

The effect of group size on vigilance in Ruddy Turnstones *Arenaria interpres* varies with foraging habitat

RICHARD A. FULLER,^{1,2*} STUART BEARHOP,³ NEIL B. METCALFE⁴ & THEUNIS PIERSMA^{5,6}

¹*School of Biological Sciences, University of Queensland, St Lucia, Qld, Australia*

²*CSIRO Climate Adaptation Flagship and CSIRO Ecosystem Sciences, Qld, Australia*

³*Centre for Ecology and Conservation, School of Biosciences, University of Exeter, Penryn, UK*

⁴*Institute of Biodiversity, Animal Health & Comparative Medicine, University of Glasgow, Glasgow, UK*

⁵*Department of Marine Ecology, Royal Netherlands Institute for Sea Research (NIOZ), Den Burg, Texel, The Netherlands*

⁶*Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, Groningen, The Netherlands*

Foraging birds can manage time spent vigilant for predators by forming groups of various sizes. However, group size alone will not always reliably determine the optimal level of vigilance. For example, variation in predation risk or food quality between patches may also be influential. In a field setting, we assessed how simultaneous variation in predation risk and intake rate affects the relationship between vigilance and group size in foraging Ruddy Turnstones *Arenaria interpres*. We compared vigilance, measured as the number of ‘head-ups’ per unit time, in habitat types that differed greatly in prey energy content and proximity to cover from which predators could launch surprise attacks. Habitats closer to predator cover provided foragers with much higher potential net energy intake rates than habitats further from cover. Foragers formed larger and denser flocks on habitats closer to cover. Individual vigilance of foragers in all habitats declined with increasing flock size and increased with flock density. However, vigilance by foragers on habitats closer to cover was always higher for a given flock size than vigilance by foragers on habitats further from cover, and habitat remained an important predictor of vigilance in models including a range of potential confounding variables. Our results suggest that foraging Ruddy Turnstones can simultaneously assess information on group size and the general likelihood of predator attack when determining their vigilance contribution.

Keywords: competition, density, group-size effect, predation.

Animals often reduce individual predation risk by forming larger groups (Krause & Ruxton 2002), particularly when the risk of predation is high (Hager & Helfman 1991, Tegered & Krause 1995, Spieler 2003). This brings benefits because the vigilance effort required of individuals usually declines as group size increases (Pulliam 1973, Vine 1973). There are two main hypotheses to explain this group size effect. First, in larger groups, a smaller individual contribution is

required to maintain a given level of overall group vigilance (Elgar 1989). Secondly, the reduction in individual predation risk through numerical effects such as dilution (Foster & Treherne 1981), predator confusion (Milinski 1979) and co-operative warning and escape effort (Humphries & Driver 1967, Proctor *et al.* 2003) implies that a lower level of individual vigilance is required in larger groups, everything else being equal.

Although this effect has been widely documented (Elgar 1989, Lima & Dill 1990, Roberts 1995), some studies have reported no detectable effect of group size on individual vigilance levels

*Corresponding author.

Email: r.a.fuller@dunelm.org.uk

(Catterall *et al.* 1992, Scheel 1993, Jones 1998, Treves 2000, Barbosa 2002). Thus, it seems likely that factors other than group size may influence vigilance contributions of foragers (Beauchamp 2008). Predation danger and variation in energy intake rate might be important factors, and these can both vary independently among potential foraging patches. When patches differ in predation danger, the combined vigilance effort of the group should vary. Independent of this, the intake rate that can be achieved at a patch may also affect the relationship between group size and vigilance; for example, a high rate of food acquisition might free time for vigilance. Thus, between-patch variation in predation danger and intake rate may both affect the relationship between group size and vigilance.

One system in which predation risk and energy intake rate both vary among foraging patches is shorebirds foraging on intertidal and supratidal coastal habitats. The main risk of predation for coastal shorebirds is surprise attacks by raptors launched from terrestrial areas of cover (Cresswell 1996). Because supratidal habitats are closer to suitable areas of raptor cover than intertidal habitats, risk of predation is higher for supratidal foragers (Whitfield 1985a,b, Whitfield 1988). Predation rates of Common Redshanks *Tringa totanus* were 21 times higher on saltmarsh, a habitat that is close to predator-concealing cover, than on mudflats (Yasué *et al.* 2003). Nearshore-feeding Red Knots *Calidris canutus* at the Banc d'Arguin in Mauritania are disproportionately juveniles, and suffer much higher rates of predator attack than adults (van den Hout *et al.* 2008).

Ruddy Turnstones *Arenaria interpres* form large foraging flocks on supratidal deposits of beach-cast macroalgae and strandline debris over the high water period (Baker 1981). It has been suggested that foragers take on the extra risk of foraging supratidally because prey in those habitats have a high calorific value (Marshall 1981, Whitfield 1985a,b, Cresswell & Whitfield 2008). However, the relative energetic value of supratidal and intertidal habitat types is unknown. Because supratidal foragers form large flocks, the group size effect predicts that individual vigilance rates will be lower in birds feeding supratidally, whereas the increased predation risk associated with foraging above the high water mark implies that such foragers should be more vigilant. If foraging Ruddy Turnstones can simultaneously

account for group size and habitat effects when assessing their vigilance contribution, we might expect negative relationships between group size and vigilance within the two habitat types but the level of vigilance for any given group size to be higher in supratidal habitats.

We measure the energetic value of prey items on intertidal and supratidal habitats, and assess whether foraging habitat type explains additional variation in vigilance levels beyond the group size effect by comparing vigilance levels of foragers in the two habitats, while simultaneously accounting for the effects of group size and a range of other plausible predictors of vigilance.

METHODS

Study area and habitats

The study was conducted along a broadly linear 40-km stretch of coastline in northeast England between Warkworth Harbour (55°20'25"N, 1°35'33"W) in the north and St. Mary's Island (55°4'37"N, 1°27'8"W) in the south. The area comprises a mix of sandy beaches and rocky shore backing onto dunes or low cliffs typically about 4 m in height. Rocky intertidal habitats extended up to 1.5 km from the high water mark at low tide, typically in the form of long rocky outcrops running perpendicular to the coast. Rocky intertidal habitat was dominated by two substrates: *Fucus*-covered rock (i.e. with a complete overgrowth of macroalgae *Fucus* spp.), and barnacle-covered rock (with a near-complete cover of barnacles; Crustacea: Cirripedia). The two main supratidal foraging substrates were loose aggregations of debris along the high water mark, and more discrete and dense aggregations of beach-cast macroalgae (wrack), thrown up above the high water mark close to the base of the cliff or dune backing the beach. Thus, there were two substrate types within each habitat.

Energetic content of prey species

We ran one transect in each intertidal substrate for 300 m upshore from the low tide mark during a spring tide series in early March 2003. In the case of *Fucus*-covered rock, we arbitrarily selected 30 locations along the transect, and removed all animals in a 10 × 10 cm quadrat at each location. Any mobile animals escaping before they could be

removed were counted. In the case of barnacle-covered rock, we randomly selected 10 locations along the transect. In a 10 × 10 cm quadrat at each location we counted the number of live barnacles and invertebrates colonizing empty barnacle cases (e.g. gastropod molluscs or small mussels *Mytilus edulis*), and then scraped all live barnacles off the substrate into a sealed container.

To sample potential prey in supratidal habitats, 66 1-L samples were taken from three typical deposits of beach-cast macroalgae in November 2001 and January 2002. Field observations indicated that 10 cm was the maximum depth reached by foraging birds, although such depths were rarely achieved. Actual prey availability will vary according to factors such as season, the precise characteristics of the deposit itself, such as stage of decomposition, degree of wave action, or stage in the tidal cycle. Although the timing of the sampling supratidal habitats differed from intertidal habitats, and is thus potentially affected by seasonal variation in prey densities (Whitfield 1985b), the aim of the supratidal sampling was to measure food densities within individual deposits of beach-cast macroalgae, rather than measure total food availability along the coast. The number of each identified invertebrate taxon in each sample was recorded, together with life stage (larva, pupa, adult) in the case of wrack flies *Coelopa* (Diptera: Coelopidae). Strand-line invertebrates were sampled in a similar way using 20 1-L samples of strand material, including the sandy substrate underneath where the strand material was <10 cm in depth. Half the samples were taken from loose, dry strandline debris and the other half from strandline comprising previously beach-cast material in the process of resuspension, reflecting the two major types of strandline habitat used by Ruddy Turnstones in the study area.

Samples were washed through a 1-mm sieve and all macroinvertebrates were extracted and killed by rapid freezing and stored in a dry sealed container. They were then divided into single species samples, freeze-dried to constant weight, homogenized with a grinding mill, and combusted in a Gallenkamp bomb calorimeter. After combustion, remaining ash was weighed to provide a measure of indigestible content. The proportion of organic material was calculated as $1 - aw/dw$ (where aw = ash weight and dw = dry weight), and water content as $1 - dw/ww$ (where ww = wet weight).

Energy requirements of foraging Ruddy Turnstones

The regression equation in Kersten and Piersma (1987) predicts an existence metabolism of 250 kJ per day for Ruddy Turnstones experiencing an average daily temperature of 6.6 °C as in this study. Existence metabolism is the energy required by a non-breeding bird for survival under normal free-living conditions but excluding behaviours such as flying or preening (Kendeigh 1970). Net energy intake (NEI) will be substantially higher than this figure, and a value of 300 kJ per day is probably more representative of the NEI of free-living Ruddy Turnstones, given that Common Ringed Plovers *Charadrius hiaticula* (a slightly smaller bird) in northeast England used 159–192 kJ per day and Grey Plovers *Pluvialis squatarola* (slightly larger bird) 309–392 kJ per day (Pienkowski 1982). Assuming an assimilation efficiency of 85% (Evans *et al.* 1979), we estimated that the gross daily energy requirement of foraging Ruddy Turnstones in our study area would be about 350 kJ, corresponding well with a field metabolic rate of 348.1 kJ per day for incubating Ruddy Turnstones (Piersma & Morrison 1994, Morrison *et al.* 1997, Piersma *et al.* 2003). Incubating Red Knots show similar energetic requirements to birds wintering at temperate latitudes (Piersma 2002).

Ruddy Turnstone foraging measures

We watched foraging Ruddy Turnstones across the full range of tidal states on intertidal and supratidal habitats to measure vigilance rate, group size and a number of potential confounding variables that might also contribute to vigilance rate. A flock was defined as a group of birds all within 10 m of each other. The area occupied by each flock was estimated with reference to known distances measured between various physical features in the environment to allow calculation of flock density. Data were discarded if any observer-related disturbance was apparent.

A focal bird was selected arbitrarily from a flock. Habitat, time of year (days since 1 November), time of day (proportion of the daylight period for that day that had elapsed), temperature, time to the nearest high tide and flock size were recorded before beginning observations. Each focal bird was observed for 30 s and the following

measures of foraging behaviour were collected: number of pecks, number of swallows, number of head-ups and number of aggressive encounters. A peck was an attempt by the bird to capture a single prey item, as distinct from a bill movement to bulldoze seaweed, turn stones or clear away debris. Where it could not be ascertained whether a food item had been ingested, the number of swallows was not recorded for that particular bird. Head-ups were recorded to provide a measure of vigilance for predators or competitors as distinct from visual searching for foraging areas or food items. Head-ups were defined as postures in which the bird's head was raised accompanied by a marked interruption of the search path of the bird, tilting of the head and/or pronounced scanning eye movements. In contrast, postures in which the bird's head was raised accompanied by limited interruption of the forager's walking rhythm, the head remaining in a vertical orientation, and limited scanning eye movements were interpreted as foraging behaviour. The distinction was usually easy to make in the field. In ambiguous cases or cases where the bird went out of view, data for that observation period were discarded. After each 30-s observation period, a new focal bird was chosen and the process repeated, the flock measurements being updated as necessary. The number of birds observed per flock varied among flocks and was not contingent on flock size. Flocks were dynamic over time, such that the values of key predictor variables could change as we were watching a flock. To account statistically for this dynamism, a new flock identity was assigned if any of the flock variables changed (i.e. habitat, flock density or flock size). However, because this approach treats major differences in group context (e.g. changing habitat type) in the same way as minor changes in group composition (birds leaving or joining the flock), we also ran the analysis assigning flock identity only when group composition and not foraging context changed.

Analyses

For initial analyses exploring differences among habitats in energetic and behavioural variables, we used a standard hypothesis-testing approach. To examine predictors of vigilance levels (the number of head-ups per 30 s, log-normalized), we constructed mixed effects models using the `lme4` package in R (R Development Core Team. 2009,

Bates & Maechler 2010), taking an information-theoretic approach to model selection (Johnson & Omland 2004, Whittingham *et al.* 2006). We used the 10 predictor variables described above: flock size, habitat type, flock density, time of day, time of year, number of pecks, number of swallows, number of aggressive encounters, temperature and time since high tide (see Supporting Information Table S1 for a correlation matrix among the continuous variables). All variables, including the response variable, were either already approximately normally distributed, or transformed to fit a normal distribution. Because all predictor variables have been shown individually to affect vigilance in previous studies, we had no *a priori* reason to select some combinations of predictors over others, so we constructed 1023 models based on all possible combinations of predictors as main effects, and ranked them according to Akaike's information criterion (AIC; Bolker *et al.* 2009). We did not consider interaction terms between predictors because (1) we simultaneously accounted for a range of predictors of vigilance, (2) there is a very large number of potential interactions in an analysis of this size, complicating interpretation, and (3) it is not obvious *a priori* which interactions are biologically relevant. However, because of its potential importance, we tested for the presence of an interaction between habitat and flock size using exploratory linear models.

For each model included in the model selection analysis, we calculated the Akaike weight, as a measure of the probability that it provides the most parsimonious fit to the data of the models considered. Each predictor variable appeared in the same number of models, and to estimate the relative importance of each predictor, we calculated the summed Akaike weights of all models in which the predictor was present (Burnham & Anderson 2002). We took this approach rather than model averaging or choosing the single most parsimonious model because we were primarily interested in qualitative understanding rather than quantitative prediction (Bolker *et al.* 2009). Summed Akaike weights were standardized between 0 and 1, with higher values indicating that the variable consistently appeared in the most parsimonious models (i.e. those with the lowest AIC). In particular, we wanted to assess whether habitat was a consistent predictor of vigilance levels in the

presence of various combinations of the potential confounding variables.

RESULTS

Energetics of alternative foraging habitats

The density of potential invertebrate prey species was similar on intertidal and supratidal habitats ($t = 0.69$, $df = 108.5$, $P = 0.422$). Supratidal habitats contained only amphipods and coelopids, the latter reaching high densities in wrack (Table 1). With the exception of barnacles, which reached a maximum density of 400 individuals/dm², all potential prey items in intertidal habitats occurred at < five individuals/dm² (Table 1). Invertebrate density was only very weakly related to distance upshore from the low tide mark ($r = -0.28$, $n = 30$ quadrats, $P = 0.128$).

Energy value and organic content varied markedly among prey types (Table 1). Coelopid larvae had by far the highest energy content (0.147 kJ per individual), and also a very low ash content (9%). All other prey types had much lower values for energy content (0.044–0.072 kJ per individual). The three shelled prey types (littorinids, *Mytilus* and barnacles) contained a very high proportion of ash (63–87%) and a low proportion of water (33–54%). The relatively low energy value per individual amphipod was due to their small size, since their energy value per gram of dry weight was relatively high (15.15 kJ/g). The mean value of potential prey items was much higher in supratidal than intertidal samples (Fig. 1a, $t = 14.67$, $df = 118$, $P < 0.001$), variation in prey

energy value between habitats being driven by the differing proportions of energy-rich coelopid flies.

Peck rate and head-up data were collected for 764 focal birds in 44 flocks, and accurate observation of number of swallows was achieved for 336 focal birds in 18 flocks. Peck rate did not differ between habitats ($t = 1.01$, $df = 762$, $P = 0.314$) but birds foraging supratidally swallowed food items at a slower rate than birds foraging intertidally (Fig. 1b; $t = 4.54$, $P < 0.001$). However, this effect was not strong enough to offset the difference in net energy intake rate, which was higher on supratidal than intertidal habitats (Fig. 1c; $t = 5.33$, $P < 0.001$). This translated into foragers requiring about 4.4 h to fulfil their daily energy requirement on supratidal habitats, but about 6.7 h on intertidal habitats (Fig. 1d), if foragers always selected the foraging substrate yielding the greater energy intake rate in both intertidal and supratidal habitats. In contrast, and regardless of selectivity, a forager would only have to spend 46% of the daylight period feeding on beach-cast macroalgae to achieve daily energy balance. These results suggest a considerable energetic advantage to feeding in supratidal habitat.

Group size and context effects on vigilance rate

Flocks foraging supratidally were much closer to cover for predators than those foraging intertidally (Fig. 2a; mean supratidal distance = 10.4 m, intertidal = 175 m; $t = 34.7$, $P < 0.001$), and supratidal flocks were larger and denser than those on intertidal habitats (mean supratidal flock size = 18.9, intertidal = 7.2; $t = 3.1$, $df = 36$, $P = 0.004$;

Table 1. Prey densities per prey group, and energy values of prey items in the four substrate types. Densities are individuals per dm² sample.

| | Prey densities | | | | Energy content | | | | |
|----------------|-------------------------|------------------|-------------------|------------------|----------------|-------|----------|-----------|-------------|
| | Intertidal | | Supratidal | | n_1 | % ash | kJ/g dry | kJ/g AFDM | kJ per item |
| | <i>Fucus</i> $n_2 = 30$ | Rocks $n_2 = 10$ | Strand $n_2 = 20$ | Wrack $n_2 = 66$ | | | | | |
| Amphipods | 4.2 | 0 | 5.5 | 0.05 | 2 | 24 | 15.15 | 19.94 | 0.044 |
| Littorinids | 2.2 | 4.4 | 0 | 0 | 1 | 63 | 6.35 | 17.15 | 0.072 |
| <i>Mytilus</i> | 1 | 3.9 | 0 | 0 | 1 | 72 | 4.97 | 17.75 | 0.051 |
| Barnacles | 41.3 | 265 | 0 | 0 | 6 | 87 | 3.64 | 15.82 | 0.054 |
| Coelopids | 0 | 0 | 14.9 | 442 | 5 | 9 | 29.48 | 32.39 | 0.147 |

n_1 : number of combustions; n_2 : number of dm² samples.

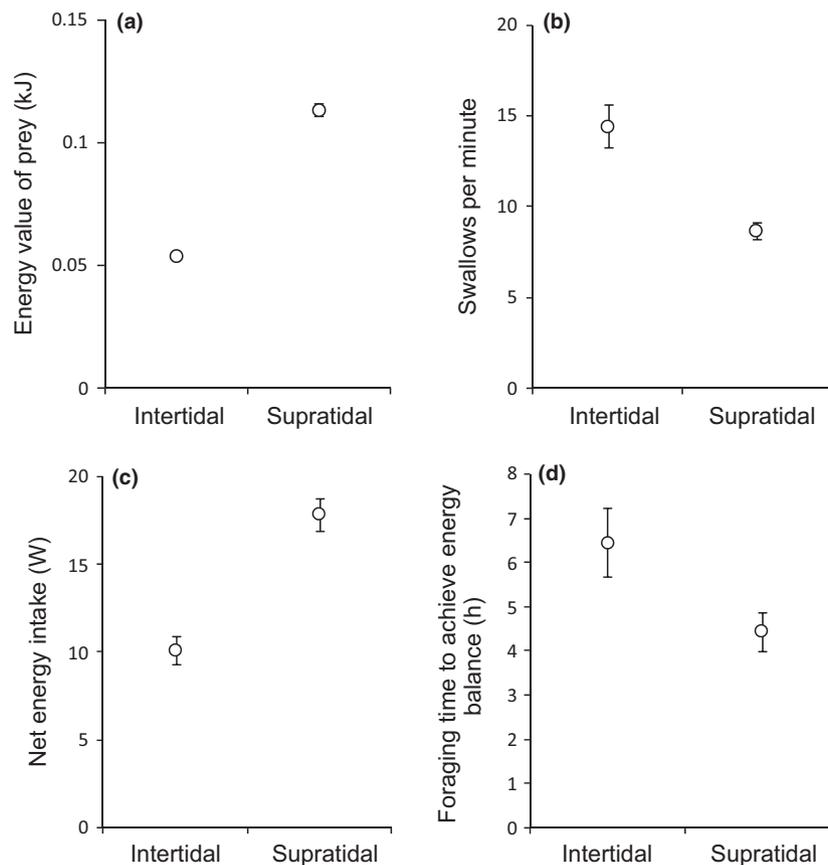


Figure 1. (a–d) Prey energy values and foraging measures of Ruddy Turnstones foraging in intertidal and supratidal habitats. Error bars indicate ± 1 se, too small to be seen in (a).

Fig. 2b, mean supratidal flock density = 0.46 birds per m^2 , intertidal = 0.1; $t = 6.27$, $df = 36$, $P < 0.001$; Fig. 2c). Supratidal foragers were involved in more aggressive encounters than intertidal foragers (Fig. 2d; $t = 8.0$, $df = 762$, $P < 0.001$), and performed more head-ups (Fig. 2e; $t = 3.97$, $df = 762$, $P < 0.001$).

Despite considerable statistical power, there was no correlation between the rate of aggressive encounters and vigilance rate in supratidal foragers ($r_s = -0.008$, $n = 438$, $P = 0.875$). Thus, it seems likely that the head-up posture is associated with vigilance for predators rather than purely for tracking competitors. Vigilance rate declined with increasing flock size on both intertidal and supratidal habitats. Indicative OLS regression plots show these negative relationships to share a similar slope but to differ greatly in intercept (Fig. 3), suggesting a context effect as well as a group size effect on vigilance. To test formally for a difference in slope, we constructed a linear model containing

habitat, flock size and their interaction. The interaction term was marginally significant ($F_{1,760} = 3.50$, $P = 0.062$), suggesting a weak tendency for the effect of habitat on vigilance to increase with flock size. We chose not to include this interaction term in further modelling, but we discuss further the implications of this possible interaction below.

Of the 10 predictor variables entered into the information-theoretic modelling of vigilance rate, four showed a high probability of inclusion in the best approximating model, as measured by ΣW_i , the summed Akaike weights of the models in which the variable appears: number of swallows ($\Sigma W_i = 1$), habitat ($\Sigma W_i = 0.975$), flock size ($\Sigma W_i = 0.943$) and time of day ($\Sigma W_i = 0.901$). Flock density was intermediate ($\Sigma W_i = 0.361$) and the remaining five variables were of very low importance: number of aggressive encounters ($\Sigma W_i = 0.037$), temperature ($\Sigma W_i = 0.012$), number

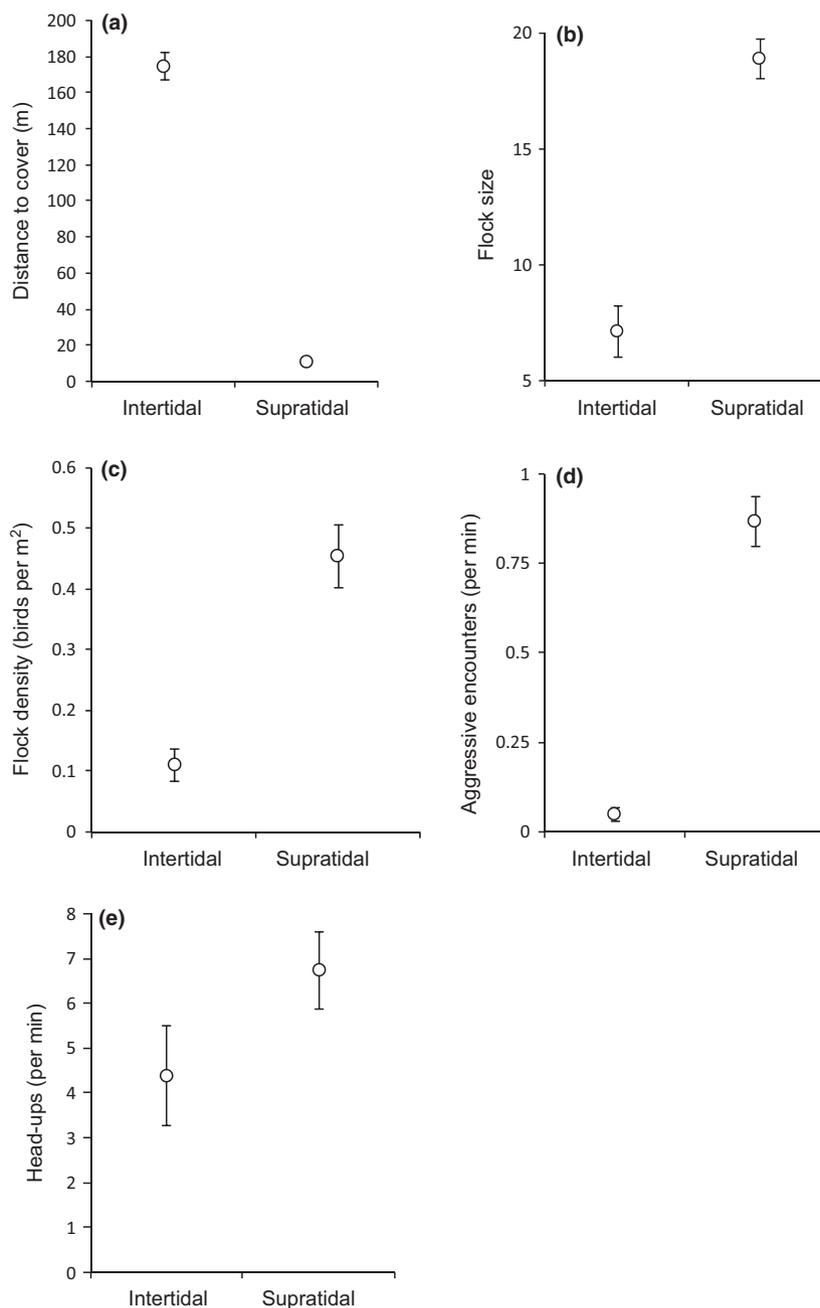


Figure 2. (a–d) Flock attributes and behaviour of Ruddy Turnstones foraging in intertidal and supratidal habitats. Error bars indicate ± 1 se.

of pecks ($\Sigma W_i = 0.005$), time of year ($\Sigma W_i = 0.002$) and time since high tide ($\Sigma W_i = 0.001$).

The most parsimonious model of vigilance rate ($W_i = 0.507$) included three predictors: flock size, habitat and time of day, and the next most parsimonious model also contained number of swallows and flock density. The combined Akaike weight of

these two models was 0.8 (see Supporting Information Table S2 for a full list of the models), and the 95% model set contained only nine models (Table 2). These models generally explained a high proportion (> 60%) of the deviance of the null model. Vigilance rate was related negatively to flock size, and positively to number of swallows

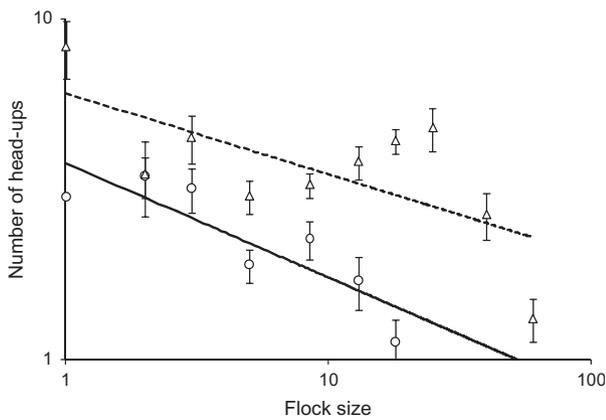


Figure 3. (a–d) Relationship between individual vigilance rate and flock size for foraging Ruddy Turnstones on intertidal (circles) and supratidal (triangles) habitats. OLS regression lines are shown separately for each habitat (solid line, intertidal habitats: $r^2 = 0.76$, broken line, supratidal habitats: $r^2 = 0.45$). Error bars indicate ± 1 se. Both axes are plotted on a log scale, and for display purposes data are grouped into flock sizes of 1 ($n = 9$), 2 ($n = 30$), 3 ($n = 59$), 4–6 ($n = 136$), 7–10 ($n = 163$), 11–15 ($n = 92$), 16–20 ($n = 120$), 21–30 ($n = 23$), 31–50 ($n = 30$), 51–72 ($n = 68$).

in most of the models in the 95% set, and vigilance was higher among foragers in supratidal habitats for all but one of the models in the 95% set (Table 2). The model from which habitat was absent had an Akaike weight of only 0.016. Habitat had a strong independent effect, as evidenced by its partial D^2 values of *c.* 11–22% (Table 2); there was always a significant increase in deviance if habitat was removed from each model in the 95% set (chi-squared tests of change in deviance: all $P < 0.001$).

The results of models re-run assigning flock ID only when group composition and not foraging context changed were qualitatively similar. Habitat remained a significant, albeit slightly weaker, predictor of vigilance rate, appearing in the top four most parsimonious models and eight of the 13 models comprising the 95% set (Table S3). Taken together, these results indicate that, superimposed on the negative relationship between vigilance rate and group size, there is a context effect, whereby foragers were more vigilant on supratidal habitats. This result is robust to different approaches to assigning flock ID.

Our analysis included various components of a time budget in both the predictor variables and the response variable, so there is potential for non-independence. However, because we use counts of

Table 2. Mixed models of vigilance rate in foraging Ruddy Turnstones. The table shows parameter estimates for each predictor appearing in the nine models (of 1023 constructed) comprising the 95% set (i.e. cumulative Akaike weight > 0.95), ranked according to their AIC value. Standard errors of parameter estimates are included in parentheses. The reference habitat is supratidal, such that negative parameter estimates for habitat indicate lower vigilance rates in intertidal habitats. The model weight indicates the probability that the model provides the most parsimonious fit to the data out of all possible models (of those constructed). Three predictors (Flock size, Number of swallows and Habitat) appear in all nine of the most parsimonious models. Explanatory power (D^2) is indicated by the percentage of the null model deviance explained by the focal model, and a partial D^2 is also presented indicating the percentage of the deviance of the model with the habitat term removed explained by the focal model.

| Parameter estimates | | | | | | | | | | | | | |
|---------------------|----------------|---------------------------------|-----------------|--------------------|----------------|-------------|----------------|--------------|-------------------|---------------|---------------|---------------|------|
| Flock density | Flock size | Number of aggressive encounters | Number of pecks | Number of swallows | Habitat | Temperature | Time of day | Time of year | Time to high tide | Akaike weight | Partial D^2 | Partial D^2 | |
| – | –0.285 (0.082) | – | – | – | –0.377 (0.075) | – | –0.001 (0.004) | – | – | 116.4 | 0.507 | 67.3 | 22.1 |
| 0.241 (0.134) | –0.385 (0.097) | – | – | 0.001 (0.005) | –0.296 (0.086) | – | 0.439 (0.138) | – | – | 117.5 | 0.294 | 68.7 | 13.5 |
| – | –0.238 (0.085) | – | – | 0.001 (0.005) | –0.319 (0.077) | – | – | – | – | 121.1 | 0.047 | 63.5 | 15.4 |
| – | – | – | – | 0.003 (0.004) | –0.331 (0.081) | – | – | – | – | 122 | 0.03 | 62.6 | 14.8 |
| – | –0.28 (0.083) | –0.024 (0.036) | – | 0.001 (0.005) | –0.386 (0.076) | – | – | – | – | 122.9 | 0.02 | 67.5 | 22.5 |
| 0.217 (0.142) | –0.326 (0.102) | – | – | 0.001 (0.005) | –0.244 (0.09) | – | – | – | – | 123 | 0.019 | 64.5 | 12.7 |
| – | – | – | – | 0.003 (0.005) | –0.29 (0.081) | – | – | – | – | 123.2 | 0.017 | 60.3 | 11.3 |
| 0.478 (0.124) | –0.435 (0.104) | – | – | 0.001 (0.005) | – | – | 0.348 (0.144) | – | – | 123.4 | 0.015 | 63.8 | – |
| 0.24 (0.135) | –0.379 (0.098) | –0.022 (0.036) | – | 0.001 (0.004) | –0.304 (0.087) | – | 0.445 (0.139) | – | – | 124.1 | 0.011 | 68.9 | 13.8 |

behavioural events rather than time allocations, the data are not strictly compositional, and so they are not constrained to sum to 1, as would be the case if the variables were measured per unit time. For example, there was no significant correlation between vigilance and aggressive encounters ($r = 0.04$, $n = 764$, $P = 0.33$), number of pecks ($r = 0.03$, $n = 764$, $P = 0.45$) or number of swallows ($r = -0.09$, $n = 764$, $P = 0.1$).

DISCUSSION

In common with many studies (see reviews in Elgar 1989, Lima & Dill 1990, Roberts 1995), we found a negative effect of group size on vigilance, but habitat type explained additional variation in vigilance levels after accounting for this group size effect. Vigilance was higher in supratidal habitats than intertidal habitats, consistent with the hypothesis that foraging context moderates the effect of group size on vigilance. At least in this system, foragers seemed able to assess habitat-specific predation danger and group size information when making decisions about their vigilance contribution. Although vigilance is affected by several parameters (Elgar 1989, Li *et al.* 2009), a meta-analysis has revealed a high proportion of unexplained variation in avian vigilance rates (Beauchamp 2008). This highlights the importance of determining the impact on vigilance of a range of candidate driving variables simultaneously, as we do in this study. The effect of habitat on vigilance showed a tendency to increase with group size and, although the effect was not significant, this hints that the size of the context effect might itself vary with group size.

Although variation in predation risk is a likely explanation for the habitat-specific variation in vigilance that we report here (see also Metcalfe 1984, Whittingham *et al.* 2004, Butler *et al.* 2005a,b), there are other possibilities. Indeed, the group size effects we uncovered were noisy, particularly in supratidal habitats, and it is possible the relationships are not linear (Fig. 3). First, vigilance usually declines as flock density increases (Fernández-Juricic *et al.* 2007) but we found the opposite effect, suggesting a possible role for competition. Indeed, vigilance in Common Starlings *Sturnus vulgaris* is associated with gathering social information from conspecifics (Fernández-Juricic *et al.* 2005), and the very high supratidal densities of foragers that we document here could lead to competition-

mediated effects on vigilance. However, the number of aggressive encounters was not a strong predictor of vigilance in our study, and experimental evidence suggests that effects of forager density on vigilance are limited in Ruddy Turnstones (Vahl *et al.* 2005). If social vigilance were playing an important confounding role, we would not expect to find a strong negative effect of group size on vigilance (Favreau *et al.* 2010).

Secondly, prey types differed between intertidal and supratidal habitats, which could potentially lead to differences in vigilance if certain foraging techniques reduced the ability of foragers to maintain some level of baseline vigilance whilst feeding (e.g. Pays *et al.* 2012). This seems unlikely in this case, given that mobile and sessile prey were available in both habitat types (Table 1), leading to no obvious predictions for an effect on vigilance.

Thirdly, increased food density in supratidal habitats might reduce hunger and the motivation to feed, freeing more time for vigilance (Beauchamp 2009). However, given the risk of foraging supratidally, and the fact that most birds transfer to roost sites over the high water period (Eaton 2001), we would expect foragers to feed supratidally only when energetically necessary. Indeed, we found a positive relationship between time of day and vigilance (Table 2), indicating that foragers were becoming more vigilant as the day progressed. One might expect time-stressed foragers to invest less in vigilance when foraging in richer food patches (McNamara & Houston 1986, Swennen *et al.* 1989) but perhaps because the difference in predation risk and food density vary in the same direction in this instance, we do not see the expected vigilance adjustment. This could also explain the positive relationship between number of swallows and vigilance, in that birds are taking on additional predation risk when foraging in more profitable sites. It is also worth noting that direct comparisons of prey abundance between intertidal and supratidal habitats are inherently difficult because prey in the former occur over a hard substrate and prey in the latter are uncovered by excavation to a potentially variable depth.

Lastly, the relationship between individual vigilance and group size has been shown also to depend on foraging techniques and foraging strategy (Beauchamp 2001, Barbosa 2002), and as Ruddy Turnstones show clear individual foraging strategies in response to both phenotype and

environment (Whitfield 1990), it would be worthwhile looking for such effects in this species.

Intertidal habitats contained relatively few different potential prey types, and those that were present tended to have low energetic value per individual. The results of the energetic analyses indicate that on intertidal habitats amphipods were the most calorific prey item, although it is possible that our values for ash content of barnacles are overestimates, given that not all of the outer plates are typically ingested by a foraging bird (Groves 1978). Supratidal habitats also contained relatively few different potential prey types, but they had far higher energy value and lower ash content per individual than prey on intertidal habitats. Coeloped flies had a high energy and water content, and also contained very little indigestible material. This suggests that both energy intake and digestive efficiency would be higher for birds foraging supratidally than for birds foraging intertidally. Further investigation of prey handling times, mechanical breakdown and digestibilities of alternative prey items is required to complete this picture, but this study has at least demonstrated a large differential in potential energy intake rates between intertidal and supratidal foraging habitats.

The difference in energy intake rate among the alternative foraging substrates led to a substantial inequality in the time required for a forager to achieve daily energy balance. This was approximately 4.4 h in supratidal habitats and 6.7 h in intertidal habitats. We did not take account of additional costs and further reductions in digestive and assimilation efficiency caused by the high ash content of many intertidal invertebrates but these values fit well with existing information on the length of time that Ruddy Turnstones spend feeding in a day in this study area (Eaton 2001).

Foragers in risky situations show greater vigilance than predicted by the flock size effect alone (Mathot *et al.* 2009). For example, the vigilance of Common Starlings foraging declines more slowly with increasing flock size on the periphery of a flock than at its centre (Jennings & Evans 1980). Further investigation of spatial variation of the group size effect across individuals constituting a flock could therefore prove fruitful. For example, Semipalmated Sandpipers *Calidris pusilla* foraging on the riskier side of a group showed increased vigilance and lower peck rates, suggesting that collective detection of predator attack is unlikely to be the sole mechanism driving the group size

effect (Beauchamp & Ruxton 2008, Folmer *et al.* 2012). In a similar vein, it would be worth investigating the impact of distance to cover upon the group size effect within each of the habitat types we consider here.

A further logical extension to our study would be to consider differences in risk management between the different high water feeding strategies. Lima and Bednekoff (1999) predict that where high-risk situations are rare, foragers should show the greatest anti-predation behaviour in those high risk situations, and that the strength of this anti-predation response must necessarily decline as they become commoner. Our study system presents an ideal opportunity to test this hypothesis empirically. The model of Lima and Bednekoff (1999) predicts that average vigilance in supratidal habitat should decline as the propensity of an individual to feed supratidally increases, because it is exposed to higher predation risk more frequently.

In this study, habitats differed markedly in both energy intake rate and proximity to predation risk, and these parameters may vary more subtly but still influentially in other study systems. Field studies of relationships between group size and vigilance behaviour should therefore attempt to identify and control for variation in both energy intake rate and predation risk among alternative foraging areas.

This work was funded through the Environment Programme of Northumbrian Water plc through a grant to Peter R. Evans. We thank Wouter Vahl for helpful insight, and for reviewing previous versions of this manuscript. Phil Whitfield and Will Cresswell also provided helpful comments on a previous version of this manuscript. Thanks also to Robin Ward, Michael Bone, Mark Eaton, Claire Fuller and Alexandra Lognonné for assistance during data collection and to Steve Oswald, Jon Bennie and Steve Willis for helpful discussions. Peter Evans sadly died during the early stages of this project, and we dedicate this study to his memory.

REFERENCES

- Baker, J.M.** 1981. Winter feeding rates of Redshank *Tringa totanus* and Turnstone *Arenaria interpres* on a rocky shore. *Ibis* **123**: 85–87.
- Barbosa, A.** 2002. Does vigilance always covary negatively with group size? Effects of foraging strategy. *Acta Ethol.* **5**: 51–55.
- Bates, D. & Maechler, M.** 2010. *lme4: Linear Mixed-Effects Models using Eigen and S4 Classes*. R package version 0.999375-35.
- Beauchamp, G.** 2001. Should vigilance always decrease with group size? *Behav. Ecol. Sociobiol.* **51**: 47–52.

- Beauchamp, G.** 2008. What is the magnitude of the group-size effect on vigilance? *Behav. Ecol.* **19**: 1361–1368.
- Beauchamp, G.** 2009. How does food density influence vigilance in birds and mammals? *Anim. Behav.* **78**: 223–231.
- Beauchamp, G. & Ruxton, G.D.** 2008. Disentangling risk dilution and collective detection in the antipredator vigilance of semipalmated sandpipers in flocks. *Anim. Behav.* **75**: 1837–1842.
- Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. & White, J.-S.S.** 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.* **24**: 127–135.
- Burnham, K.P. & Anderson, D.R.** 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd edn. New York: Springer-Verlag.
- Butler, S.J., Bradbury, R.B. & Whittingham, M.J.** 2005a. Stubble height affects the use of stubble fields by farmland birds. *J. Appl. Ecol.* **42**: 469–476.
- Butler, S.J., Whittingham, M.J., Quinn, J.L. & Cresswell, W.** 2005b. Quantifying the interaction between food density and habitat structure in determining patch selection. *Anim. Behav.* **69**: 337–343.
- Catterall, C.P., Elgar, M.A. & Kikkawa, J.** 1992. Vigilance does not covary with group size in an island population of Silvereyes (*Zosterops lateralis*). *Behav. Ecol.* **3**: 207–210.
- Cresswell, W.** 1996. Surprise as a winter hunting strategy in Sparrowhawks *Accipiter nisus*, Peregrines *Falco peregrinus* and Merlins *F. columbarius*. *Ibis* **138**: 684–692.
- Cresswell, W. & Whitfield, D.P.** 2008. How starvation risk in Redshanks *Tringa totanus* results in predation mortality from Sparrowhawks *Accipiter nisus*. *Ibis* **150**(Suppl. 1): 209–218.
- Eaton, M.A.** 2001. *Determinants of Habitat and Site Use by Turnstones and Purple Sandpipers in N.E. England, and Possible Effects of the Removal of Coastal Nutrients*. PhD Thesis, University of Durham.
- Elgar, M.A.** 1989. Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biol. Rev.* **64**: 13–33.
- Evans, P.R., Herdson, D.M., Knights, P.J. & Pienkowski, M. W.** 1979. Short-term effects of reclamation of part of Seal Sands, Teesmouth, on wintering waders and Shelduck. *Oecologia* **41**: 183–206.
- Favreau, F.-R., Goldizen, A.W. & Pays, O.** 2010. Interactions among social monitoring, anti-predator vigilance and group size in eastern grey kangaroos. *Proc. R. Soc. Lond. B* **277**: 2089–2095.
- Fernández-Juricic, E., Smith, R. & Kacelnik, A.** 2005. Increasing the costs of conspecific scanning in socially foraging starlings affects vigilance and foraging behaviour. *Anim. Behav.* **69**: 73–81.
- Fernández-Juricic, E., Beauchamp, G. & Bastain, B.** 2007. Group-size and distance-to-neighbour effects on feeding and vigilance in brown-headed cowbirds. *Anim. Behav.* **73**: 771–778.
- Folmer, E.O., Olf, H. & Piersma, T.** 2012. The spatial distribution of flocking foragers: disentangling the effects of food availability, interference and conspecific attraction by means of spatial autoregressive modelling. *Oikos* **121**: 551–561.
- Foster, W.A. & Treherne, J.E.** 1981. Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature* **295**: 466–467.
- Groves, S.** 1978. Age-related differences in ruddy turnstone foraging and aggressive behavior. *Auk* **95**: 95–103.
- Hager, M.C. & Helfman, G.S.** 1991. Safety in numbers: shoal size and choice by minnows under predatory threat. *Behav. Ecol. Sociobiol.* **29**: 271–276.
- van den Hout, P.J., Spaans, B. & Piersma, T.** 2008. Differential mortality of wintering shorebirds on the Banc d'Arguin, Mauritania, due to predation by large falcons. *Ibis* **150**(Suppl. 1): 219–230.
- Humphries, D.A. & Driver, P.M.** 1967. Erratic display as a device against predators. *Science* **156**: 1767–1768.
- Jennings, T. & Evans, S.M.** 1980. Influence of position in the flock and flock size on vigilance in the starling, *Sturnus vulgaris*. *Anim. Behav.* **28**: 634–635.
- Johnson, J.B. & Omland, K.S.** 2004. Model selection in ecology and evolution. *Trends Ecol. Evol.* **19**: 101–108.
- Jones, M.** 1998. The function of vigilance in sympatric marsupial carnivores: the eastern quoll and the Tasmanian devil. *Anim. Behav.* **56**: 1279–1284.
- Kendeigh, S.C.** 1970. Energy requirements for existence in relation to size of bird. *Condor* **72**: 60–65.
- Kersten, M. & Piersma, T.** 1987. High levels of energy expenditure in shorebirds: metabolic adaptations to an energetically expensive way of life. *Ardea* **75**: 175–187.
- Krause, J. & Ruxton, G.D.** 2002. *Living in Groups*. Oxford: Oxford University Press.
- Li, Z., Jiang, Z. & Beauchamp, G.** 2009. Vigilance in Przewalski's gazelle: effects of sex, predation risk and group size. *J. Zool.* **277**: 302–308.
- Lima, S.L. & Bednekoff, P.A.** 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *Am. Nat.* **153**: 649–659.
- Lima, S.L. & Dill, L.M.** 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* **68**: 619–640.
- Marshall, W.** 1981. *The feeding behaviour and ecology of the Turnstone *Arenaria interpres* on a rocky shore and in captivity*. PhD Thesis, University of Edinburgh.
- Mathot, K.J., van den Hout, P.J. & Piersma, T.** 2009. Differential responses of red knots, *Calidris canutus*, to perching and flying Sparrowhawk, *Accipiter nisus*, models. *Anim. Behav.* **77**: 1179–1185.
- McNamara, J.M. & Houston, A.I.** 1986. The common currency for behavioral decisions. *Am. Nat.* **127**: 358–378.
- Metcalf, N.B.** 1984. The effects of habitat on the vigilance of shorebirds: is visibility important? *Anim. Behav.* **32**: 981–985.
- Milinski, M.** 1979. Can an experienced predator overcome the confusion of swarming prey more easily? *Anim. Behav.* **27**: 1122–1126.
- Morrison, R.I.G., Davidson, N.C. & Piersma, T.** 1997. Daily energy expenditure and water turnover of shorebirds at Alert, Ellesmere Island, N.W.T. *Can. Wildl. Service Prog. Notes* **211**: 1–8.
- Pays, O., Blanchard, P., Valeix, M., Chamaillé-Jammes, S., Duncan, P., Périquet, S., Lombard, M., Ncube, G., Tarakini, T., Makuwe, E. & Fritz, H.** 2012. Detecting predators and locating competitors while foraging: an experimental study of a medium-sized herbivore in an African savanna. *Oecologia* **169**: 419–430.
- Pienkowski, M.W.** 1982. Diet and energy intake of grey and ringed plovers, *Pluvialis squatarola* and *Charadrius hiaticula*, in the non-breeding season. *J. Zool.* **197**: 511–549.
- Piersma, T.** 2002. Energetic bottlenecks and other design constraints in avian annual cycles. *Integr. Comp. Biol.* **42**: 51–67.

- Piersma, T. & Morrison, R.I.G. 1994. Energy expenditure and water turnover of incubating ruddy turnstones – high costs under high Arctic climatic conditions. *Auk* **111**: 366–376.
- Piersma, T., Lindström, Å., Drent, R.H., Tulp, I., Jukema, J., Morrison, R.I.G., Reneerkens, J., Schekkerman, H. & Visser, G.H. 2003. High daily energy expenditure on incubating shorebirds on High Arctic tundra: a circumpolar study. *Funct. Ecol.* **17**: 356–362.
- Proctor, C.J., Broom, M. & Ruxton, G.D. 2003. A communication-based spatial model of antipredator vigilance. *J. Theor. Biol.* **220**: 123–137.
- Pulliam, H.R. 1973. On the advantages of flocking. *J. Theor. Biol.* **38**: 419–422.
- R Development Core Team. 2009. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Roberts, G. 1995. A real-time effect of changes in group size on vigilance behaviour. *Anim. Behav.* **50**: 1371–1374.
- Scheel, D. 1993. Watching for lions in the grass: the usefulness of scanning and its effects during hunts. *Anim. Behav.* **46**: 695–704.
- Spieler, M. 2003. Risk of predation affects aggregation size: a study with tadpoles of *Phrynomantis microps* (Anura: Microhylidae). *Anim. Behav.* **65**: 179–184.
- Swennen, C., Leopold, M.F. & de Bruijn, L.L.M. 1989. Time-stressed oystercatchers, *Haematopus ostralegus*, can increase their intake rate. *Anim. Behav.* **38**: 8–22.
- Tegeder, R.W. & Krause, J. 1995. Density-dependence and numerosity in fright simulated aggregation behaviour of shoaling fish. *Philos. Trans. R. Soc. B* **350**: 381–390.
- Treves, A. 2000. Theory and method in studies of vigilance and aggregation. *Anim. Behav.* **60**: 711–722.
- Vahl, W.K., van der Meer, J., Weissing, F.J., Van Dullemen, D. & Piersma, T. 2005. The mechanisms of interference competition: two experiments on foraging waders. *Behav. Ecol.* **16**: 845–855.
- Vine, I. 1973. Detection of prey flocks by predators. *J. Theor. Biol.* **40**: 207–210.
- Whitfield, D.P. 1985a. Raptor predation on wintering waders in southeast Scotland. *Ibis* **127**: 544–558.
- Whitfield, D.P. 1985b. *Social organisation and feeding behaviour of wintering turnstone *Arenaria interpres**. PhD thesis, University of Edinburgh.
- Whitfield, D.P. 1988. Sparrowhawks *Accipiter nisus* affect the spacing behavior of wintering Turnstone *Arenaria interpres* and Redshank *Tringa totanus*. *Ibis* **130**: 284–287.
- Whitfield, D.P. 1990. Individual feeding specializations of wintering turnstone *Arenaria interpres*. *J. Anim. Ecol.* **59**: 193–211.
- Whittingham, M.J., Butler, S.J., Quinn, J.L. & Cresswell, W. 2004. The effect of limited visibility on vigilance behaviour and speed of predator detection: implications for the conservation of granivorous passerines. *Oikos* **106**: 377–385.
- Whittingham, M.J., Stephens, P.A., Bradbury, R.B. & Freckleton, R.P. 2006. Why do we still use stepwise modelling in ecology and behaviour? *J. Anim. Ecol.* **75**: 1182–1189.
- Yasué, M., Quinn, J.L. & Cresswell, W. 2003. Multiple effects of weather on the starvation and predation risk trade-off in choice of feeding location in redshanks. *Funct. Ecol.* **17**: 727–736.

Received 1 November 2010;
revision accepted 2 December 2012.
Associate Editor: Francis Daunt.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Matrix of Pearson correlation coefficients among the eight continuous predictor variables.

Table S2. Full list of models forming the main analysis.

Table S3. Mixed models of vigilance rate in foraging Ruddy Turnstones.