Vigilance and flocking behaviour of tactilely foraging Dunlins *Calidris alpina*

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Abstract - Field observations of the relationship between vigilance, foraging, and flocking behaviour in Dunlins *Calidris alpina* were carried out under optimal field conditions.
The results show that central Dunlins within larger flocks devote less time to vigilant behaviour and more time to feeding (higher probing rate) than more peripheral conspecifics. The most coherent explanation for the difference in vigilance level between peripherally and centrally foraging Dunlins is the individual birds´ perception of a higher predation risk when exposed. It is argued that vigilance for predators in Dunlins constrains foraging activity rather than vice versa. Hence, the adaptive significance of flocking in Dunlins may be an increased feeding activity without jeopardising predator surveillance.

Introduction

A selective force usually emphasised as important for the evolution of flocking behaviour in birds, is the need for the individual to avoid predation (Pulliam 1973, Thompson *et al.* 1974, Stinson 1980, Myers 1984, Elgar 1989, Lima and Dill 1990). Flock formation may have at least three obvious advantages in this respect: (1) a dilution effect where the probability of a given flock member to be killed during a predatory attack decreases as the flock size increases (e.g. Myers 1984, Dehn 1990); (2) the possibility of co-operative evasive behaviour, confusing the predator during attack (e.g. Boyce 1985, Lima 1993); (3) an increased group vigilance against predators with increasing flock size, allowing a reduction in time spend on scanning for predators at the level of individual. Time saved can in turn be allocated to other essential activities such as feeding (Bertram 1980, Elgar 1989, Lima and Dill 1990). The latter has received considerable empirical attention in both observational and experimental studies, of which the vast majority have shown the expected negative relationship between flock size and individual vigilance level (Elgar 1989, Burger and Gochfeld 1991, Creswell 1994, Alonso *et al.* 1994, Saino 1994, Roberts 1995, Benkman 1997, Reboreda and Fernandez 1997). Since this observation usually is accompanied by a positive relationship between flock size and foraging rate, it is regularly concluded

that vigilance for predators constrains feeding, and therefore it is adaptive for the individual to join flocks in order to optimise both energy intake and predator avoidance. However, the apparently clear message from such relationships can be confounded by other variables as well as obtained through mechanisms unrelated to anti-predator behaviour (see Elgar 1989). For instance, birds are prone to aggregate on patches with high prey accessibility or quality where feeding priority temporally may exceed that of scanning for predators. Hence, foraging may constrain vigilance, rather than vice versa. In most observational studies this possibility is usually not adequately addressed (see Elgar 1989), probably because a detailed knowledge of the often patchy distribution of food items and their quality can be difficult to obtain. In experimental studies where food availability normally is controlled, the little controllable possibility of intra-group competition (that the presence of other flock members per se enhance individual feeding rate) may also result in erroneous conclusions (Clark and Mangel 1984, Elgar 1989). Other confounding variables listed in Elgar (1989) includes the 'edge effect'; difference in breeding status and age; distance from cover; time of day; ambient temperature; presence of predators and observers; habitat obstructions and visibility.

In purely observational studies on e.g. waders feeding on large intertidal flats many of the above mentioned

confounding variables can be difficult to rule out or control. Here we report on field observations of vigilance levels in peripherally and centrally foraging Dunlins *Calidris alpina* obtained under conditions that may minimise the influence of some of these variables, though it must be emphasised, that the many potentially confounding variables could not be controlled for.

Materials and methods

Study area and conditions

The study was conducted in early spring from 31 March to 8 April 1996 at the scientific reserve Tipperne, positioned on the tip of a peninsula in the southern part of Ringkøbing Fjord, Denmark (55°53'N, 08°14'E) (see Meltofte 1987). All observations were achieved within a 400 ha large area composed of meadows and reed swamps, surrounded by extensive nontidal brackish shallow waters and mudflats where the Dunlins were feeding.

The observations were carried out between 10 a.m. and 4 p.m. in light winds and good visibility only. The mean minimum and maximum ambient temperature was -1.7°C ± 0.9 (SD) and 6.5 ± 3.0 (SD), respectively during the study period. About 400 Dunlins were staging in the area during the study period.

Behavioural parameters

Dunlins foraging in the centre of flocks containing ≥100 individuals (range: 100-300) were classified as central feeders, while those foraging more isolated in the periphery of flocks containing <50 individuals (range: 2-50) were defined as peripheral feeders.

An individual was defined as vigilant when its head was raised to at least horizontal position, and individual vigilance level was measured as the frequency per minute of such vigilant behaviour (see Fig. 1). The probing rate was recorded as the number of times the bill was inserted into the sediment per minute. Multiple probing at the same site without bill retraction was registered as a single feeding attempt.

General method

Registration of behavioural parameters were carried out using trip meter, stop watch, and telescope (x20). Each day the observations of both central and peripheral birds were mixed unsystematically between time of day, and between sites within the study area. Hence, records of the two behavioural categories were obtained under approximately the same temperature, range of prey density, and distance to cover (reed swamps, meadows etc.). In all cases the observer was clearly visible to the birds. Since increasing water depth can cause a decrease in foraging rate (Petersen 1981), only probing birds feeding in about 1-2 cm deep water (toes submerged, joint of tarsus above water, see Fig. 1) was selected for observation. Precaution was taken to avoid double registration when the behaviour of more than one individual in a given flock was recorded. Accordingly, the number of recordings in each flock were adjusted to its size.

Since the number of birds in the study area was rather low, the obtained observations can not be expected to be entirely independent. This problem, however, was judged to be small and a statistical test assuming independent observations was nevertheless applied on the present data (Welch's appropriate t-test, see Sokal and Rolf 1995).

Prey availability

Prior to behavioural observations of Dunlins, the density of potential prey organisms within the substrate was estimated on the basis of five core samples (area: 78.5 cm^2, depth: 20 cm) from each of two stations (~2 km apart) known to cover the range of prey density within the study area. Collected sediment was sieved through a 600 µm mesh, and retained animals were stored in 96% ethanol and later counted in the laboratory. Dry weights of the organisms were obtained following 24 hours at 110°C.

Additional information on prey density (mean dry weight from five sub-samples from each of the two stations) also in previous years was obtained from the running prey monitoring program at Tipperne (National Environmental Research Institute (NERI)), following the same procedure as mentioned above.

Figure 1. A Dunlin showing the regularly observed vigilant posture with an angle of vision above the horizontal level.

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Presence of predators

Potential predators on Dunlins recorded during the study period comprised Hen Harriers *Circus cyaneus*, Marsh Harriers *Circus aeruginosus*, Peregrine falcons *Falco peregrinus*, Merlins *Falco columbarius*, and Red foxs *Vulpes vulpes*. All species do attack Dunlins regularly or occasionally (pers. obs.).

Results

Peripherally foraging Dunlins had a significantly higher scanning rate than centrally feeding birds ($t'_s = 6.53$, $p<0.001$), whereas the probing rate was significantly less in peripherally than in centrally foraging individuals ($t'_s = 3.74$, $p<0.001$) (Fig. 2).

The abundance of potential prey organisms to Dunlins was unusually low during the study and comprised almost exclusively the small tubificid oligochaete worm *Tubificoides benedeni* (Fig. 3). The density of this dominant prey species differed between the two stations with averagely 12 and 33 individuals per sample (78.5 cm^2), respectively (Student's t-test, $t_8 = 5.55$, $p < 0.001$). A similar conclusion apply to animal dry weights. Regarding prey density, the variance to mean ratio (s^2/x) was at the two stations 1.2 and 2.3, respectively, suggesting a random or only slightly aggregated prey distribution.

Discussion

Present results indicate that Dunlins foraging within larger flocks devote less time to vigilant behaviour and more time to feeding (higher probing rate) than more peripheral conspecifics, in general agreement with several similar studies on birds, including waders (Pulliam 1973, Thompson et al. 1974, Stinson 1980, Myers 1984, Elgar 1989, Lima and Dill 1990, Burger and Gochfeld 1991). In this study *T. benedeni* appeared to be the only available prey item, and this species does neither make permanent burrows from which it can appear, retract upon a disturbance, or otherwise produce significant cues on the sediment surface revealing its presence (Prof. O. Giere, in litt.). Hence, the only effective way to detect *T. benedeni* is through tactile feeding, which apply both to peripheral and central Dunlins during this study. Consequently, our records of probing rates gives us an indirect mesure of relative food intake since each probing event had the same chances of success in a given feeding patch.

However, before it can be concluded accordingly that vigilance constrains foraging and, in turn, the adaptive significance of joining flocks is to reduce time allocated scanning for predators, alternative interpretations and confounding variables (see introduction) should be addressed.

This study was carried out during the spring migration period far from the breeding grounds, and there is no
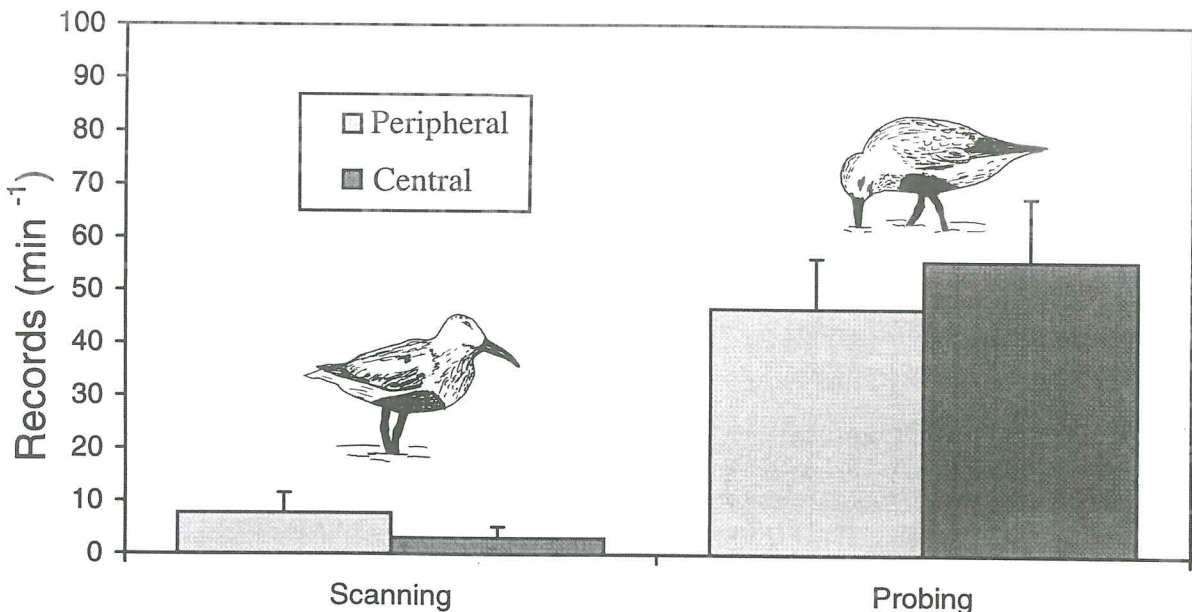

Figure 2. The scanning and probing rate (+SD) of centrally and peripherally foraging Dunlins.
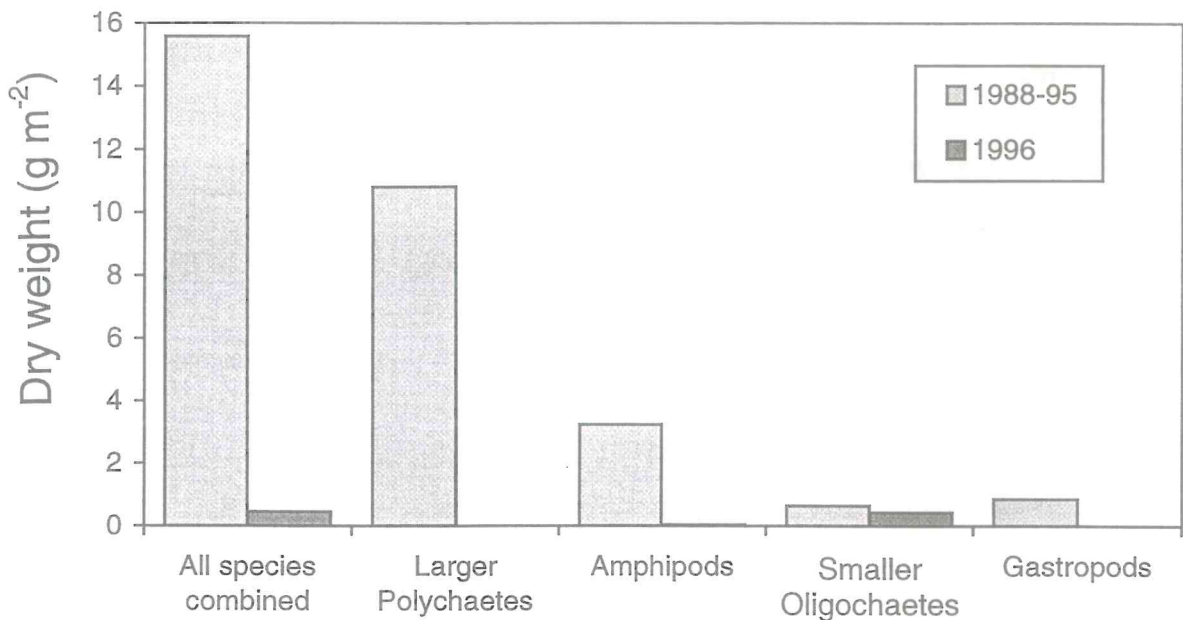
Figure 3. Mean dry weight of the four groups of invertebrates during springs following mild winters (1988-95) and following a severe winter (1996, this study). Larger polychaetes: *Hediste diversicolor, Malacoceros fuliginosus*, and *Heteromastus filiformis*. Amphipods: *Corophium volutator*. Gastropods: *Hydrobia ventrosa* and *Potamopyrgus jenkinsi*. Smaller oligochaetes: *Tubificoides benedeni*.

evidence suggesting that 2yr Dunlins, which have managed to survive their first winter, behave significantly different from their older conspecifics.

Distance to cover, time of day, ambient temperature, presence of observers and predators, habitat obstructions, and visibility can be excluded as significantly confounding variables because records of peripheral and central birds were obtained at the same time (within nine days) at the same sites.

Shorebirds commonly aggregate on optimal feeding patches in which foraging activity is intensified (Goss-Custard 1970, 1977, Evans 1979, Connors et al. 1981, Rands and Barkham 1981, Puttick 1984, Mouritsen and Jensen 1992). Hence, foraging priority may constrain a perhaps default level of vigilance for predators inherently independent of flock size or intra-flock position. Such interpretation is, however, unlikely in the present case because: (1) observations were carried out in a non-tidal habitat excluding large variation in prey accessibility in time and space due to tidal oscillations; (2) with any significance, only one prey species was available in the study area, excluding the possibility of patches of other prey species showing e.g. a pattern of accessibility or quality different from *T. benedeni*; (3) The distribution of *T. benedeni* seemed rather homogeneous both on the small and large spatial scale, in comparison with many other prey organisms usually encountered in e.g. tidal

habitats (see e.g. Mouritsen 1994); (4) central and peripheral birds were observed at the same sites which minimise, but not control for, the influence of prey density/quality on the behaviour of the two Dunlin categories.

Birds feeding under optimal conditions might eventually reach a digestive bottle-neck (Zwarts and Dirksen 1990), and thus have to reduce the intake rate for a period of time. Such birds can be expected to lack behind (and eventually loose contact with) the actively feeding flock of conspecifics. Vigilance for predators may be higher in such individuals, simply because they have nothing better to do, thereby causing negative relationship between flock size and scanning rate. This (to our knowledge) hitherto not recognised confounding variable, is nevertheless unlikely to operate here. Probably because of a severe winter, the overall prey density and biomass observed in the present study was extremely low in comparison with previous years (Fig. 3) as well as values usually seen in alternative intertidal habitats. Based on 4 times a BMR (Basic Metabolic Rate) of 9 Kcal d^{-1}, the necessary energy intake for an average Dunlin individual equals 36 Kcal d^{-1} (Evans et al. 1979, Pienkowski et al. 1984). The mean dry weight of small oligochaete specimens is given by Evans et al. (1979) to be 0.15 mg (similar to our value on *T. benedeni*). Using a calorific value of 5.1

Kcal per g dry weight (Evans et al. 1979), a Dunlin has to ingest 7.06 g dry weight *T. benedeni* d⁻¹ to meet daily requirements. This correspond to an intake rate of 32 specimens min⁻¹. With a common probing rate of about 50 min⁻¹ (see Fig. 2), this necessitates success at more than every second feeding attempt during the entire 24 h cycle. Considering the low prey density in the study area and the tactile feeding mode, we believe that the Dunlins must have experienced severe difficulties in obtaining sufficient energy intake to subsist, rather than have experienced a digestive bottle-neck.

The low prey density and ambient temperature, together with the season these observations were carried out (period of migratory fattening), suggest that Dunlins always should optimise feeding rate, leaving no room in their time budget for intragroup competition.

The final artefact emphasised by Elgar (1989) is the edge effect. Because flock members usually are selected for observation at random, the proportion of birds originating from the flock periphery is declining as group size increases. Since birds at the periphery often are more vigilant than central individuals (see Elgar 1989 and references therein), an unreal negative relation between average individual vigilance and flock size may emerge. In the present case this possibility can be excluded because birds where not selected at random (see materials and methods). This also emphasise the main weakness of the present study: we are not able to separate the effect of flock size from position within the flock. However, if other influencing factors can be disregarded, higher vigilance among birds in the flock periphery and within smaller groups will be the consequence of the same process, namely a higher priority of anti-predator behaviour where predation risk is high.

The above discussion prerequisite that the Dunlins have the ability to behave optimally. However, the possibility that some of the observed birds do not have this ability can not be ruled out entirely. Hence, variance in food availability could theoretically be an operating confounding variable, since this variable can not be controlled for in field studies. We nevertheless find that the most likely explanation for the difference in vigilance level between peripherally and centrally foraging Dunlins at Tipperne, spring 1996, is the individual birds´ perception of predation risk, and that vigilance behaviour consequently constrains foraging activity and not vice versa. Hence, the adaptive significance of flocking in Dunlins may be an increased feeding activity without jeopardising predator surveillance.

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