



Dynamic group size and displacement as avoidance strategies by eiders in response to hunting

Authors: Laursen, Karsten, Møller, Anders Pape, and Holm, Thomas Eske

Source: Wildlife Biology, 22(4) : 174-181

Published By: Nordic Board for Wildlife Research

URL: <https://doi.org/10.2981/wlb.00197>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Dynamic group size and displacement as avoidance strategies by eiders in response to hunting

Karsten Laursen, Anders Pape Møller and Thomas Eske Holm

K. Laursen (kl@dmu.dk) and T. E. Holm, Inst. of Bioscience, Aarhus University, Grenåvej 14, Kalø, DK-8410 Rønde, Denmark. – A. P. Møller, Laboratoire d'Ecologie, Systématique et Evolution, CNRS UMR 8079, Univ. Paris-Sud, Bâtiment 362, FR-91405 Orsay Cedex, France

Hunting by humans constitutes a major source of mortality that selects for avoidance strategies. Group formation in eiders *Somateria mollissima* in response to hunting from motorboats was studied in the Danish Wadden Sea as an avoidance strategy to humans. In autumn the birds' food demand and energy consumption are relatively low and the need for optimal feeding opportunities are not as essential as during winter. We tested the hypothesis that eiders aggregate in groups of variable size dependent on predation risk (hunting), season and site. During autumn at the preferred feeding sites eiders occur in small numbers and group size increase together with hunting activity. Opposite during winter, eiders occur in large numbers and group size decrease when hunting activity increase. Hunting activity displaced eiders to adjacent sites with no or low hunting intensity and low food availability where group size of eiders increase during both autumn and winter in relation to the overall hunting activity. The formation into larger groups when hunting activity increase is probably due to increasing effects of vigilance and dilution, whereas formation into smaller groups is assumed to reduce the eiders conspicuousness to hunters. This change in group size made it possible for eiders to forage in areas with high food availability and high hunting intensity, while minimizing the risk of being detected by hunters. When the largest numbers of hunters were present at the preferred feeding site, group sizes during both autumn and winter were 110–125 eiders, indicating an optimal group size in relation to hunting density. Eiders located outside preferred feeding sites were in poorer body condition, suggesting that displacement was a suboptimal decision caused by hunting. We conclude that eiders adopted regrouping and displacement as two different strategies during hunting. Both strategies are tradeoffs between the risks of being detected by hunters and killed, and the benefits of feeding on mussel stocks thereby increasing body condition and hence fitness.

Major challenges for prey species are the continual problem of balancing the tradeoff between reducing predation risk and maintaining or increasing reproductive fitness (Clark 1994, Lind and Cresswell 2005). To avoid predation, prey show a complexity of anti-predator defences that constitute behavioural mechanisms that are shaped by natural selection to avoid premature death (Caro 2005). Responses to the threat of predation are often characterized as a sequence of interactions between predator and prey in which group formation is considered a main anti-predator behaviour (Cresswell 2008). Members belonging to a group have often lower predator-induced mortality than solitary individuals (Coulson 1968, Alberts and Altmann 1995, Clutton-Brock et al. 1999) due to increased response distance in groups allowing for early detection of approaching predators (Miller 1922, Pulliam 1973, Kenward 1978, Elgar 1989, Laursen et al. 2005). However,

in some cases predator induced mortality can increase with group size (Botham et al. 2005). The dilution effect is another group advantage. If a predator takes only one or a few prey per attack, the risk of being killed is rapidly reduced when group size increases (Hamilton 1971, Cresswell and Quinn 2011). The gains for group members in addition to reduced predation risk are increased fitness due to time devoted to other activities such as foraging, which increases in large groups (Lima and Dill 1990, Cresswell et al. 2003). Disadvantages of being in a group derive from intra-specific competition and spacing (Minderman et al. 2006, Caro 2005). In addition, large groups of prey are more likely to be detected visually in open habitats or easily encountered in dense habitats by a predator than small groups and solitarily living prey (Cullen 1960, Vine 1973).

Prey responses to predators can be modified by the location of food, food demand and hunting strategy. When food resources are limited or food demand is high, prey species take larger risks during feeding (e.g. by increasing distance to cover), and they are less vigilant. Group size can change in response to type of predator and hunting strategy i.e.

This work is licensed under a Creative Commons Attribution 4.0 International License (CC-BY) <<http://creativecommons.org/licenses/by/4.0/>>.

attack in open space or by surprise (Metcalf and Furness 1984, Cresswell et al. 2003, Cresswell and Whitfield 2008, Cresswell and Quinn 2010). These findings suggest that an optimal group size of prey exists due to a balance between costs and benefits for group members (Cresswell and Quinn 2011).

A particular type of predator–prey interaction occurs between hunters and wild animals, and principles similar to those that apply to predators and prey should also apply to hunters and their prey. However, this important and widespread interaction is poorly understood despite there are several opportunities of this kind of studies since millions of animals are harvested annually by thousands of hunters. When waterbirds are hunted by man they change activity pattern, escape distance and displace to alternative sites and habitats just as described for birds hunted by natural predators (Bell and Owen 1990, Madsen and Fox 1995, Fox and Madsen 1997, Frid and Dill 2002, Holm et al. 2011). This allows scientists to use knowledge obtained from natural predator–prey systems to predict interactions between hunters and their prey. Hunter–prey systems have less often been used for research on the relationship between group formation and density of hunters. Prey aggregate in groups when a predator is approaching, and group size increases with predation risk in mammals (Caro 2005), birds (Thiollay 2005, Jaatinen et al. 2011) and fish (Seghers 1974). However, when predator risk is sufficiently high, group size may decrease, e.g. fish skulls attached by predators (Kenyon et al. 2007). Most studies of birds and mammals have been performed in extensive areas with a uniform distribution of food resources and a stable food demand by prey. In contrast, few studies have focused on prey species with variable seasonal food demands in landscapes with patchily distributed food resources and a predator with variable hunting strategies (Caro 2005).

The daily food demand by eiders increases from autumn to winter from 2.2×10^6 J to 2.9×10^6 J (Brinkman et al. 2003), and the weight of the females increase accordingly (Milne 1976), when they build up body resources on the wintering grounds for subsequent breeding (Descamps et al. 2011, Sénéchal et al. 2011, Hobson et al. 2015, Waltho and Coulson 2015). Individual eiders arriving at the breeding grounds in prime condition produce larger clutches with higher duckling survival than individuals in poor condition (Hanssen et al. 2002, Hario and Selin 2002, Öst et al. 2008). Blue mussels *Mytilus edulis* are a key prey species allowing eiders to build up more body mass than e.g. cockles (Nehls and Ketzenberg 2002, Laursen et al. 2010, Cervencel et al. 2014). In addition, the amount of mussel stocks and other food resources seems to regulate the number of eiders and group size (Guillemette et al. 1993, Laursen and Frikke 2008).

Here we study complex behavioural interactions between eiders *Somateria mollissima* and hunters in motorboats in marine areas. We have information of three variables: hunting intensity, site quality (with and without mussel stocks) and season (high and low food demand of eiders). This gives several possible combinations of which we have the information of combinations: (a) sites with mussel stocks and high hunting activity during autumn and winter, and (b) sites without mussel stocks and low hunting activity during autumn and winter.

In this study we put forward the following hypotheses: 1) at preferred feeding sites during autumn, when food demand is low and eiders occur in low number, group size in hunted eiders increases when density of hunters increases, because the eiders aggregate in larger flocks when density of hunters increases due to dilution and vigilance effects; 2) at preferred feeding sites during winter, when food demand is high and eiders occur in large number, group size of eider decreases in preferred feeding sites because large numbers of eiders are present that split up in smaller groups to reduce conspicuousness when density of hunters increases; 3) during autumn and winter eiders aggregate in adjacent sites with low or no hunting activities and low mussel stocks when the overall hunting activity increase, due to dilution and vigilance effects and 4) spatial displacement of eiders from prime food resources by hunters has consequences in terms of reduced body condition. These hypotheses were tested in the Danish Wadden Sea where eiders were hunted from motorboats in autumn and winter in the Central Wadden Sea until 1992 (Fig. 1), when hunting was prohibited except for the Offshore area (Fig. 1). This provided us with an opportunity in a natural experiment to compare group size formation in eiders at sites with different hunting regimes, food stocks and food demand.

Methods

Study sites

The Danish Wadden Sea (1225 km²) constitutes the northern tenth of the Wadden Sea (Fig. 1), shared by Germany and the Netherlands. It is of global international importance as breeding, staging and wintering area for over fifty populations of migratory waterbird species (Van Roomen et al. 2012). A peninsula and three major islands define the Danish Wadden Sea to the west, separating it from the North Sea.

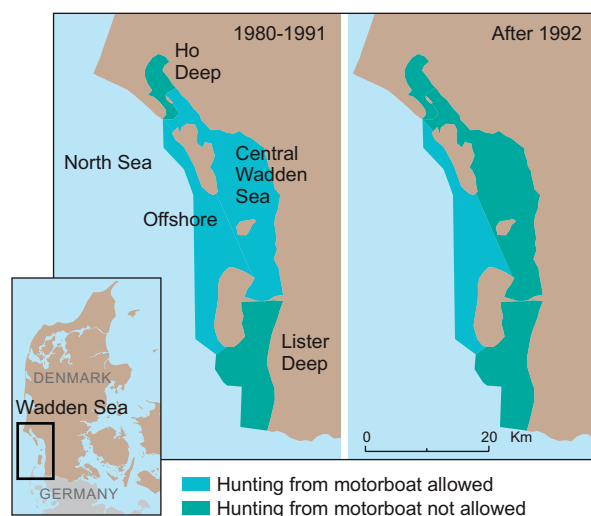


Figure 1. Map showing the Danish Wadden Sea, divided into Refuge Areas (Ho Deep and Lister Deep), the Central Wadden Sea and the Offshore area. Hunting from motorboats was allowed in the Central Wadden Sea and the Offshore area until 1992. After 1992 hunting was prohibited in the Central Wadden Sea.

The site became a wildlife reserve in 1979, when hunting from motorboats was no longer allowed in the Ho Deep (to the north) and Lister Deep (to the south), hereafter named the Refuge Areas, 315 km² (Fig. 1). Elsewhere, hunting from motorboats was allowed until 1992. Due to differences in hunting strategy and number of eiders shot, this area was divided into two parts: the area between the mainland coast and the islands (named the Central Wadden Sea, 641 km²) where a high numbers of eiders was shot, and the area west of the islands (named the Offshore area, 269 km²), where few eiders was shot (Laursen 1985). The combined three areas (the Central Wadden Sea, the Refuge Areas and the Offshore area) are hereafter referred to as the Danish Wadden Sea.

Aerial surveys

Eiders occur mainly from October to the end of February in the Danish Wadden Sea, and in the periods 1980–1992 and 1992–2010 (before and after hunting was prohibited in the Central Wadden Sea) a total of 37 and 15 aerial surveys were performed in these months. The reduced number of flights after 1992 was caused by a reduction in the monitoring scheme. Surveys in periods with > 25% ice cover and intensive mussel fishery (1988) were excluded from the analyses because they strongly affected the abundance and distribution of eiders (Laursen et al. 2010). The entire Danish Wadden Sea was covered by each flight. Two observers in the aircraft located and estimated the size of all eider flocks (including single birds) and the number of motorboats with hunters. Surveys were carried out at high water, lasting 3–4.5 h following the methods by Pihl and Frikke (1992). Simultaneous counts of eiders from aircraft and from the ground showed an overall negligible difference in numbers of 1.1% (19.0%) (mean (SE)) (Laursen et al. 2005).

Hunting activity

Hunting from motorboats is a traditional Danish method for hunting diving ducks. Motorboat speeds are restricted to 2.7 knots during hunting, and the open season lasts from 1 October to the end of February. Hunting bouts can last the entire day, and half the Central Wadden Sea can be accessed during a bout. In the Central Wadden Sea hunters actively search for eider flocks and flush them several times during a day. Due to more exposed conditions in the Offshore area, motorboats are anchored near sand banks along the deeps between the islands where hunters wait for eiders to pass during their tidal movements (Laursen and Frikke 2008). Thus hunting density and bag size was larger in the Central Wadden Sea compared to the Offshore area, ca 350 versus ca 75 shot eiders annually (Laursen 1985). After 1992 hunting was forbidden in the Central Wadden Sea and only permitted Offshore.

Because hunter motorboats observed in the Offshore area had sailed through the Central Wadden Sea and may have caused some disturbance while passing, we use the overall number of hunter motorboats recorded in the Danish Wadden Sea to quantify the daily density of hunters.

Sample of eiders

During January and February 1986 and 1987 a sample of 191 eiders was collected by hunters in the Central Wadden

Sea and the Offshore area. The eiders were sexed, aged and body mass measured (g) together with the length of wing (mm).

Food stocks

The eider is predominantly a mussel eater (Swennen 1976, Nehls 1995, Kats 2007), and the vast majority (> 98%) of mussel stocks was located between the islands and the mainland coast. The annual mussel stocks in the Danish Wadden Sea during 1986–2007 varied between 6000 and 117 000 metric tonnes with an average of 38 400 metric tonnes of which 82% were situated in the Central Wadden Sea and the rest in the Refuge Areas (Laursen et al. 2010). However, no data exists on mussel stocks before 1986, but information from the 1960s indicate the presence of mussel stocks (Theisen 1968).

Statistical analysis

Group size

From 52 aerial surveys the mean group size of eiders was estimated at four sites (Central Wadden Sea, Offshore area, Lister Deep and Ho Deep) in autumn (1 October – 31 December) and winter (1 January – 28 February).

To analyse group size of eiders in relation to hunting density we made a stepwise test scheme, first analysing all data and based on these results we analysed the significant variables to determine if there were effects of sites and season. First, for all data we tested if eider group size (as response variable) could be explained by site, season and the density of hunting motorboats and the interaction effects of site and hunting motorboats, season and hunting motorboats, site and season together with site, season and hunting motorboats as predictor variables. Year and total number of eiders in the Danish Wadden Sea were random effects in this and in the following tests of group size. Second, if the predictor variable 'site' was statistically significant ($p < 0.05$), we ran a set of tests (a) for the Offshore and the Refuge Areas (sites with low or no hunting activities) and (b) the Central Wadden Sea (high hunting activities), respectively. In the second test (a), for the Offshore and the Refuge Areas and the second test (b) for the Central Wadden Sea we tested if eider group size (as response variable) could be explained by season, the density of hunting motorboats and the interacting effects of season and density of hunting motorboats as predictor variables. If the predictor variable 'season' became statistically significant, we ran a third set of tests for autumn (a) and winter (b) for the Offshore and the Refuge Areas and likewise for autumn (c) and for winter (d) for the Central Wadden Sea. In the third test (a, b, c and d) we tested if eider group size (as response variable) could be explained by density of hunting motorboats as predictor variables. For the analyses of group size we used mixed models (SAS 2010).

Body condition

We tested whether the body condition (scaled body mass index (Peig and Green 2009)) of eiders (as a response variable) depended on sex, age, body size, site (in the Central part of Wadden Sea or in the Offshore area) and the interaction

between these variables and site (as predictor variables). In the tests we used general linear models (GLM) (SAS 2010).

In all the tests variables for which $p < 0.1$ were stepwise excluded from the models. Data for hunting motorboats, total number of eiders and mean group size of eiders were log-transformation ($\log + 1$) to achieve normal distributions. Numbers are given as mean (SE).

Results

Eider numbers, phenology and displacement by hunting

The total number of eiders in the Danish Wadden Sea before 1992 increased from ca 13 800 (SE = 3000) birds in October to ca 31 500 (2100) in January ($F = 12.11$, $DF = 1,43$, $p = 0.040$, estimate (SD) = 3.9734 (1.1416); Fig. 2). This pattern was evident for the number of eiders in both the Refuge Areas and the Offshore area with most eiders being found in the latter area except for February. In contrast, numbers in the Central Wadden Sea were small and stable at ca 3000 (800) eiders during October–December, increasing to ca 10 000 (2500) eiders during January and February ($F = 19.23$, $DF = 1,54$, $p < 0.0001$).

During days with low densities of hunter motorboats a large proportion of eiders were found in the Central Wadden Sea during all months (Fig. 3). The proportion of eiders decreased when the density of hunter motorboats increased ($F = 5.75$, $DF = 1,35$, $p = 0.0219$, $r^2 = 0.14$, estimate (SD) = -6.6173 (2.7589)) and the eiders moved to the Offshore area or the Refuge Areas.

Group size of eiders

Mean group size of eiders in relation to density of hunting motorboats for the Central Wadden Sea, Offshore area, Lister Deep and Ho Bay is shown in Fig. 4 for autumn and winter.

The first statistical test based on all data show that site and the interaction between site, season and density of hunting motorboats had significant effects on the group size of

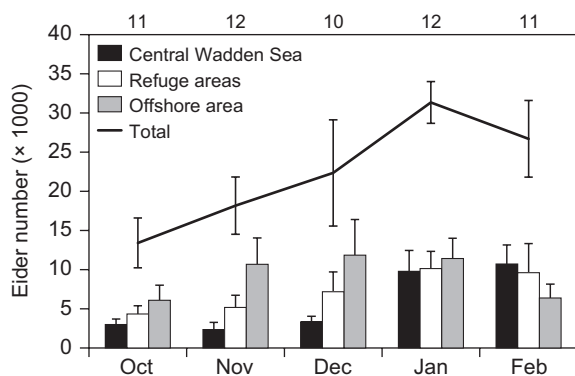


Figure 2. Total number (mean (SE)) of eiders in the Danish Wadden Sea during October–February 1980–1992 and numbers in the Central Wadden Sea, Refuge Areas and the Offshore area. At the top: number of surveys.

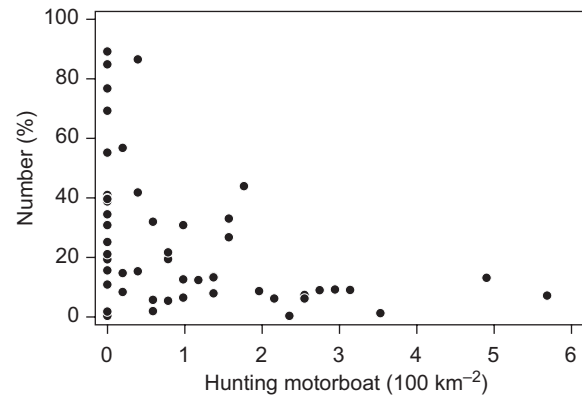


Figure 3. Relationships between the proportion of eiders in the Central Wadden Sea and density of hunter motorboats per 100 km².

eider (Table 1; results of primary model are given in the Supplementary material Appendix 1 Table A1). Since the variable 'site' (as part of the interaction between site, season and motorboats) was significant we performed the second test. The second test shows for the Refuge Areas that group size of eiders increases when the density of hunting motorboats was high (results of the primary and final models for this and the following tests are given in the Supplementary material Appendix 1 Table A2). The second test for the Central Wadden Sea shows that season and the interaction of season and density of hunting motorboats (Supplementary material Appendix 1 Table A3) had a significant effect of group size of eider. Since the variable 'season' (as part of the interaction between season and density of motorboats) was statically significant in the second test for Central Wadden Sea, we performed the third test for this site. This test shows for the Central Wadden Sea during autumn that group size of eider was large when the densities of hunters were high (Supplementary material Appendix 1 Table A4). When this test is focused on the period when hunting occurred in the Central Wadden Sea (before 1992) the relationship between density of hunters and the group size of eiders was marginally significant ($F = 4.23$, $DF = 1,21$, $p = 0.052$, estimate (SE) = 0.7483 (0.3640)). In contrast for the Central Wadden Sea during winter group size of eider decreased when the density of hunters increased (Supplementary material Appendix 1 Table A5). Year and total number of eiders was selected as random effects and have the statistics: (year) $F = 12.79$, $p = 0.00004$, $DF = 1,199$, estimate = -0.01211 (0.00339), (total number of eider) $F = 27.28$, $p < 0.0001$, $DF = 1,199$, estimate = 0.45300 (0.08674).

Body mass and site in the Wadden sea

The analysis of scaled body mass index of eiders in relation to sex, site and wing length explained 26% of the variance (Table 2). This model fitted the data (goodness of fit: $F = 0.63$, $DF = 170, 5$, $p = 0.83$). Males were heavier than females (Table 2). Eiders from the Offshore area on average had a lower body mass index (2164.14 units (24.76)) compared to those from the Central Wadden Sea (2342.40 units (0.40)), a difference by 8%.

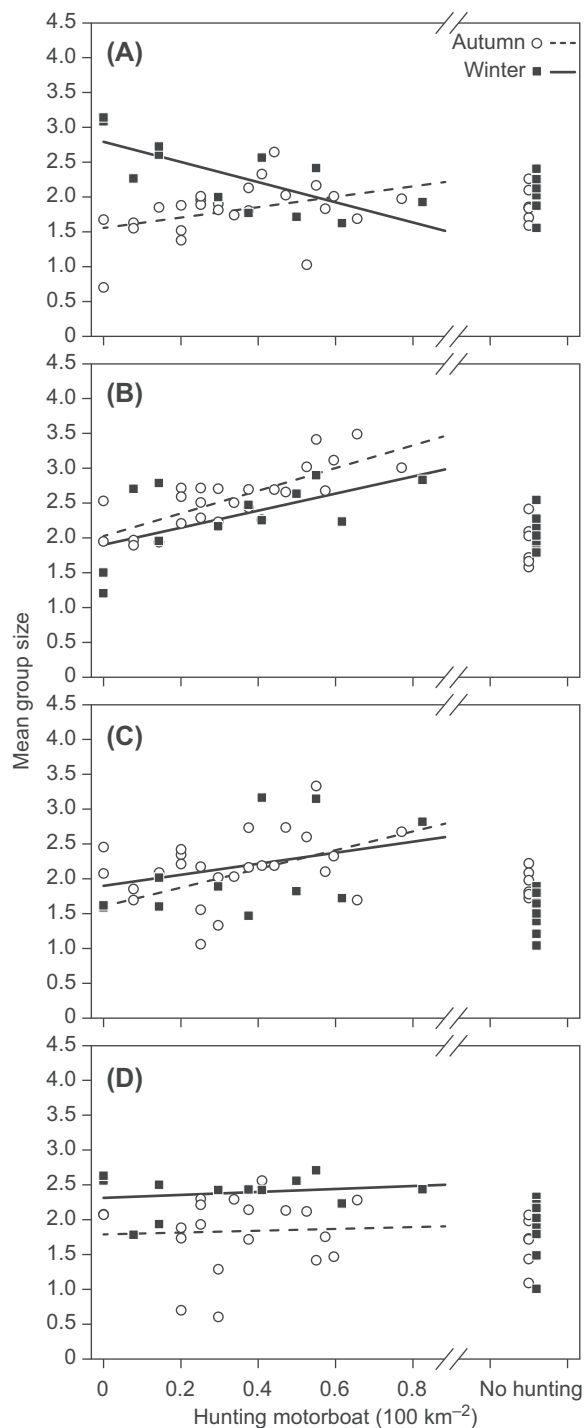


Figure 4. Relationship between density of hunter motorboats per 100 km² and the mean group size of eiders during autumn and winter in (A) Central Wadden Sea, (B) Offshore area, (C) Lister Deep and (D) Ho Bay. The regression lines are shown for autumn (dash line) and winter (full line). To the right: eider group size after 1992 when hunting was prohibited in the Central Wadden Sea.

Discussion

Group size

Eider numbers in the Danish Wadden Sea increase during autumn when birds arrive from the breeding grounds

Table 1. Final result of mix-model analysis of group size of eiders in the Danish Wadden Sea in relation to site, season, density of hunting motorboats and the interaction between site, season and density of hunting motorboats. Total number of eiders and year is random variables. AIC = 258.0, DF = 1,191.

Fixed effects	Solution		Type III tests	
	Estimate	SE	F	p
Intercept	11.5283	5.8369	3.9	0.0497
Site	0.0871	0.0294	8.79	0.0034
Site × Season × Log Hunting Density	0.1139	0.0363	9.86	0.0020

along the coasts of the Baltic Sea and the Wadden Sea (Noer 1991). During autumn (October–December) in the years until 1992, when hunting was allowed in the Central Wadden Sea, the largest numbers occurred in sites with no hunting (the Refuge Areas) or with low hunting activity (the Offshore area). During winter (January–February) eiders build up parts of the body stores for the subsequent breeding season (Meijer and Drent 1999, Blums et al. 2005), and numbers increase in the Central Wadden Sea, where the vast majority of mussel stocks are located, despite high hunting activity (Laursen and Frikke 2008, Laursen et al. 2010). On days when hunting activity was high in the Central Wadden Sea, eiders moved to adjacent sites with low (the Offshore area) or no hunting activity (the Refuge Areas), where the group size of eiders increased. For the Offshore area and Lister Deep group size during autumn and winter increased several fold when overall density of hunters increased. The increase in group size in Ho Bay was modest, probably due to its small size and an insufficient buffer zone to the Central Wadden Sea where hunting activity was high (Fox and Madsen 1997).

During autumn the number of eiders was small despite large mussel stocks in the Central Wadden Sea, but the high hunting activity together with a low food demand for eiders in this season prevents the use of this area by great numbers. However, when hunting activity increased, eiders gathered in larger groups probably due to greater vigilance in large flocks that increases individual feeding time together with dilution effects that reduce predation rate (Lima and Dill 1990, Cresswell et al. 2003). Eiders occur in large numbers in the Central Wadden Sea during winter to feed on mussel stocks for building up body stores (Laursen and Frikke 2008). On days with no or low hunting activity the number of birds was high and they occurred in large groups. However, when hunting activity increased, flock size decreased. The reason for changes in group size was probably that large flocks were easier for hunters to locate and chase. During this process some birds left the Central Wadden Sea, while birds that stayed were flushed repeatedly during the day causing them to gather in smaller and less detectable groups. These groups stabilized at a small size.

Group sizes in the Central Wadden Sea change in opposite directions during autumn and winter and thus tend towards the same level of 110–125 birds when hunting activity increased. This level is assumed to be a balance between the advantages and disadvantages of staying in a group under given hunting conditions. When group size increased, the dilution effect increased thus reducing the risk of being

Table 2. Body mass of eiders in relation to sex, age, Offshore area or Central Wadden Sea and wing length.

Term	Sum of squares	DF	F	p	Estimate	SE
Sex	0.0142	1	9.57	0.0023	2.8711	0.1042
Offshore–Central Wadden Sea	0.0200	1	13.52	0.0003	0.0114	0.0031
Wing length	0.0294	1	19.95	< 0.0001	0.0516	0.0516

killed. In contrast, when group size increased conspicuousness of eider groups also increased, and they became easier for hunters to detect. On the other hand, when members of the group left, group size decreased and thereby reducing vigilance and dilution effects. We hypothesize that this intermediate group size can be considered an 'optimal group size' for eiders exposed to intensive hunting. The mechanism behind the formation of increasing and decreasing group sizes in autumn and winter is probably the number of flushes (attacks) by hunters during a day, which again depends on the density of hunting motorboats.

Assessments of optimal group size are few in wild bird populations. On the breeding grounds in Finland 2–3 eider females were the optimal number of tenders that maximized daily survival of ducklings (Öst et al. 2008). In England redshank *Tringa totanus* flocks were hunted by the Eurasian sparrowhawk *Accipiter nisus* and its attack rate peaked at a flock size of 55 redshanks and the attack rate declined when flock size were lower than 40 or above 70 individuals (Cresswell and Quinn 2011). Furthermore, redshank commonly formed group sizes far larger than those expected for advantages from dilution effects or reduced attack rates. We found similar results with eiders forming flocks of more than 1000 individuals in the Offshore area and in Lister Deep at high hunting intensity, which is far above the group size of 110–125 birds found in the Central Wadden Sea.

Eider group size increased at adjacent sites when overall hunting activity increased. Several mammal species also show behavioural responses to predator presence, and group sizes increase when predation risk increases. This was shown for eastern grey kangaroo *Macropus giganteus* hunted by foxes *Vulpes vulpes*, white-tailed deer *Odocoileus virginianus* hunted by coyotes *Canis latrans* and musk ox *Ovibos moschatu* hunted by wolves *Canis lupus* (LaGory 1987, Heard 1992, Banks 2001, Caro 2005). However, other factors as distance to cover, the ability of prey individuals to survey the group, and vegetation structure may all influence flock formation (Caro 2005).

In the Wadden Sea there could be a continuum from the situation of no hunting, over low intensity of hunting to the highest level of hunting, except for the Central Wadden Sea. The different patterns between the Offshore area, Ho Bay and Lister Deep on one hand and the Central Wadden Sea on the other may depend on hunting strategy and hunting activity. In Ho Bay and Lister Deep there was no hunting and in the Offshore area hunting activity was low and the hunting strategy was passive (hunters wait for eiders to pass close to anchored boats or sand banks). This allowed eiders to build up large groups without being disturbed and flushed by hunters. In the Central Wadden Sea group formation differed from the other sites between autumn and winter due to the large mussel stocks and the high food demand of eiders

during winter. The large food stocks in the Central Wadden Sea is supposed to drive eiders to take larger risks when feeding during winter as found by Cresswell and Whitfield (2008), Cresswell et al. (2003) and Cresswell and Quinn (2010). However, eiders may counteract the risk by formation of dynamic flock sizes in response to hunting activity and change in food demand.

Effect of displacement

Body condition increased with sex and size. In addition eiders were in considerably worse condition in the Offshore area than in the Central Wadden Sea. Eiders feeding on blue mussels have better body condition than those taking other food items (Laursen et al. 2009). Eiders feeding in the Offshore area had mostly eaten cockles whereas those in the Central Wadden Sea had taken blue mussels (Laursen et al. 2009). This support the results that eiders displaced to the Offshore area are in poor condition compared to eiders in the Central Wadden Sea. In other words, it is unlikely that eiders were located in the Offshore area because of superior foraging conditions. This suggests that the response in terms of displacement due to hunting activity was a suboptimal choice as evidenced by the reduced condition. Eiders have to build up body condition during winter for the coming breeding season, and the reduced body condition may influence reproduction and thus have non-lethal effects.

Conclusion

Motorboat hunting in the Danish Wadden Sea displaced eiders to suboptimal feeding sites with no or little hunting activity, where group size increases due to increasing hunting activity. The Central Wadden Sea has prime feeding conditions due to large mussel stocks but a high level of hunting activity. Eiders occurred in small numbers during autumn, but the number increased due to high food demand during winter. The responses to hunting activity were opposite in the two seasons approaching group sizes of 110–125 individuals at the highest hunting activity, which we hypothesise to be the optimal group size during intensive hunting. The hunting induced displacement to suboptimal sites may have fitness consequences for eiders due to reductions in body condition. Thus hunting may have non-lethal effects that have to be added to the total number of eiders shot.

Acknowledgements – We thank Karen Asferg for morphological and diet data of eiders and Will Cresswell for valuable comments on the manuscript.

Funding – This study was supported by the 15 June Foundation.

References

- Alberts, S. C. and Altmann, J. 1995. Balancing costs and opportunities: dispersal in male baboons. – *Am. Nat.* 145: 279–306.
- Banks, P. B. 2001. Predation-sensitive grouping and habitat use by eastern grey kangaroos: a field experiment. – *Anim. Behav.* 61: 1013–1021.
- Bell, D. V. and Owen, M. 1990. Shooting disturbance – a review. – In: Matthews, G. V. T. (ed.), *Managing waterfowl populations*. IWRB Special Publications No. 12. Slimbridge, UK.
- Blums, P. et al. 2005. Individual quality, survival variation and patterns of phenotypic selection on body condition and timing of nesting in birds. – *Oecologia* 143: 365–376.
- Botham, M. S. et al. 2005. Predator choice in the field; grouping guppies, *Poecilia reticulata*, receive more attacks. – *Behav. Ecol. Sociobiol.* 59: 181–184.
- Brinkman, A. G. 2003. Modelling the energy budget and prey choice of eider ducks. – *Alterra-rapport* 839. Alterra, Wageningen, the Netherlands.
- Caro, T. 2005. Antipredator defences in birds and mammals. – Univ. of Chicago Press.
- Cervenc, A. et al. 2014. Distribution of wintering common eider *Somateria mollissima* in the Dutch Wadden Sea in relation to available food stocks. – *Mar. Biol.* 162: 153–168.
- Clark, A. W. 1994. Antipredator behaviour and the asset-protection principle. – *Behav. Ecol.* 5: 159–170.
- Clutton-Brock, T. H. et al. 1999. Selfish sentinels in cooperation mammals. – *Science* 284: 1640–1644.
- Coulson, J. C. 1968. Differences in the quality of birds nesting in the centre and on the edge of a colony. – *Nature* 217: 478–479.
- Cresswell, W. 2008. Non-lethal effects of predation in birds. – *Ibis* 150: 3–17.
- Cresswell, W. and Quinn, J. L. 2010. Attack frequency, attack success and choice of prey group size for two predators with contrasting hunting strategies. – *Anim. Behav.* 80: 643–648.
- Cresswell, W. and Quinn, J. L. 2011. Prediction the optimal group size from predator hunting behaviour. – *J. Anim. Ecol.* 80: 310–319.
- Cresswell, W. and Whitfield, D. P. 2008. How starvation risk in redshanks results in predation mortality from sparrowhawks. – *Ibis* 150: 209–218.
- Cresswell, W. et al. 2003. Does an opportunistic predator preferentially attack nonvigilant prey? – *Anim. Behav.* 66: 643–648.
- Cullen, J. M. 1960. Some adaptations in the nesting behaviour of terns. – *Proc. Int. Ornithol. Congr.* 12: 153–157.
- Descamps, S. et al. 2011. Individual optimization of reproduction in a long-lived migratory bird: a test of the condition-dependent model of laying date and clutch size. – *Funct. Ecol.* 25: 671–681.
- 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.
- Fox, A. D. and Madsen, J. 1997. Behavioural and distributional effects of hunting disturbance on waterbirds in Europe: implications for refuge design. – *J. Appl. Ecol.* 34: 1–13.
- Frid, A. and Dill, L. M. 2002. Human-caused disturbance stimuli as a form of predation risk. – *Conserv. Ecol.* 6:11.
- Guillemette, M. et al. 1993. Habitat selection by common eiders in winter and its interaction with flock size. – *Can. J. Zool.* 71: 1259–1266.
- Hario, M. and Selin, K. 2002. Cohort-specific differences in reproductive output in a declining common eider *Somateria mollissima* population. – *Dan. Rev. Game Biol.* 16: 33–45.
- Hamilton, W. D. 1971. Geometry for the selfish herd. – *J. Theor. Biol.* 31: 295–311.
- Hanssen, S. A. et al. 2002. Incubation start and egg size in relation to body reserves in the common eider. – *Behav. Ecol. Sociobiol.* 52: 282–288.
- Heard, D. C. 1992. The Effect of wolf predation and snow cover on musk-ox group size. – *Am. Nat.* 139: 190–204.
- Hobson, K. A. et al. 2015. Differential contribution of endogenous and exogenous nutrients to egg components in wild Baltic common eiders (*Somateria mollissima*): a test of alternative stable isotope approaches. – *Auk* 132: 624–633.
- Holm, T. E. et al. 2011. The feeding ecology and distribution of common coots *Fulica atra* are affected by hunting taking place in adjacent areas. – *Bird Study* 58: 321–329.
- Jaatinen, K. et al. 2011. Adult predation risk drives shifts in parental care strategies: a long-term study. – *J. Anim. Ecol.* 80: 49–56.
- Kats, R. 2007. Common eiders *Somateria mollissima* in the Netherlands: the rise and fall of breeding and wintering populations in relation to the stock of shellfish. – PhD thesis, Rijksuniversiteit Groningen, the Netherlands.
- Kenward, R. E. 1978. Hawks and doves: factors affecting success and selection in goshawk attacks on woodpigeons. – *J. Anim. Ecol.* 47: 449–460.
- Kenyon, J. K. et al. 2007. Can redistribution of feeding colonies on a landscape mitigate changing predation danger? – *J. Avian Biol.* 38: 541–551.
- LaGory, K. E. 1987. The influence of habitat and group characteristics on the alarm and flight response of white-tailed deer. – *Anim. Behav.* 35: 20–25.
- Laursen, K. 1985. Waterfowl and wader shooting in the Danish Wadden Sea and southern Jutland. – *Danske Vildtundersøgelser* 39: 1–60, in Danish.
- Laursen, K. and Frikke, J. 2008. Hunting from motorboats displaces Wadden Sea eiders *Somateria mollissima* from their favoured feeding distribution. – *Wildl. Biol.* 14: 423–433.
- Laursen, K. et al. 2005. Factors affecting escape distances of staging waterbirds. – *Wildl. Biol.* 11: 13–19.
- Laursen, K. et al. 2009. Mussel fishery affects diet and reduces body condition of eiders *Somateria mollissima* in the Wadden Sea. – *J. Sea Res.* 62: 22–30.
- Laursen, K. et al. 2010. Mussel fishery affects diet and reduces body condition of eiders *Somateria mollissima* in the Wadden Sea. – *J. Sea Res.* 62: 22–30.
- Lima, S. L. and Dill, L. M. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. – *Can. J. Zool.* 68: 619–640.
- Lind, J. and Cresswell, W. 2005. Determining the fitness consequences of antipredation behaviour. – *Behav. Ecol.* 16: 945–956.
- Madsen, J. and Fox, A. D. 1995. Impacts of hunting disturbance on waterbirds: a review. – *Wildl. Biol.* 1: 193–207.
- Meijer, T. and Drent, R. 1999. Re-examination of the capital and income dichotomy in breeding birds. – *Ibis* 141: 399–414.
- Milne, H. 1976. Body weight and carcass composition of the common eider. – *Wildfowl* 27: 115–122.
- Metcalf, N. B. and Furness, R. W. 1984. Changing priorities: the effect of pre-migratory fattening on the tradeoff between foraging and vigilance. – *Behav. Ecol. Sociobiol.* 15: 203–206.
- Miller, R. C. 1922. The significance of the gregarious habitat. – *Ecology* 3: 122–126.
- Minderman, J. et al. 2006. Behaviourally mediated indirect effects: interference competition increases predation mortality in foraging redshanks. – *J. Anim. Ecol.* 75: 713–723.
- Nehls, G. 1995. Strategien der Ernährung und ihre Bedeutung für Energiehaushalt und Ökologi der Eiderente (*Somateria mollissima*). – PhD thesis, Christian-Albrechts-Univ. zu Kiel, Germany.
- Nehls, G. and Ketzenberg, C. 2002. Do common eiders *Somateria mollissima* exhaust their food resources? A study on natural mussel *Mytilus edulis* beds in the Wadden Sea. – *Dan. Rev. Game Biol.* 16: 47–61.

- Noer, H. 1991. Distributions and movements of eider *Somateria mollissima* populations wintering in Danish waters analysed from ringing recoveries. – Dan. Rev. Game Biol. 14: 1–32.
- Öst, M. et al. 2008. Social and maternal factors affecting duckling survival in eiders *Somateria mollissima*. – J. Anim. Ecol. 77: 315–325.
- Peig, J. and Green, A. J. 2009. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. – Oikos 118: 1883–1891.
- Pihl, S. and Frikke, J. 1992. Counting birds from aeroplane. – In: Komdeur, J. et al. (eds), Manual for aeroplane and ship surveys of waterfowl and seabirds. IWRB Spec. Publ. 19: 8–23.
- Pulliam, H. R. 1973. On the advantage of flocking. – J. Theor. Biol. 38: 419–422.
- SAS 2010. SAS Institute, Cary, NC, USA.
- Seghers, B. H. 1974. Schooling behaviour in guppy (*Poecilia reticulata*): an evolutionary response to predation. – Evolution 28: 486–489.
- Sénéchal, E. et al. 2011. Do purely capital layers exist among flying birds? Evidence of exogenous contribution to arctic-nesting common eider eggs. – Oecologia 165: 593–604.
- Swennen, C. 1976. Population structure and food of the eider *Somateria mollissima* in the Dutch Wadden Sea. – Ardea 64: 311–371.
- Theisen, B. 1968. Growth and mortality of culture mussels in the Danish Wadden Sea. – Meddelelser Danmarks Fiskeri- og Havundersøgelser 6: 47–78.
- Thiollay, J.-M. 2005. Effects of hunting on Guianan forest game birds. – Biodiver. Conserv. 14: 1121–1135.
- Vine, I. 1973. Detection of prey flocks by predators. – J. Theor. Biol. 40: 207–210.
- Van Roomen, M. et al. 2012. Signals from the Wadden Sea: population declines dominate among waterbirds depending on intertidal mudflats. – Ocean Coastal Manage. 68: 79–88.
- Waltho, C. and Coulson, J. 2015. The common eider. – T & AD Poyser.

Supplementary material available online as Appendix wlb-00197 at <www.wildlifebiology.org/appendix/wlb-00197>). Appendix 1.