Table 1). Interscan interval increased with increasing flock size (Fig. 1); therefore individual vigilance decreased with increasing flock size. Time spent foraging varied significantly with flock size (Table 2). Individuals spent a greater proportion of their time foraging as flock size increased (Fig. 2). Stepping rate (number of steps taken in 1 min) showed a significant change with flock size (see Table 3), with the number of steps taken per minute increasing with flock size. Stepping rate also varied significantly with flock size squared which suggests an asymptotic increase in stepping rate. This is indicative of a nonlinear increase in interference competition with flock size; in larger flocks fewer prey are available and birds must move to new patches more rapidly to find food, thus taking more steps.

There was no significant change in intake with flock size (Table 4). Stepping rate and time spent foraging were both significant factors predicting intake rates. However, their effects act in opposing directions (Table 4). As flock size increased, the potential increase in intake from the increased time available to forage and the decreased intake due to increased interference competition (reflected in stepping rate) balance each other (see Fig. 3). Therefore as flock size increases there was no apparent increase or

Table 1. Prediction 1: GLM for transformed interscan interval, investigating the effect of flock size on individual vigilance

	Type III sum of squares	df	F	P	b	
	Intercept	0.740	1	3.94	0.048	1.314
	Intercept error	45.97	244.5			
Random	Bird	15.6	42	1.98	0.001	
Fixed	Position in flock	0.54	1	2.87	0.092	
	Season	1.17	1	6.25	0.013	-0.366 (2004/2005)
Covariates	Day	0.09	1	0.50	0.483	
	Day squared	0.10	1	0.51	0.478	
	Time of day	0.06	1	0.302	0.583	
	Flock spacing	0.01	1	0.054	0.817	
	Flock size	3.80	1	20.26	<0.001	0.01
	Metres to cover	0.78	1	4.14	0.043	-0.003
	Pecks per minute	3.24	1	17.30	<0.001	0.12
	Steps per minute	3.76	1	20.06	<0.001	-0.005
	Error	45.15	241			

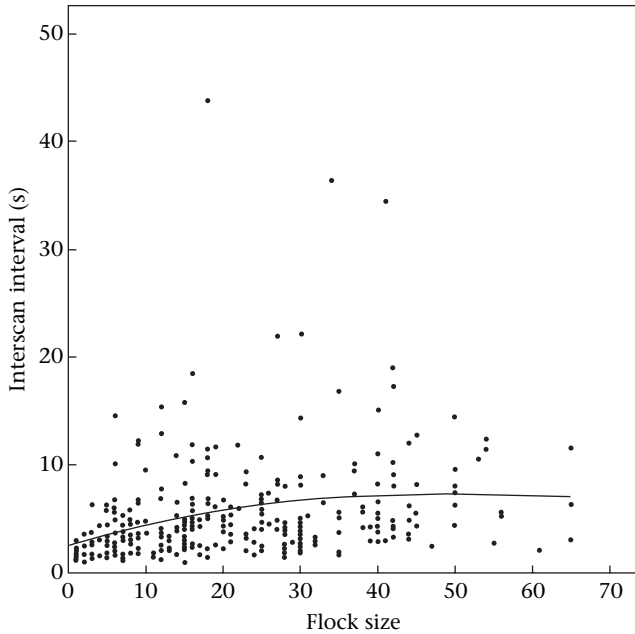


Figure 1. Prediction 1. Interscan interval increases as flock size increases. The line was fitted using curve fitting functions in SPSS to maximize variance explained and is for illustration only to show clearly the direction and magnitude of the effect: the significance of the effects should be assessed only from the models presented in Tables 1–4.

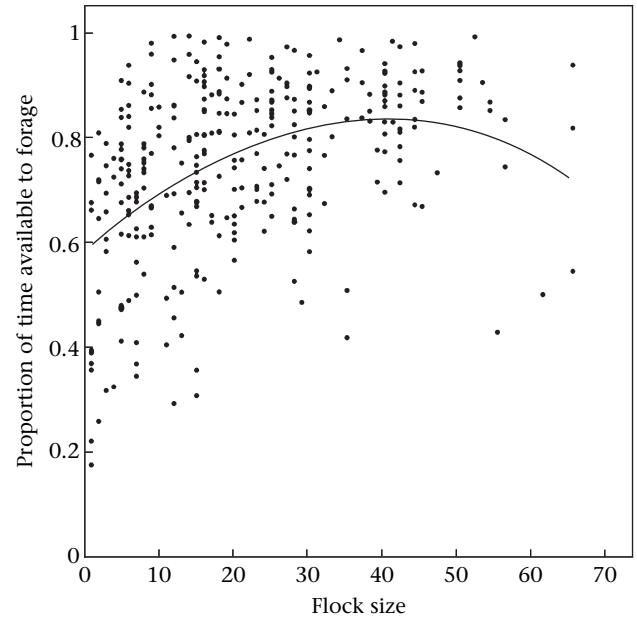


Figure 2. Prediction 2. Proportion of time individuals spend foraging increases with flock size. The line was fitted using curve fitting functions in SPSS to maximize variance explained and is for illustration only to show clearly the direction and magnitude of the effect: the significance of the effects should be assessed only from the models presented in Tables 1–4.

decrease in intake (Table 4). Birds in larger flocks used the extra time available to maintain their intake under conditions where increased competition made prey harder to locate.

DISCUSSION

When we investigated the change in vigilance with flock size we found that, as predicted, individual vigilance levels decreased with flock size. This is consistent with the majority of studies investigating the effect of flocking on vigilance (Elgar 1989; Lima & Dill 1990; Roberts 1996). Additionally, vigilance decreases with flock size in this system (Cresswell 1994b). As predicted, we found that

individuals spent more time foraging as flock size increased. When investigating the effect of flock size on competition we found that competition also increased with flock size, which was indicated by a significant increase in stepping rate with flock size. With increasing flock size, foraging redshanks moved between food patches more quickly because disturbance decreases prey availability as more birds pass through an area (Minderman et al. 2006).

The increase in the proportion of time spent foraging does not appear to translate into a foraging benefit because redshanks show no change in intake with flock size. The lack of a foraging benefit is not consistent with many other studies investigating the effect of decreased vigilance on intake. In a review examining mean food

Table 2. Prediction 2: GLM for transformed time spent foraging, investigating the effect of flock size

		Type III sum of squares	df	F	P	b
	Intercept	0.03	1	1.0	0.317	
	Intercept error	6.74	250.8			
Random	Bird	1.04	42	0.919	0.617	
Fixed	Position in flock	0.10	1	3.577	0.06	
	Season	0.15	1	5.62	0.019	-0.125 (2004/2005)
Covariates	Day	0.03	1	0.926	0.337	
	Day squared	0.02	1	0.862	0.354	
	Time of day	0.13	1	4.79	0.03	0.017
	Flock spacing	0.01	1	0.364	0.547	
	Flock size	0.16	1	6.068	0.014	0.002
	Metres to cover	0.17	1	6.202	0.013	-0.001
	Pecks per minute	1.95	1	72.59	<0.001	0.009
	Error	5.6	246			

Table 3. Prediction 3: GLM for the number of steps taken in 1 min, investigating the effect of flock size on the intensity of competition

		Type III sum of squares	df	F	P	b
	Intercept	3990.89	1	6.01	0.015	14.06
	Intercept error	168 035.59	252.97			
Random	Bird	74 189.68	42	2.676	<0.001	
Fixed	Position in flock	1930.7	1	2.925	0.088	
	Season	11 164.62	1	16.92	<0.001	34.46 (2004/2005)
Covariates	Day	394.21	1	0.597	0.44	
	Day squared	9.94	1	0.015	0.902	
	Time of day	210.1	1	0.318	0.573	
	Flock spacing	31.41	1	0.048	0.827	
	Flock size	5527.74	1	8.375	0.004	1.293
	Flock size squared	3591.85	1	5.442	0.02	-0.018
	Metres to cover	5829.87	1	8.83	0.003	0.252
	Pecks per minute	15 570.16	1	23.59	<0.001	-0.779
	Error	163 683.5	248			

intake (not individuals) [Beauchamp \(1998\)](#) found that of 40 studies where vigilance decreased as a function of group size only eight showed no change in intake. However, when competition also increases with flock size this may limit intake and may cause a decrease in intake with flock size ([Caraco 1979](#)) often because individuals lose foraging time when interacting with others ([Ens & Goss-Custard 1984](#); [Stillman et al. 1997](#)). We have demonstrated in this study that individuals gain foraging time as flock size increases. However, the decrease in prey availability as flock size increases has the potential to lower the intakes of birds in larger flocks ([Minderman et al. 2006](#)). Prey disturbance has previously been suggested as a potential cause of decreased intake with flock size ([Beauchamp 1998](#)), operating in a way similar to that of prey depletion, but it has not often been demonstrated empirically. However, in a result similar to that of this study, [Petit & Bildstein \(1987\)](#) found that white ibis, *Eudocimus albus*, foraging at the centre of flocks spent more of their time foraging but did not increase their intake due to disturbance of their crab prey by other flock members. We found that, as flock size increased, individuals were able to maintain their intake despite the increased competition making prey harder to locate.

When in larger flocks, individuals are able to put more effort into foraging as reflected in the increased proportion of time spent on this activity; however, any potential gains in intake are constrained by interference competition. Our results thus suggest that the main function of flocking for redshanks in this system is to reduce predation risk rather than to gain foraging benefits. The extra time available to forage that occurs in larger groups means that individuals can gain the antipredation benefits of being in a larger flock without incurring the full costs of competition. This may result in flocks that are larger than would otherwise be sustainable, thus providing a less risky feeding environment where individuals do not need to compromise their safety to maintain their intake. This may be particularly important in redshanks because they do not accumulate significant energy reserves ([Mitchell et al. 2000](#)) and so are constantly under pressure to maintain their intake rates to meet their energy budget.

Our results suggest that an 'optimal' group size in terms of the trade-off between food and safety, which has been suggested and demonstrated for group foraging animals ([Higashi & Yamamura 1993](#); [Williams et al. 2003](#)), is not seen in this case as individuals maintain the same intake

Table 4. Prediction 4: GLM for the transformed intake rate (number of swallows made in 1 min), investigating the effect of flock size, stepping rate (level of competition) and time spent foraging

		Type III sum of squares	df	F	P	b
	Intercept	2.9	1	13.5	<0.001	1.27
	Intercept error	54.6	249.25			
Random	Bird	16.3	42	1.8	0.003	0.311
Fixed	Position in flock	0.1	1	0.4	0.508	
	Season	0.5	1	2.2	0.144	
Covariates	Day	0.1	1	0.6	0.448	0.008
	Day squared	0.01	1	0.03	0.865	0.000
	Time of day	0.01	1	0.05	0.822	0.005
	Flock spacing	0.1	1	0.5	0.504	-0.006
	Flock size	0.001	1	0.01	0.914	-0.001
	Metres to cover	1.7	1	7.6	0.008	-0.004
	Pecks per minute	0.3	1	1.4	0.240	0.004
	Steps per minute	5.4	1	24.6	<0.001	-0.006
	Transformed time spent foraging	2.2	1	10.1	<0.001	0.621
	Error	53.8	246			

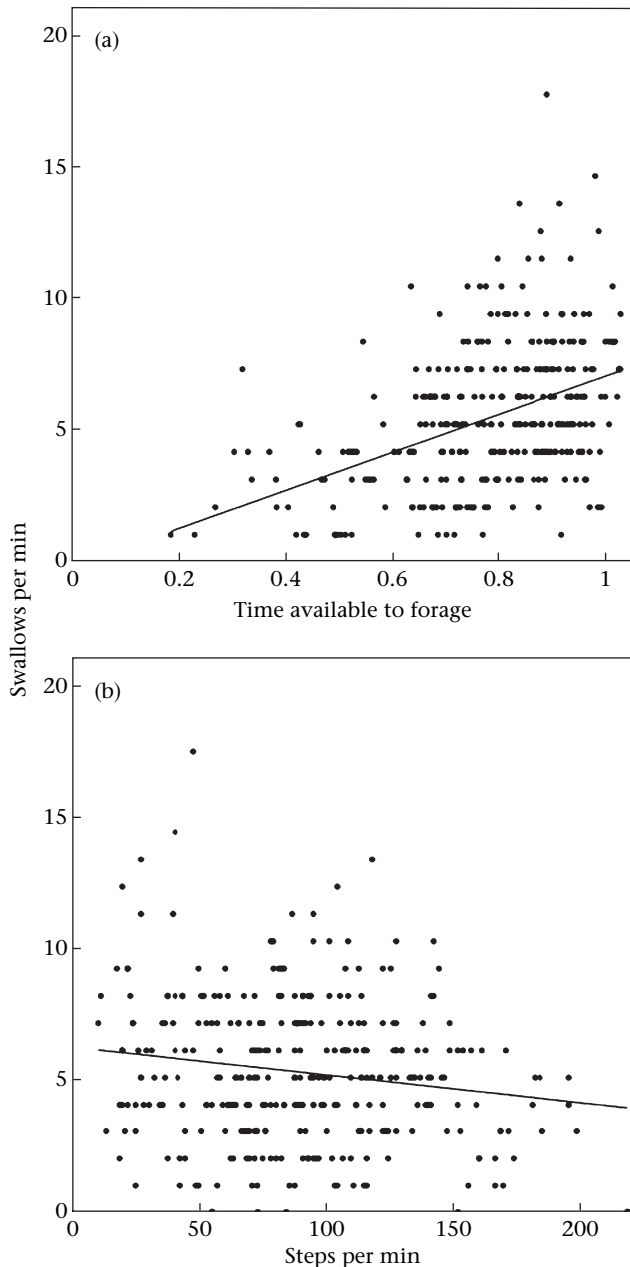


Figure 3. (a) Intake (swallows per min) increases with percentage of time spent foraging and (b) decreases with increased stepping rate. Lines are linear regressions fitted through the untransformed data ($P = 0.013$ for time foraging and $P < 0.01$ for stepping rate). Using the parameter estimates from the GLM of intake rate (Table 4), it was calculated that the approximate decrease in intake rate (swallows per min) due to the increased number of steps being taken was 0.39 swallows per min (0.23–0.49, 95% confidence interval) and the increase in intake rate due to the extra time available to forage was 0.39 swallows per min (0.10–0.76, 95% confidence interval), controlling for confounding factors. Therefore the opposing effects of competition and increased time to forage cancel any change in intake with flock size.

across flock sizes. It may be that individual redshanks seek to forage in the largest possible groups to minimize their predation risk. However, when large numbers of birds are present flocks might reach a maximum size at the point

at which the balance between the positive effect of increased time available to forage and the negative effect of competition breaks down and intake rates cannot be maintained. This seems likely because individual redshanks will still have to spend a certain proportion of their time scanning for predators and therefore will reach a point where they cannot dedicate any more time to foraging; also, given that competition depresses prey availability over a large area at very high levels of competition (i.e. large flock sizes), all patches are likely to become unprofitable.

Our results also provide another example of how flock dynamics could also be influenced by individual competitive ability (Rowcliffe et al. 2004) and its interaction with competitor density (Cresswell 1998a), prey availability (Cresswell 1998b) and patch conditions (Cresswell et al. 2001). Individuals better able to cope with high levels of competition may be able to use the extra foraging time to gain a higher intake in larger flocks as well as the antipredator benefits, whereas less competitive redshanks may gain only antipredator benefits and may not be able to maintain their intake rates in larger flocks. The roles of individual variation in competitive ability and other behaviours such as vigilance are therefore likely to be important in determining individual decisions about which flock to feed in and when to leave a flock. Interference competition is frequently neglected in studies of vigilance and its influence in the evolution of social behaviour, but, as our redshank system shows, it is probably critical in elucidating the costs of social behaviour, and this seems likely to apply more generally.

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