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Factors affecting escape distances of staging waterbirds

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Escape distances (EDs) have been used to study sensitivity of waterbirds to different sources of disturbance, to design reserves for waterbirds, and to define eco-targets for the Wadden Sea management plan. However, the use of ED as an index of sensitivity has been criticised because it can be highly variable. Although some factors affecting variation in the EDs of species have been studied, there is still a need for further analysis of factors that may affect it. In this study, we analysed the EDs of 19 waterbird species (geese, ducks, waders and gulls) exposed to a walking person (N = 1,371) during autumn and spring 1980-1984 under controlled conditions in the Danish Wadden Sea. We analysed how EDs varied between species in relation to body mass and hunting and within species in relation to flock size and weather conditions. EDs increased significantly with species body mass, and quarry species (dabbling ducks, curlew *Numenius arquata*, golden plover *Pluvialis apricaria*, common gull *Larus canus* and black-headed gull *L. ridibundus*) had longer EDs than non-quarry species when corrected for body mass. EDs increased with flock size in dabbling ducks and nine waterbird species in autumn and two waterbird species in spring. In autumn an inverse relationship was found between visibility and ED for dabbling ducks and five wader species. An inverse relationship was also found between wind force and ED for three wader species, but this relationship was found to be positive for two wader species. Several factors affected EDs, and EDs measured in one region may not apply to other regions. Based on our results it is recommended that reserve borders (core area and buffer zones) are designed to take into account mean EDs as well as variation in EDs, with respect to local disturbance levels, flock size and target species.

Key words: body mass, disturbance, flock size, hunting, reserve models, weather

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When a potential predator approaches a group of birds, at what stage will they take flight? Birds must optimise their investment in vigilance with respect to other important activities, but at the same time their reaction to a specific stimulus must not lead to a waste of energy on unnecessary escape flights (Metcalfe & Furness 1984, Cresswell et al. 2000). Each reaction therefore involves a trade-off between an early escape and the continuation of an on-going activity as long as predation can be successfully avoided.

Escape distance (ED) of waterbirds is defined as the shortest distance at which birds flush when a person or another disturbing stimulus approaches (Smit & Visser 1993). EDs have been used to demonstrate relative susceptibility of waterbirds to different types of disturbance, e.g. the differences between a walking person, a car or a boat (Batten 1977, Keller 1989, Platteeuw & Henkens 1997), and in relation to hunting (Owens 1977, Madsen 1998). For many years, EDs have also been used in bird protection. Knight & Knight (1984) suggested that EDs could be used to develop zones with restricted human activity in relation to different sources of disturbance. The use of EDs has also been developed to assist in the design of reserves and in defining management goals. Thus, Fox & Madsen (1997) presented a model of reserve design in which the core area and a buffer zone were defined in relation to the EDs of target species. The integrated management plan for the Wadden Sea introduced an ecological target whereby it was defined that "The waterfowl species staging in the Wadden Sea should have a natural ED" (Anon. 1998). Recently, EDs were used to calculate standardised lengths of buffer zones for protection of waterbirds from human disturbance in Florida (Rodgers & Schwikert 2002).

On the other hand it has been argued that EDs vary among species, habitat and site, making it impossible to generate generic tolerance distances (Hill et al. 1997). Therefore, it is relevant to analyse EDs in relation to a set of potential modifying factors to identify which factors may influence it. Such results could be useful in understanding under which conditions the measurement of EDs could be used. Up to now, relatively few studies have considered the confounding effects that could modify ED with the notable exceptions of flock size (Owens 1977, Madsen 1985, Spilling et al. 1999) and body mass in resident and migrant species (Burger & Gochfeld 1991). In the present study, we analyse EDs of waterbirds disturbed by a person walking towards them and explore how EDs of staging waterbirds varies both within species and between species as a function of the species' body mass, hunting status, flock size and ambient weather conditions.

Material and methods

Locality and data

The study was conducted in the Danish Wadden Sea, which consists of extensive intertidal mudflats, shallow waters and salt marshes. Waders feed on mudflats during low tide and roost in large flocks on adjacent salt marshes or on islets during high tide (Meltofte et al. 1994). Dabbling ducks and geese roost or feed at the water edge on tidal flats or on salt marshes (Madsen 1988).

The EDs of waterbirds were measured during spring and autumn 1980-1984 at both high and low tide on the intertidal flats and in the salt marshes. A single person, dressed in dark colours, walked at a regular speed of ca 5 km/hour directly towards a selected bird or a flock of birds. In total, 1,371 EDs were measured for 19 species of waterbirds at 15 sites.

The distance at which the bird(s) flushed was measured by pacing out the distance between the observer and the bird or, if a flock, to the centre of the flock. When the observer approached a flock, some individuals flushed before others. On such occasions the distance between the observer and the centre of the flushing portion of the main flock (> 50% of the individuals) was measured. For larger flocks of > 1,000 individuals of e.g. dunlins *Calidris alpina* the ED was measured to the centre of the part of the main flock which flushed first. Measurements from flocks of mixed species were included in the material, but flocks of just one species were preferred when data were collected. A bird or a flock was used for only one observation, and only two, intercalibrated observers, collected the data. For each ED the following parameters were recorded: number of individuals, weather conditions (visibility in kilometres and estimated wind force in Beaufort) and date.

Between-species comparisons

Data for 19 species were used to analyse the effect of body mass and hunting status (quarry or non-quarry species in Denmark). Information on species body mass was taken from Cramp & Simmons (1977,1983).

To reduce skewness in the distribution of the ED data, they were log-transformed in the statistical analysis. Variation in ED was described as a linear regression function of body mass including data from both autumn and spring. An ANCOVA analysis was used to test the hypothesis that quarry species have longer EDs than non-quarry species.

Within-species comparisons

For each species, effects of flock size, visibility and wind force were investigated. Data for mallard *Anas platyrhynchos*, teal *A. crecca*, pintail *A. acuta* and wigeon *A. penelope* were pooled in one category, i.e. 'dabbling ducks', to obtain sufficient data.

The data were analysed using stepwise regression anal-

Table 1. Mean, minimum and maximum escape distances (in m ± 95% confidence interval) for 19 species of waterbirds measured in autumn and spring. The maximum escape distances are rounded to the nearest multiple of 50 m.

Species	Escape distance Mean	Minimum	Maximum	95% C.I.	N
Wildfowl					
Brent goose *Branta bernicla*	319	130	1000	265-384	31
Shelduck *Tadorna tadorna*	225	55	700	206-246	102
Mallard *Anas platyrhynchos*	236	60	400	195-285	25
Teal *Anas crecca*	197	80	450	158-244	24
Pintail *Anas acuta*	294	100	500	255-338	31
Wigeon *Anas penelope*	269	150	1000	239-303	42
Waders					
Oystercatcher *Haematopus ostralegus*	119	20	400	109-130	172
Lapwing *Vanellus vanellus*	142	45	450	122-165	47
Grey plover *Pluvialis squatarola*	132	42	400	119-147	80
Golden plover *Pluvialis apricaria*	143	45	450	117-173	38
Ringed plover *Charadrius hiaticula*	42	18	100	38- 47	59
Curlew *Numenius arquata*	298	58	650	273-326	110
Bar-tailed godwit *Limosa lapponica*	156	40	450	142-170	120
Redshank *Tringa totanus*	137	40	450	120-158	73
Greenshank *Tringa nebularia gunnerus*	94	38	250	80-111	35
Dunlin *Calidris alpina*	70	15	450	65- 75	317
Avocet *Recuvirostra avocetta*	113	75	250	95-133	17
Gulls					
Common gull *Larus canus*	120	70	350	90-160	13
Black-headed gull *Larus ridibundus*	116	50	450	98-137	35

ysis, which was executed for each species and for spring and autumn, respectively, provided that at least 10 observations were available. This way it was shown whether flock size, visibility and wind force contributed significantly to the variation in ED. Flock size was log-transformed as this improved the explanatory power of this factor with respect to ED. Entry and stay in regression models were allowed at P = 0.05.

Results

Between-species comparisons

Brent goose *Branta bernicla* had the longest mean ED of all wildfowl (Table 1), significantly longer than the mean EDs of shelduck *Tadorna tadorna*, mallard and teal (one-way ANOVA, multiple t-test with Bonferroni's correction: t > 2.96, P < 0.05). Of the waders, curlew *Numenius arquata* and bar-tailed godwit *Limosa lapponica* had the longest EDs, and their EDs were both significantly different from each other and from those of the other wader species (t > 3.33, P < 0.05). The ringed plover *Charadrius hiaticula* had the shortest ED, which was significantly shorter than for all other examined wader species (t > 3.33, P < 0.05).

The results presented in Table 1 may suggest that the size of the bird species could be an important explanatory factor of the variation in EDs. Thus brent goose and shelduck are the heaviest wildfowl species, while curlew and bar-tailed godwit are the heaviest waders. In addition, the hunting status of the species differed. Hunting was permitted on dabbling ducks, curlew, golden plover *Pluvialis apricaria* (up to 1983) and the two gull species. Analysis of covariance showed that EDs increased significantly with body mass (ANCOVA: F = 21.46, df = 1, P < 0.001), and that quarry species had longer EDs when corrected for body mass (ANCOVA: F = 5.51, df = 1, P < 0.05; Fig. 1). The significant difference between EDs of quarry and non-quarry species prevailed even if ringed plover, which had a significantly shorter ED than the other non-quarry species (see Fig. 1 and Table 1), was excluded from the data set. Hence, the result seemed resilient to exclusion of this potential outlier.

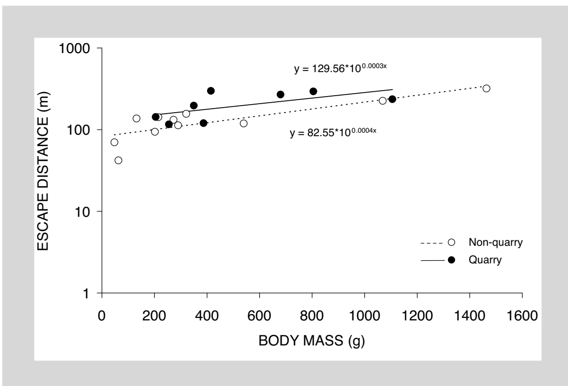

Figure 1. Relationship between body mass (in g) and the mean escape distances for 11 non-quarry species (○; from left: dunlin, ringed plover, redshank, grey plover, greenshank, lapwing *Vanellus vanellus*, avocet, bar-tailed godwit, oystercatcher, shelduck and brent goose) and eight quarry species (•; from the left: golden plover, teal, black-headed gull, common gull, curlew, wigeon, pintail and mallard).

Table 2. Relative importance in autumn and spring of flock size (number of individuals), visibility (in km) and wind force (Beaufort scale) for predicting escape distances for nine waterbird species and dabbling ducks. Stepwise regression was used allowing entry and retention in the model for estimates of slopes at P = 0.05.

Species	Season	N	Independent Variable	Parameter Estimate	Partial R^2
Shelduck	Autumn	40	Flock size	0.195	0.317
Dabbling ducks	Autumn	52	Visibility	-0.060	0.251
			Flock size	0.114	0.101
	Spring	67	Flock size	0.089	0.085
Oystercatcher	Autumn	103	Flock size	0.184	0.280
			Visibility	-0.046	0.095
			Wind force	-0.037	0.027
Lapwing	Autumn	30	Visibility	-0.041	0.251
			Flock size	0.290	0.200
Golden plover	Autumn	36	Flock size	0.256	0.422
			Wind force	-0.102	0.203
			Visibility	-0.024	0.066
Ringed plover	Autumn	44	Flock size	0.176	0.290
			Wind force	0.062	0.208
Curlew	Autumn	84	Flock size	0.175	0.175
			Visibility	-0.031	0.130
Bar-tailed godwit	Autumn	71	Flock size	0.158	0.182
Redshank	Autumn	43	Flock size	0.203	0.327
			Visibility	-0.029	0.080
	Spring	30	Flock size	0.270	0.220
Dunlin	Autumn	245	Flock size	0.189	0.298
			Wind force	-0.034	0.035
	Spring	66	Flock size	0.105	0.084
			Wind force	0.060	0.076

Within-species comparisons

In autumn, a significant linear relationship was found between flock size and ED for dabbling ducks and nine species of waterbirds (Table 2). In spring, dabbling ducks, redshank *Tringa totanus* and dunlin also showed a significant, positive relationship between flock size and ED. The relationship between flock size and ED is shown for dunlin during autumn, the species and season with the highest number of observations (Fig. 2).

In autumn, an inverse relationship between visibility and ED was found for dabbling ducks and five species of waders (see Table 2). This indicates that the ED is shorter in bright weather than in misty weather.

In autumn, inverse relationships were found between wind force and ED for three species of waders (see Table 2). By contrast a positive relationship between wind force and ED was found for ringed plover in autumn and for dunlin in spring.

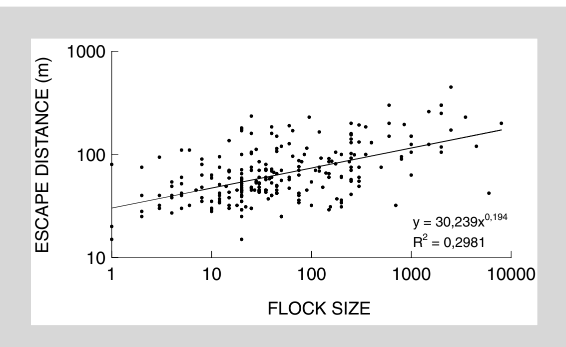

Figure 2. Relationship between flock size (number of individuals per flock) of dunlins and escape distance (in m) in autumn.

The EDs of brent goose, grey plover *Pluvialis squatarola*, greenshank *Tringa nebularia*, avocet *Recuvirostra avocetta*, common gull *Larus canus* and black-headed gull *L. ridibundus* were also analysed in relation to flock size and weather parameters, but no significant relationships were found.

Discussion

Between-species comparisons

It was found that species with greater body mass have longer EDs than smaller species suggesting that size is an important factor affecting ED. Investigation of ED in relation to total length and body mass of 23 waterbirds species in Florida, USA, showed a positive correlation to both parameters (Rodgers & Schwikert 2002). Studies of 138 migrant and resident species in India also showed a correlation between ED and body length (Burger & Gochfeld 1991). Previous studies have not clearly explained why, for instance, body length and body mass were correlated with ED. However, we venture to speculate that large body mass, which is highly correlated with body length, could increase the time and distance necessary for the larger birds to ensure successful avoidance of a predator. The rationale is based on the idea that increasing wing load, and thus body mass, is known to reduce take-off speed (Witter & Cuthill 1993). In addition small species such as dunlin and ringed plover are more manoeuvrable than larger species, and some smaller species even perform an initial leap during take-off which increases escape speed (Witter & Cuthill 1993). For this reason a larger bird may not allow a human being to come as close as a small bird would allow. However, a proper test of these suggestions is lacking.

Hunting

Our study showed that quarry species had longer EDs than non-quarry species, when controlling for species body mass (see Fig. 1). A long ED caused by hunting during the open season in autumn and winter was also reported for geese in both Germany and Denmark (Gerdes & Reepmayer 1983, Madsen 1985), and in both studies EDs were shorter in spring after the open season. Studies in India where birds are not hunted (due to the Hindu religion) showed EDs of up to 35 m for both resident and migratory species including waterbirds. This is much shorter than found for all species in our study. However, in India migratory species had longer EDs than resident species. This was caused by the fact that the migrants came from areas north of India, where disturbance and hunting of birds were common (Burger & Gochfeld 1991). These results indicate that hunting influences the flushing distance of birds even in regions where it is not practised, but on the other hand the birds habituate to the new conditions by generally reducing their EDs (Burger & Gochfeld 1991).

Within-species comparisons

Flock size

We found that flock size had a strong effect on ED. Spilling et al. (1999) found that in white-fronted *Anser albifrons* and bean geese *A. fabalis* wintering in the Elbe Valley, Germany, EDs were shorter in smaller than in larger flocks. They also showed that the EDs of geese responding to approaching cars did not increase further when flocks grew larger than 150 individuals. For pink-footed geese *A. fabalis brachyrhynchus* in western Denmark this threshold appeared at 400-600 individuals (Madsen 1985). In our study, the ED of dunlins continued to increase with flock size up to the largest flock of 9,000 individuals (see Fig. 2). Hence, the nature of the relationship between flock size and ED may differ across species.

Visibility

Lima & Bedenkoff (1999) found that detection distances were shorter when predator attacks occurred against a camouflaged background. In our study this would mean that on days with poor visibility a predator or a person would be better camouflaged than on days with good visibility. However, we found the opposite relationship. The EDs of five waterbird species and dabbling ducks increased with decreasing visibility in autumn, i.e. birds took off at shorter distances in bright than in misty weather. This inverse relationship may originate from the fact that in misty weather birds are more alert and take off at a longer distance to be safe. Alternatively, on bright days humans (and predators) are more conspicuous, and the waterbirds continue their activities for a longer time letting the potential predator come closer before taking off, possibly a result of predator inspection, i.e. assessment of predation risk (see Fishman 1999, Cresswell et al. 2000).

Wind force

Fruzinski (1977) found a linear relationship between wind force and the ED of pink-footed geese which supported the main part of our result concerning the effect of wind force. Both the larger wader species such as oystercatcher *Haematopus ostralegus* and golden plover as well as the smaller species such as ringed plover and dunlin showed significant relationships between wind force and ED (see Table 2). This indicates that the influence of wind speed on ED is not restricted to certain size categories of wader species. However, wind speed generally had the lowest explanatory power with regard to variation in ED. Also the pattern at which ED changed as a function of wind force was not consistent. For example, in dunlin the relationship between the two factors was positive during spring, but negative during autumn. For these reasons it must be concluded that the influence of wind force on ED is not a factor from which general predictions can be made about ED.

Management

A comparison of ED of waders and gulls measured in the Dutch Wadden Sea (Smit & Visser 1993) with our results, shows that for oystercatcher, golden plover, curlew, bar-tailed godwit and black-headed gull the mean ED is 1.4-2 times as long in the Danish Wadden Sea as in the Dutch Wadden Sea. There may be at least two reasons for this. Firstly, birds may have habituated to the far higher number of people walking along the beaches and on the intertidal flats in the Dutch Wadden Sea compared to the Danish Wadden Sea (Laursen et al. 1997, Jong et al. 1999). Secondly, a far greater hunting activity in the Danish Wadden Sea may have led to higher EDs there than in the Dutch Wadden Sea (Jong et al.1999). These results indicate that EDs vary between regions, possibly depending on local disturbance levels and the extent of habituation. This means that when using EDs in design of reserves, measurements of EDs from one region can not be applied in another region, and that local measurements of EDs must be used.

Fox & Madsen (1997) suggested that information about EDs could be applied when designing reserves for birds. They argued that a disturbance-free core area of a reserve should have a minimum diameter of three times the ED of the most sensitive species present. Evidently, our study confirmed that waterbirds show a wide range of sensitivity levels (see Table1), which should be taken into account when designing reserves protecting bird species from disturbance from walking persons or hunting activity. However, knowing that ED converges (in a statistical sense) to normal distribution, especially when data are log-transformed, the definition of core areas and buffer zones could be based not solely on mean ED but also on its variance. Hence, depending on the level of protection required in a given area the mean ED plus one or two standard deviations could be considered in calculating the size of the core area and the buffer zone. The suggested definition corresponds to the protection of about 84 and 98% of the flocks of a given species, respectively. We are fully aware that standard deviation may be reduced by increasing sample size in the data set used as a reference, and this may require that a standard sample size is defined.

Furthermore, the aim of the reserve model presented by Fox & Madsen (1997) was to give protection especially to quarry species during the open season in autumn. We found that flock size increased EDs in several waterbird species. This information may be useful when defining the goals of establishing a reserve. For example, the presence of large flocks of waterbirds and thus a potentially large number of birds may be unrealistic in some reserves simply because human activity occurs too close to the core area of the reserve or due to other factors in the area which restrict the number of birds. Inadequate reserve design may explain why an increase in bird numbers did not occur in some areas after the establishment of reserves (see example in Bregnballe et al. 2001).

One of the objectives of the Wadden Sea Plan adopted by the Netherlands, Germany and Denmark is to restore natural EDs for all species of waterbirds (Anon. 1998). It is argued that the ED in relation to humans is unnaturally long due to hunting. Our results support the assertion for the hunted species, which showed longer EDs than the non-quarry species. Concerning the non-quarry species, the fact that the EDs measured in the Danish Wadden Sea for oystercatcher, bar-tailed godwit and redshank, are about 1.4-2 times longer than EDs measured in the Dutch Wadden Sea could indicate that hunting also influences these species. The results show that the ED is influenced by several factors, which leads to the conclusion that the natural ED for a given species can probably only be considered as a theoretical parameter.

Jong et al. (1999) argued that standardised methods should be developed for measurements of ED to be included in a monitoring program for the Wadden Sea. Our results show that it is possible to identify factors that influence ED and to include these parameters into a model for selected species. However, comparisons with measurements from different regions of the Wadden Sea indicate that EDs differ between areas with different levels of recreational use. Besides, we expect that factors other than those studied here influence EDs. For example, internal factors such as hunger and migratory motivation, and the tide might affect the motivation of individuals to depart from the roosting or the feeding areas if disturbed. Our results could contribute to formulate a preliminary, standardised method to monitor EDs in waterbirds. We conclude that EDs can be a useful tool in designing wildlife refuges for waterbirds and in determining their sensitivity to human disturbances.

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