

Behaviourally mediated indirect effects: interference competition increases predation mortality in foraging redshanks

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Summary

1. The effect of competition for a limiting resource on the population dynamics of competitors is usually assumed to operate directly through starvation, yet may also affect survival indirectly through behaviourally mediated effects that affect risk of predation. Thus, competition can affect more than two trophic levels, and we aim here to provide an example of this.
2. We show that the foraging success of redshanks *Tringa totanus* (L.) foraging on active prey was highest in the front of flocks, whereas this was not the case for redshanks foraging on inactive prey. Also, when foraging on active prey, foraging success in a flock decreased as more birds passed through a patch, while overall foraging success was not lower on subsequent visits to the same patch. Thus, redshanks foraging on active prey suffered from interference competition, whereas this was not the case for redshanks foraging on inactive prey.
3. This interference competition led to differences in activity: redshanks attaining a lower foraging success had a higher walking rate. Greater activity was associated with wider flock spacing and shorter distances to cover, which has previously been shown to increase predation risk and mortality from sparrowhawks *Accipiter nisus* (L.).
4. We conclude that behavioural adaptations of prey species can lead to interference competition in foraging redshanks, and thus can affect their predation risk and mortality through increased activity. This study is one of the first to show how interference competition can be a mechanism for behaviourally mediated indirect effects, and provides further evidence for the suggestion that a single species occupying an intermediate trophic level may be simultaneously top-down controlled by a predator and bottom-up controlled by a behavioural response of its prey.

Key words: activity, *Orchestia*, redshanks, top-down control, trophic levels.

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Introduction

Competition for a limited resource is generally assumed to have a direct negative effect on individual fitness (Lomnicki 1980, 1988) and this competition can thus affect population dynamics of competitors (Begon, Harper & Townsend 1986; Sutherland 1996; Newton 1998). Interference competition, a more-or-less immediate and reversible reduction in feeding rate when

competitor density increases (Goss-Custard 1980), is an important form of competition for food (Milinski & Parker 1991). For example, interference competition between foraging oystercatchers *Haematopus ostralegus* (L.) leads to reduced intake rates, which leads to increased starvation mortality (Goss-Custard *et al.* 2001), thus linking susceptibility to interference competition and population dynamics (Stillman *et al.* 2000). However, interference competition may affect population dynamics indirectly because the resultant reduced intake rates can have large consequences for the predicted distribution of animals across habitats (Kacelnik, Krebs & Bernstein 1992; Sutherland & Dolman 1994; Van der Meer & Ens 1997). The fitness of these animals may

then be affected by properties of the habitats other than resource availability, for example by variation in predation risk (McNamara & Houston 1987). Instead of directly influencing population dynamics of competitors through starvation, interference competition may thus lead to mortality of the competitors due to increased predation levels.

Interference competition may therefore provide a good example of where interactions between three trophic levels determine population dynamics of the middle trophic level ('behaviourally mediated indirect effects', reviewed in Bolker *et al.* 2003 and Werner & Peacor 2003). For example, a population of organisms that appears to be mainly top-down controlled may actually also be bottom-up controlled by their competitive response to a limiting resource (the 'predation-sensitive food hypothesis', Sinclair & Arcese 1995). Such a hypothesis may be of general application because many prey animals use refuges as a response to predators (Dill & Fraser 1997; Sih 1997) and so become temporarily unavailable under increased risk of predation. Predators of such refuge using prey are thus forced to be active to find prey, and it has been demonstrated in a wide variety of taxa that increased activity can lead to increased predation risk (Sih 1986; Schwarzkopf & Shine 1992; Skelly 1994; Anholt & Werner 1995; Wisenden, Cline & Sparkes 1999; Persons, Walker & Rypstra 2002; Biro, Post & Parkinson 2003). Examples such as those by Sinclair & Arcese (1995) and referenced by Werner & Peacor (2003) and Bolker *et al.* (2003) are important because they increase our understanding of how populations are structured within and between trophic levels, and how behaviourally mediated effects play a part in interactions between these levels (reviewed in Lima 1998).

We aim here to describe a natural system where a predator's own foraging behaviour results in temporary disappearance of its prey so that the predator takes greater risks when foraging, which in turn results in an increase of the predator's own predation mortality. Thus we provide an example of a possible pathway by which interference competition can indirectly affect population dynamics, via an effect on predation risk. We use a well studied system of wintering redshanks at the Tynninghame Estuary in Scotland. Earlier studies suggested that redshanks at Tynninghame forage in two different habitats on a salt marsh. Prey availability in one area consists mostly of *Orchestia* sp. (hereafter referred to as *Orchestia*), amphipod crustaceans (Cresswell 1994a), which are very active (Bowers 1964; Friend & Richardson 1986) and use refuges when disturbed (pers. obs.). In contrast, the prey available in the second area mostly consists of (relatively) inactive gastropod (mainly *Hydrobia* sp., hereafter referred to as *Hydrobia*) and isopod species. Flocks of foraging redshanks in the *Orchestia* area are widely spaced and active, while flocks in the other area are relatively dense and inactive (pers. obs.) suggesting that interference

competition may be structuring feeding flocks (Goss-Custard 1976, 1980). Finally, predation risk for the redshanks by hunting sparrowhawks has been well quantified in this system, with the consequences of most redshank behaviours known in terms of predation risk (Cresswell 1994a, b; Cresswell & Quinn 2004; Quinn & Cresswell 2004, and unpublished).

We hypothesize that a behavioural response of *Orchestia* to increased predation pressure by foraging redshanks results in a change of behaviour of the redshanks, and that this interference through prey depression (Charnov, Orians & Hyatt 1976) affects the predation risk of the redshanks. This will not occur when redshanks are feeding on the other (gastropod or isopod) prey species that lack such a behavioural response. We test that

1. The areas differ in their availability of active (*Orchestia*) prey and inactive prey.
 2. *Orchestia* respond to disturbance while other potential prey species do not.
- Having confirmed these differences between areas, a number of testable predictions are generated by the hypothesis of *Orchestia* activity determining predation risk of the redshanks via interference competition.
3. In areas where redshanks forage on *Orchestia*, birds in front of a flock will have higher intake rates than birds foraging in the back of flocks.
 4. As a flock moves through a patch, intake rates will decline with the number of birds that have passed through the patch.
 5. Intake rates should not be different between first and second visits of a flock to the same patch if they are well separated in time, because the decline in intake rate as a flock moves through a patch is due to depression and not depletion of *Orchestia*.
 6. The difference in intake rates between a focal bird and its predecessor passing through a patch will be negative but positively related to the time that passed between them.
 7. Foraging on *Orchestia* affects the activity of the redshanks in terms of the speed that the redshanks walk while feeding.
 8. Increased activity will result in changes in spacing and distance from predator concealing cover so that redshank predation risk is increased.

Materials and methods

STUDY SITE

Observations were made in the Tynninghame Estuary, Scotland, from October 2004 to February 2005. At the estuary, a salt marsh of approximately 15 ha is a feeding habitat for wintering redshanks, in particular for juvenile animals (Cresswell 1994a).

Based on the preferred feeding localities of the redshanks, the salt marsh was divided into two research areas, 1 and 2 (following Cresswell 1994b). Area 1 was a well-vegetated higher marsh area (c. 10 ha). This area

was delimited by the edge of the salt marsh on one side, and on the other side by creeks in the middle of the marsh. Flocks of redshanks foraging in this area were moving constantly, and prey availability and the diet of redshanks consisted mostly of *Orchestia* (Cresswell 1994a; Yasué, Quinn & Cresswell 2003).

Area 2 was a bay (c. 2 ha) along the eastern edge of the marsh, delimited on the west side by creeks in the middle of the marsh. This lower salt marsh area was mainly dominated by *Salicornia* sp. swards, and a large part of this area was covered by a layer (up to 5 cm) of channel wrack *Pelvetia canaliculata* (L.). Flocks of foraging redshanks in this area moved very little, and prey availability and the diet of the redshanks mostly consisted of *Hydrobia* and isopod species (pers. obs. and Cresswell 1994a).

PREY AVAILABILITY MEASUREMENTS

Prey availability was measured in transects running perpendicular to the edge of the marsh, in both areas. Transects varied in length between 50 and 70 m. Along each transect, five replicate counts of the number of prey were made every 10 m, c. 20 cm apart on a line perpendicular to the transect. Each replicate consisted of a count of all prey items on a square of 10 × 10 cm. All prey items were identified to species level where possible. Where present, channel wrack was removed from a square for counting and replaced directly afterwards. This wrack was checked for prey items.

In area 2, five transects were measured in November 2004, and in December 2004 these five plus an additional three were measured. This total of eight transects was measured again in January 2005. In area 1, two transects were set out and measured in January 2005.

PREY DISTURBANCE EXPERIMENTS

To test that *Orchestia* were capable of responding to increased predation risk (prediction 2), we performed a field experiment to simulate the disturbance caused by predation and measured whether this changed the availability of *Orchestia*. To this end, an area of salt marsh was covered with black plastic to create a favourable microhabitat for *Orchestia* on the surface of the salt marsh. Removal of the plastic cover would then expose *Orchestia* to potential predation and removing the plastic was thus analogous to increased predation risk.

The experiment consisted of pairs of 50 × 50 cm control and treatment plots in both areas. Prey availability was estimated throughout the experiment by counting the number of prey on squares of 10 × 10 cm repeated four times in a diagonal line across each plot.

In the first stage of the experiment ('covering stage'), prey availability was estimated in both the control and treatment plots. The treatment plots were then covered with black plastic, while control plots were left uncovered. Additionally, we tested whether any increase

on covered plots would be due to horizontal migration of prey (*Orchestia* moving over the surface of the salt marsh entering plots from the sides), or due to vertical migration of prey (*Orchestia* moving into and out of burrows below the covered plots), by fencing half of the plot pairs. Fenced plots were surrounded on all sides with a piece of cardboard of approximately 10 cm high, dug 2 cm into the substrate and restricting all sideways movement into plots, whereas unfenced plots allowed prey to move into covered plots from both the sides and the bottom. We hypothesized that differences in prey availability should arise between fenced and unfenced plots if *Orchestia* are moving horizontally as well as vertically. The plots were left overnight and prey availability was estimated when cover was removed (17–24 h after the experimental plot was covered).

Immediately following the covering stage, a second 'disturbance' stage in which all plots were uncovered and unfenced for 1.5–2.5 h was carried out. After the disturbance stage, prey availability was estimated again in all plots and compared with the availability after the initial covering stage.

Immediately following the disturbance stage, a third 'recovery' stage, repeating the first covering stage (although all plots were unfenced this time) was carried out. After one night, prey availability was estimated again and compared with availability immediately after the disturbance stage.

FOCAL OBSERVATIONS OF FORAGING REDSHANKS

Foraging rates and behaviour of redshanks was observed on 16 days between 14 January and 2 February 2005 by two observers in area 1 and one observer in area 2. Where relevant, observer identity was included in statistical analyses to account for possible confounding effects. Focal observations of foraging redshanks lasted for 30 s and were made using a telescope (30× magnification) at distances of 10–75 m. The distance between the focal bird and the closest predator-concealing cover (the edge of the salt marsh), the distance between the focal bird and its nearest neighbour (nearest-neighbour distance) and the number of birds in the flock (flock size) were recorded for each focal. A unique flock number was included in analyses to account for repeated measures from the same flock. Each focal recorded swallow rate (measure for intake rate) and step rate (measure for activity). Swallows were identified by a clear and rapid backwards movement of head and neck.

In both area 1 and 2, focals were primarily collected in a matched-pairs format. A pair consisted of one focal of a bird foraging in front of a flock, and one focal of a bird foraging in the back of a flock. In area 2, if a flock was not moving, a matched pair consisted of a focal of a bird foraging on the edge and a focal of a bird foraging in the centre of a flock. In all following analyses, edge focals were considered front focals and

centre focals were considered back focals. Matched-pair focals were collected as quickly after each other as possible to minimize variation in flock characteristics and environmental effects. The order in which pairs were collected was reversed on each pair.

In area 1, one observer also collected focals in sequence of a flock moving through a patch, being an area of salt marsh of approximately 10–50 m² delimited by two or more clear landmarks. In addition to the usual focal measurements, each focal in a sequence also recorded the bird number, being the number of birds that had passed through the patch before the focal bird, plus one. A focal in a sequence was disregarded when the bird left the observed patch before the focal was finished, or when the focal bird altered its position relative to other flock members. After passage of a flock, and if a flock then returned to the same area during the remainder of the salt marsh observation period (up to 5 h later), similar focal sequences were collected on this return. At maximum three such sequences were collected for a single patch – one initial visit and two returns.

STATISTICAL ANALYSIS

Prey availability and prey disturbance data were analysed using nonparametric tests. In case of the prey disturbance data, each of the stages was analysed separately. The proportional changes (the difference between the prey availability at the end and at the start of a stage, divided by the prey availability at the start of the stage) of both *Orchestia* densities and the densities of other prey were compared between treatment and control plots.

Focal observations were analysed using general linear models (GLMs) in SPSS 12.0, including one focal explanatory variable and all confounding variables that were recorded and relevant. Interactions were only included in a model when of direct relevance to the hypothesis being tested and interactions between confounding variables were not investigated. If it was not statistically possible to include flock number in a model, possible confounding effects of repeated measures from the same flock were controlled for by including observer, location and day number as random factors. Day number was included as a random factor, and confounding flock variables (e.g. flock size and distance to cover) were included as covariates. Where needed, both explanatory and response variables in a GLM were transformed to normality.

Prey densities are reported as a number 100 cm⁻², and swallow- and step rates as a number per second. All results are reported as mean ± 1 SE when tested parametrically, or as mean, median and interquartile range (IQR) when tested nonparametrically. Figures are to illustrate the relationships and the spread of the uncorrected and untransformed data. The true significance of the relationships is reported in the text

and the tables. The paragraph numbers in the results section follows the numbering of the predictions stated in the introduction.

Results

(1) PREY AVAILABILITY

In the period when both areas were sampled (January 2005 only), overall prey availability was on average more than four times lower in area 1 (mean = 1.99 items 100 cm⁻², median = 1.00, IQR = 3) than in area 2 (mean = 8.38 items 100 cm⁻², median = 4.00, IQR = 11, Mann–Whitney *U* (MWU) test, $N_{\text{area1}} = 100$, $N_{\text{area2}} = 250$, $Z = -6.809$, $P < 0.001$). However, the mean availability of *Orchestia* was significantly higher in area 1 than in area 2 (Fig. 1).

In area 2, where prey availability was measured multiple times during the season ($n = 1125$ samples over 82 days), total prey availability did not correlate with day number (Spearman $r = 0.019$, $P = 0.53$), neither did the *Hydrobia* availability (Spearman $r = 0.190$, $P = 0.53$). The availability of *Orchestia* decreased slightly with day number (Spearman $r = -0.105$, $P < 0.001$: a decline of 25.8% over the 82-day period), while the availability of isopods increased with day number (Spearman $r = 0.157$, $P < 0.001$: an increase of 3.3%). There was no evidence of any nonlinear seasonal effects.

(2) PREY DISTURBANCE

Orchestia densities were significantly increased by covering and this increase was not different between fenced or unfenced plots (Fig. 2, see legend for statistics).

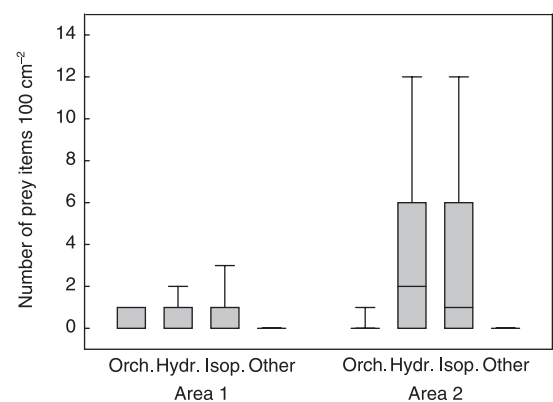


Fig. 1. Prediction 1. Boxplots of the availability (items 100 cm⁻²) of four prey categories (Orch. = *Orchestia*, Hydr. = *Hydrobia*, Isop. = Isopods) in the two areas. $N = 100$ for area 1 and $N = 250$ for area 2. Mean *Orchestia* availability was higher in area 1 than in area 2 (Mann–Whitney *U*-tests: $Z = -2.147$, $P = 0.032$). Mean availability of *Hydrobia* was higher in area 2 than in area 1 ($Z = -8.523$, $P < 0.001$), as was the availability of Isopods ($Z = -4.664$, $P < 0.001$). Availability of other prey was not different between the two areas ($Z = -1.811$, $P = 0.070$).

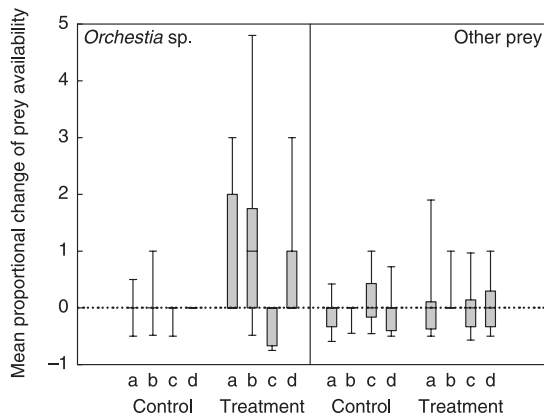


Fig. 2. Prediction 2. Boxplots of the proportional change of the availability (number 100 cm⁻²) of *Orchestia* (left panel) and other prey (right panel), in control (not covered) and treatment (covered) plots, for the four stages of the experiment. From left to right in each panel; covering stage unfenced (a), covering stage fenced (b), disturbance stage (c), recovering stage (d). Unfenced plots (a), changes in covered vs. uncovered plots; *Orchestia*: MWU $Z = -4.936$, $P < 0.001$, other prey: MWU $Z = -0.334$, $P = 0.74$. Fenced plots (b), changes in covered vs. uncovered plots; *Orchestia*: MWU $Z = -2.471$, $P = 0.013$, other prey: MWU $Z = -2.214$, $P = 0.027$. Covered plots only, changes in unfenced vs. fenced (a vs. b for treatment only); *Orchestia*: MWU $Z = -1.505$, $P = 0.132$, other prey: MWU $Z = -1.757$, $P = 0.079$. Disturbance stage (c), changes in covered vs. uncovered plots; *Orchestia*: MWU $Z = -4.121$, $P < 0.001$, other prey: MWU $Z = -1.493$, $P = 0.135$. Recovery stage (d), changes in covered vs. uncovered plots; *Orchestia*: MWU $Z = -4.626$, $P < 0.0001$, other prey: MWU $Z = -0.745$, $P = 0.456$.

On removal of covers during the disturbance stage, *Orchestia* densities declined to a degree (15-fold) significantly different from changes in controls. When they were covered again, *Orchestia* densities increased (70-fold) with a similar increase as that during the first covering, and this change was significantly greater than changes in uncovered control plots (Fig. 2). Although the availability of other prey also increased significantly with covering in both fenced and unfenced plots

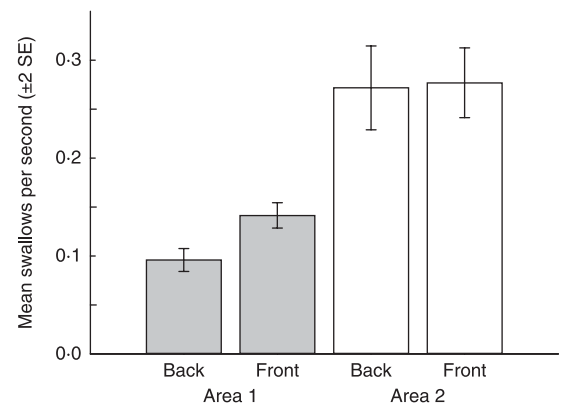


Fig. 3. Prediction 3. Mean number of swallows per second, ± 2 SEM, of the front and the back bird in a flock in each of the areas.

(both to a similar degree), the proportional increases were relatively small compared with those of *Orchestia* and there were no significant changes in the density of other prey either on removal of covers (disturbance stage) or when the plots were covered again (Fig. 2). In summary, *Orchestia* moved vertically to increase in availability when covered and decreased when uncovered and disturbed, whereas other prey did not. As the numbers of *Orchestia* again increased after the second covering, any decrease during the initial disturbance stage was unlikely to be due to destruction of the habitat.

(3) POSITION IN FLOCK

In a GLM for swallow rate, location was significant, with lower overall swallow rates in area 1 than in area 2. There was a significant effect of position in flock dependent on location (interaction position * location, Fig. 3 and Table 1): birds in front positions achieved higher intake rates in area 1. Separate GLMs for each of the areas confirmed the absence of an effect of position in flock in area 2.

Table 1. Prediction 3. GLM for transformed number of swallows per second, investigating the effect of position in flock and a possible different effect of position in each of the two locations. Including data from both areas (1 and 2)

		Sum of squares (type III)	F	d.f.	P	b
	Intercept	15.7	31.2	1	0.09	
	Intercept error	0.6		1		
Fixed:	Position in flock	0.3	1.5	1	0.43	
Random:	Location	1.2	20.4	1	0.003	0.32
	Observer	0.1	1.6	1	0.20	(area 2)
	Day number	1.7	3.5	1	< 0.001	
Covariates:	Flock size	0.3	6.9	1	0.009	0.003
	Nearest-neighbour distance	0.1	3.1	1	0.079	
	Meters to cover	0.2	5.2	1	0.023	0.002
Interaction:	Position * location	0.1	4.7	1	0.031	(see text)
	Error	11.6		293		

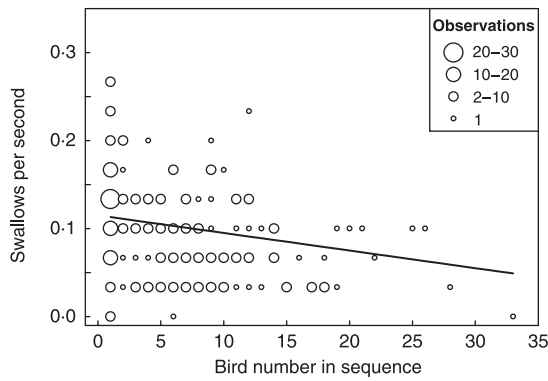


Fig. 4. Prediction 4. Mean number of swallows per second vs. bird number in a flock as it passes through a patch. Symbol size represents number of data points and the line is a linear regression fitted through all data ($y = -0.004x + 0.126$, $F_{1,232} = 47.8$, $P < 0.001$).

(4) NUMBER OF BIRDS MOVING THROUGH A PATCH

In area 1, swallow rates decreased significantly with bird number in a sequence (Fig. 4). A GLM for swallow rate in this area confirmed this decrease with bird number when controlling for a number of confounding variables (Table 2).

(5) RATES OF FEEDING ON RETURN

Swallow rates were not different between first and second visits to an area (nonsignificant effect of flock return in Table 2), and the decrease of swallow rates with bird number was similar on subsequent visits (interaction between bird number and flock return was not significant when included in the model in Table 2: $F_{1,74} < 0.1$, $P = 0.96$).

(6) RATES OF FEEDING RELATED TO TIME SINCE PREDECESSOR

The difference in swallow rate between a focal bird and the last bird visiting an area was mostly negative at

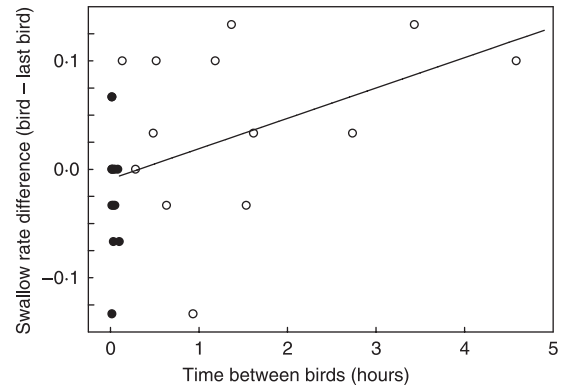


Fig. 5. Prediction 6. Difference between the number of swallows per second of a focal bird foraging in a patch and that of the previous bird passing through that patch, vs. the time that passed between these birds. Points either represent the difference between the last and second-to-last bird of a first flock passing through an area (solid circles, $n = 13$) or the difference between the first bird of a second flock and the last bird of a first flock (open circles, $n = 13$). Solid line is a linear regression fitted through all data (see text).

short time intervals, but increased to zero as more time passed between birds (linear regression, $F_{1,24} = 8.8$, $b = 0.083$, $P = 0.007$, Fig. 5). Correcting for the effect of unique flocks did not change this relationship (GLM, return interval: $F_{1,12} = 5.1$, $P = 0.044$; flock number: $F_{12,12} = 0.3$, $P = 0.97$).

(7) FORAGING BEHAVIOUR AND ACTIVITY

Step rate was negatively related to swallow rate (Fig. 6). This effect was confirmed in a GLM for step rate, controlling for the effects of confounding variables, and was independent of location (nonsignificant interaction of location * swallow rate when added to the model in Table 3: $F_{1,128} = 1.1$, $P = 0.29$).

(8) ACTIVITY AND PREDATION RISK

In turn, activity affected two parameters known to be related to predation risk. First, birds that walk more

Table 2. Predictions 4 and 5. GLM for transformed number of swallows per second, investigating the effect of bird number in a flock and whether the number of swallows per second was different between first and subsequent visits of a flock to the same patch (flock return). Including data from area 1 only, where there was an effect of position in flock

		Sum of squares (type III)	F	d.f.	P	b
	Intercept	2.8	272.8	1	< 0.001	
	Intercept error	0.4		42.2		
Random:	Flock return	0.03	2.9	1	0.089	
	Day number	0.03	0.8	4	0.52	
Covariates:	Bird number	0.06	6.8	1	0.011	-0.007
	Time since start of sequence	0.03	3.7	1	0.059	
	Flock size	0.00	0.04	1	0.84	
	Nearest-neighbour distance	0.04	4.5	1	0.037	0.036
	Metres to cover	0.001	0.2	1	0.69	
	Error	0.71		75		

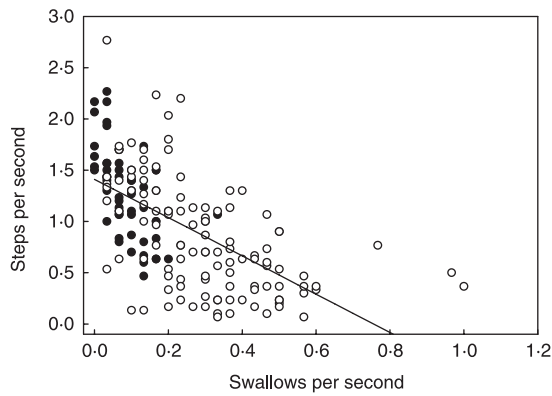


Fig. 6. Prediction 7. Number of steps per second vs. number of swallows per second in area 1 (solid circles) and area 2 (open circles). Solid line is a linear regression fitted through all data. This relationship was similar for both areas (no significant effect of area, see text).

were spaced more widely (nearest-neighbour distance increased with step rate, Fig. 7a). In a GLM, this effect of step rate on transformed nearest-neighbour distance was significant when controlling for the effect of confounding variables (Table 4).

Secondly, birds that walked more were closer to cover (distance to cover decreased as step rate increased, see Fig. 7b), and in a GLM this effect was significant when controlling for confounding variables (Table 5).

Discussion

FORAGING AND INTERFERENCE COMPETITION

As predicted, redshanks foraging on *Orchestia* in the front of a flock attained a significantly higher intake rate than birds foraging in back positions. In contrast, in an area where no *Orchestia* were available, there was no difference in intake rate between birds foraging in front (or edge) and back (or centre) positions. In addition, intake rates declined as more birds had passed through a patch, when foraging on *Orchestia*.

Table 3. Prediction 7. GLM for the transformed number of steps per second, investigating the effect of position in flock (front/back or edge/centre, depending on area, see Materials and methods). Including data from both areas (1 and 2)

		Sum of squares (type III)	<i>F</i>	d.f.	<i>P</i>	<i>b</i>
	Intercept	20.4	133.5	1	< 0.001	
	Intercept error	18.0		118.1		
Fixed:	Position in flock	1.4	9.2	1	0.003	0.20 (back)
Random:	Location	0.001	0.003	1	0.96	
	Day number	3.7	3.5	7	0.002	
Covariates:	Flock size	0.4	2.6	1	0.10	
	Nearest-neighbour distance	1.2	7.9	1	0.006	0.16
	Metres to cover	3.1	20.2	1	< 0.001	-0.01
	Swallow rate (transformed)	5.5	36.0	1	< 0.001	-0.91
	Error			129		

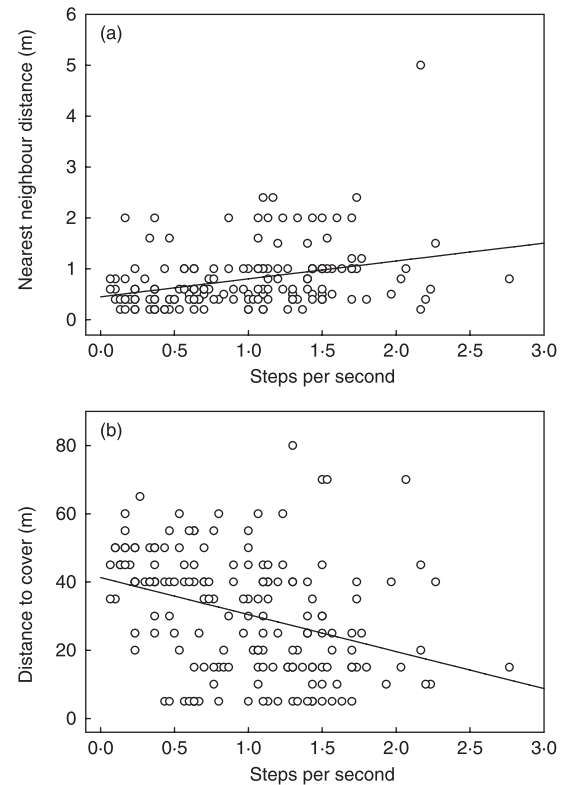


Fig. 7. Prediction 8. (a) Nearest-neighbour distance, and (b) distance to cover (untransformed, meters), vs. the number of steps per second for both areas. Regression line in (a) is significant ($P = 0.001$) even if the outlier at nearest-neighbour distance = 5 m is omitted.

Foraging in the front of a flock thus accrues benefits. This has been earlier documented in flocks of barnacle geese *Branta leucopsis* (L.) where birds in the back of the flock suffer from local depletion of the preferred food (Drent & van Eerden 1980; Prop & Loonen 1989; Black *et al.* 1992). In contrast, in our case this decline of foraging success as a flock passes cannot be explained by depletion, because we show that intake rates in an area are only temporarily depressed, recovering to initial levels over the period of a few hours.

Table 4. Prediction 8. GLM for the transformed nearest-neighbour distance, investigating the effect of steps per second (step rate). Includes data from both areas (1 and 2)

		Sum of squares (type III)	<i>F</i>	d.f.	<i>P</i>	<i>b</i>
	Intercept	1.5	3.8	1	0.054	
	Intercept error	52.6		133.1		
Fixed:	Position in flock	2.3	5.7	1	0.019	-0.27 (back)
Random:	Location	0.1	0.4	1	0.56	
	Day number	2.9	1.0	7	0.42	
Covariates:	Flock size	0.06	0.1	1	0.70	0.002
	Meters to cover	0.001	0.002	1	0.97	
	Step rate	3.9	9.6	1	0.002	0.43
	Swallow rate (transformed)	0.08	0.2	1	0.66	0.12
	Error	52.5		129		

Table 5. Prediction 8. GLM for the transformed distance to cover, investigating the effect of steps per second (step rate). Includes data from both areas (1 and 2)

		Sum of squares (type III)	<i>F</i>	d.f.	<i>P</i>	<i>b</i>
	Intercept	20.2	49.5	1	< 0.001	
	Intercept error	52.9		129.995		
Fixed:	Position in flock	2.0	5.1	1	0.025	0.25 (back)
Random:	Location	0.1	0.3	1	0.559	-0.12 (area 1)
	Day number	11.9	4.4	7	< 0.001	
Covariates:	Flock size	0.2	0.6	1	0.426	-0.004
	Nearest-neighbour distance	0.3	0.8	1	0.358	0.09
	Step rate	4.4	11.2	1	0.001	-0.44
	Swallow rate (transformed)	0.9	2.2	1	0.137	0.41
	Error	50.4		129		

Thus, we conclude that redshanks suffer from interference competition when foraging on *Orchestia*. An active mechanism for this interference is unlikely, as redshanks foraging on the salt marsh do not interact in any visible way (Cresswell 1994a). In contrast, prey depression (Charnov *et al.* 1976) is a likely mechanism because we have shown that *Orchestia* can vacate and reoccupy a surface patch of salt marsh in response to a disturbance similar to predation. The increase of the numbers of *Orchestia* after covering a patch was similar in fenced and unfenced plots, which implies that most movement of *Orchestia* takes place vertically. Thus, *Orchestia* can respond to the presence of predators by making themselves less available, probably by increased refuge use when disturbed.

INTERFERENCE COMPETITION AND PREDATION MORTALITY

We have shown that birds attaining lower foraging rates due to interference were more active and that the more active foraging birds were, the closer they were to predator-concealing cover. Proximity to cover is associated with both the probability of an attack by a sparrowhawk and with the success rate of attacks (Cresswell 1993; Cresswell 1994a; Quinn & Cresswell

2004). We have also shown that more active birds were spaced out more widely. Sparrowhawks are more likely to attack and probably kill individuals that are spaced further apart (Quinn & Cresswell 2004, and unpublished data) and more widely spaced redshanks respond more slowly to attacking sparrowhawks (Hilton, Cresswell & Ruxton 1999). Thus, combining our own observations and previous knowledge of the system, we can conclude that interference competition by prey depression, via its effects on flock activity, proximity to cover and spacing, can have fitness consequences for redshanks in terms of increased predation risk and mortality.

This effect of interference competition on predation mortality might even be more significant than outlined above. Increased activity *per se* generally results in increased mortality due to predation (Sih 1986; Schwarzkopf & Shine 1992; Skelly 1994; Anholt & Werner 1995; reviewed in Lind & Cresswell 2005), and might increase attack probability by peregrine falcons *Falco peregrinus* (L.), a raptor that also contributes significantly to mortality of redshanks in this system (Cresswell & Whitfield 1994). Sparrowhawks attack success might be affected by redshank activity, through lowered detection ability. Birds foraging on active prey (e.g. *Orchestia*) must divert much attention to the

foraging task, resulting in less effective vigilance (Krause & Godin 1996). Moreover, difficult foraging tasks *per se* can significantly impair the detection of attacking predators (Kaby & Lind 2003).

IMPLICATIONS

These findings are highly relevant for theory in (behavioural) ecology in several ways. Primarily, although interference competition has been shown in a variety of species (Hassell & Varley 1969; Ens & Goss-Custard 1984; Dickman 1991; Griffith & Poulson 1993; Cresswell 1997; Faragher & Jaeger 1998), few studies have shown that prey depression (Charnov *et al.* 1976) is the mechanism. For example, Yates, Stillman & Goss-Custard (2000) suggest a behavioural antipredatory response of the prey as the most likely mechanism for a decrease in foraging rates of redshanks, a similar relationship to what we show in Fig. 4. Thus, this study provides further support for the principle of interference competition by prey depression.

Secondly, both empirical (Ens & Goss-Custard 1984; Cresswell 1997) and theoretical (Hassell & Varley 1969; Beddington 1975; Stillman, Goss-Custard & Caldow 1997) studies of interference competition have focused on systems where individuals compete for a single resource with a limited range of properties. We here demonstrate that differences between resources (e.g. active vs. relatively inactive prey) can have repercussions on the predation risk and mortality of individuals competing for the resources. Such differences between prey species should therefore be included in models predicting population dynamics from foraging behaviour.

Furthermore, models using resource competition as a mechanism to predict population dynamics usually only consider a direct relationship between competition and fitness of the competitors. For example, reduced foraging rates at higher levels of competition lead to increased starvation (Stillman *et al.* 2000) or decreased fecundity (Fielding 2004). Although such models may incorporate reasonably complicated predator and prey behaviour, sources of mortality such as predation that may be affected by an interaction between the behaviour of prey and predator, are often omitted in models to predict population dynamics.

We have shown that antipredatory behaviour of *Orchestia* causes interference competition in redshanks hunting for them. This in turn leads to a behavioural response in foraging redshanks (increased activity), making them more susceptible to predation by sparrowhawks. This is an example, from the field, of a behaviourally mediated indirect effect (also called 'trait-mediated indirect effects', reviewed by Bolker *et al.* 2003; Werner & Peacor 2003) where behavioural adaptations in one trophic level can have indirect consequences for the fitness of organisms in another level, via changes in the behaviour in a third trophic level. For example, lab experiments on larval anurans

Rana sp. under controlled levels of resource availability and predator effectiveness, showed that predation mortality of anurans was mediated by their behaviour (increased activity) in response to low resource levels (Anholt & Werner 1995; Peacor & Werner 1997; Anholt & Werner 1998). Thus, to understand population dynamics we cannot only focus on density-mediated effects, but we must also know the behaviourally mediated effects. Our study implies that interference competition can be an important mechanism driving such behaviourally mediated indirect interactions, and is to our knowledge one of the few studies to show this in vertebrates in the field.

To conclude, because redshanks do not accumulate substantial energy reserves and are thus always vulnerable to starvation (Mitchell, Scott & Evans 2000), deterioration of abiotic conditions (e.g. weather and season) can readily force them to search for the more profitable prey, *Orchestia* (Cresswell 1994a; Yasué *et al.* 2003), and we have shown that this increases their predation risk. Thus, our study lends further support to the 'predation-sensitive food hypothesis', which states that as a resource becomes scarce, competitors are forced to take more risks while foraging and become more susceptible to predation in the process (Sinclair & Arcese 1995). Because of this behavioural interaction between competition for a limiting resource and predation risk, to classify a population as being either top-down or bottom-up controlled is not meaningful (McNamara & Houston 1987; Hunter & Price 1992; Krebs *et al.* 1995, 2001). Even for a population that appears to be primarily top-down controlled, such as the one studied here (Whitfield 1985; Cresswell & Whitfield 1994), behavioural mechanisms (e.g. antipredatory responses, interference competition) in all trophic levels of the food web need to be acknowledged to understand the population dynamics therein (Schmitz 1998; Bolker *et al.* 2003).

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