

Tools in waterfowl reserve management: effects of intermittent hunting adjacent to a shooting-free core area

Authors: Bregnballe, Thomas, and Madsen, Jesper

Source: Wildlife Biology, 10(4) : 261-268

Published By: Nordic Board for Wildlife Research

URL: <https://doi.org/10.2981/wlb.2004.031>

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.

Tools in waterfowl reserve management: effects of intermittent hunting adjacent to a shooting-free core area

Thomas Bregnballe & Jesper Madsen

Bregnballe, T. & Madsen, J. 2004: Tools in waterfowl reserve management: effects of intermittent hunting adjacent to a shooting-free core area. - Wildl. Biol. 10: 261-268.

We explored how waterfowl in a large Danish coastal wetland responded to one day of marsh shooting at intervals of three weeks (1998), two weeks (1999), and one week (2000 and 2001). Shooting took place around sunset on a section of salt marsh that usually is part of a large shooting-free refuge. The behavioural response of waterfowl was recorded, and all waterfowl were counted on the day of the hunt and on the first and second day after each hunt. The wildfowl responded to the first 1-7 shots by moving into the open water parts of the refuge (dabbling ducks) or to sites > 8 km away (geese and waders). When the salt marsh was flooded early in autumn 2001, wigeon *Anas penelope*, teal *A. crecca* and lapwing *Vanellus vanellus* restricted their response to movements to other non-hunted parts of the salt marsh. On the first day after the hunts, mallard *A. platyrhynchos* occurred in significantly lower numbers both on the adjacent shallow and on the salt marsh. Wigeon numbers on the shallows were not affected by shooting, though they returned in lower numbers to the salt marsh on the first day after the hunts in 1998-2000, but not after the hunts in 2001. A similar pattern was observed in teal numbers on the salt marsh. We conclude: 1) that shooting lead to short-term displacements of dabbling ducks, 2) that the response of wigeon and teal varied depending on prevailing conditions on the salt marsh, 3) that intermittent regulation of marsh shooting was a management tool that ensured that waterfowl continued to exploit the area shot over on days when no shooting took place, and 4) that the relatively weak responses were linked to the existence of an extensive refuge adjacent to the area with marsh shooting.

Key words: disturbance, mallard, shooting, teal, waterfowl refuges, wigeon, wildfowling

Thomas Bregnballe & Jesper Madsen*, National Environmental Research Institute, Department of Wildlife Ecology and Biodiversity, Kalø, Grenåvej 12, DK-8410 Rønde, Denmark - e-mail addresses: tb@dmu.dk (Thomas Bregnballe); jm@dmu.dk (Jesper Madsen)

*Present address: National Environmental Research Institute, Department of Arctic Environment, Frederiksborgvej 399, P.O. Box 358, DK-4000 Roskilde, Denmark

Corresponding author: Thomas Bregnballe

Received 11 June 2002, accepted 5 January 2004

Associate Editor: Hannu Pöysä

Hunting causes disturbance and displacement of migratory and wintering waterfowl in many wetlands in Europe (e.g. Meile 1991, Madsen & Fox 1995, Madsen 1998a,b, Väinänen 2001). This leads to conflict with local site management and conservation objectives, especially in EU Special Protection Areas (SPAs) and Ramsar sites designated as internationally important for migratory and wintering waterfowl. Consequently, reserves and refuge areas have been created in many parts of Europe to mitigate disturbance. However, the need for including adjacent terrestrial habitats into the shooting-free core areas in reserves is still a subject for debate (Madsen 1998b, Evans & Day 2001, Denny 2001). It is argued that especially quarry species will avoid using the inshore and terrestrial zone when shooting is allowed on adjacent land (see Madsen & Fox 1995, Guillemain, Fritz & Duncan 2002, Bregnballe, Madsen & Rasmussen 2004). Since the inclusion of adjacent land into shooting-free refuges is in conflict with local traditions for marsh shooting, it is necessary to identify tools to minimise the potential effects of wildfowling without entirely excluding hunting from the zones adjoining disturbance-free core areas (Davidson & Rothwell 1993, Fox & Madsen 1997).

Temporal regulation of hunting on a day-to-day basis has been suggested as a potentially useful tool. However, most studies have found that quarry numbers did not build up when intermittent shooting was applied (Andersson 1977, Jettka 1986, Jakobsen 1988, Ziegler & Hanke 1988, Gerhard 1994). The birds had only a few days of respite in some of these cases, and the experience of many hunters is that best practice requires periods free from hunting counted in weeks rather than in days (e.g. Bell & Owen 1990, Fox & Madsen 1997). Furthermore, in some of the studies where the interval between shootings lasted more than one week, the availability of nearby and large shooting-free areas to quarry species was limited. More manipulative studies are required to quantify bird use of buffer zones in the face of different levels of disturbance (Fox & Madsen 1997, Hill, Hockin, Price, Tucker, Morris & Treweek 1997).

To further reveal dose-response relationships between the frequency of hunting and bird use of adjacent land and inshore areas, an experiment was conducted in a large Danish coastal wetland. Marsh shooting was restricted to one day every third week in one year, one day every second week in one year, and one day every week in two years. The intervals were chosen based on previous studies which suggested between one and three week's respite time (Andersson 1977, Jettka 1986, Jakobsen 1988, Ziegler & Hanke 1988, Gerhard 1994). Based on our experiment, we explore 1) to what extent

the waterfowl remained near to the shooting site when shooting occurred, and 2) with what delay they resumed their usage of the intermittent shot-over area.

Material and methods

Study area

Our study area covered 46% of the salt marsh and 6% of the shallows (Fig. 1) included in the shooting-free area of the Ulvshale-Nyord wildlife reserve in southeast Denmark, which is also designated as a Special Protection Area (Madsen 1998b). Throughout the autumn, the salt marsh and shallows are used by large numbers of mute swans *Cygnus olor*, geese, dabbling ducks and waders (see Madsen 1998a,b, Bregnballe, Bøgebjerg & Hounisen in press). The salt marsh has large creeks and several small and large (up to 11 ha) salt-pans (see Fig. 1). It is used for cattle grazing until the last week of October, and human activities are limited to attendance of cattle and fences. The water shallows are extensive and large areas are densely vegetated with submerged macrophytes, mainly *Ruppia* spp., *Potamogeton*

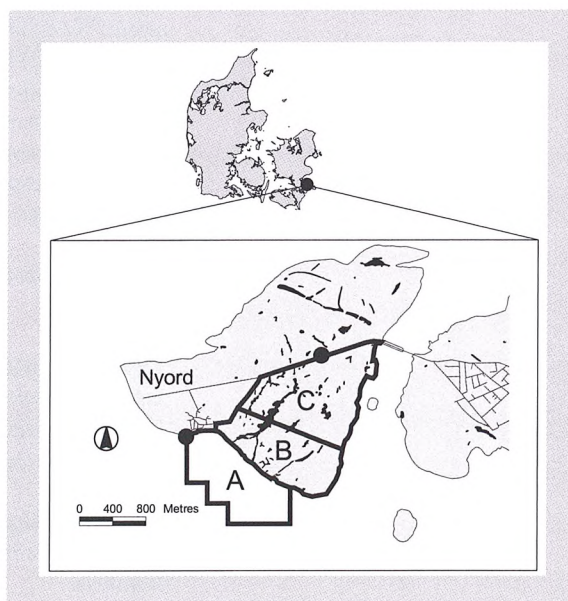


Figure 1. Location of the Nyord study area (sections A-C) in which the effect of intermittent shooting regulation was studied during September-December 1998-2001. Section A covers 6% of the shooting-free area of shallows. Section B constitutes the southernmost part of the salt marsh and is the area in which intermittent hunting was permitted during the experiment. The effect of intermittent hunting in section B on bird numbers was analysed for sections A, B and C. Black areas on the salt marsh denote creeks and salt-pans. The location of the observation tower on the north border of section C, and the site on the pier from which counts were made are shown (●).

pectinatus and *Zostera marina*, which constitute the main food source for mute swans, geese and dabbling ducks. Human activity on the shallows included in the study area was limited to tending of pound nets 1-2 times/day.

During September-December 1997-2001, water levels changed gradually over several days or shifted between high and low water levels within a single or a few days. Subsequently, water levels could remain high or low for several weeks. Day-to-day differences in water levels ranged within 1-93 cm (median: 8 cm). The timing when water filled the salt-pans varied markedly between years depending on precipitation in early autumn, and especially the timing and extent of flooding caused by high water levels.

Experiment

Shooting was prohibited on the southern salt marsh, i.e. sections B and C (205 ha; see Fig. 1), during 1990-1997. For the purpose of the experiment, hunting was introduced in September-December to section B (referred to as the hunting area; 76 ha) once every third week in 1998, once every second week in 1999, and once every week in 2000 and 2001. In 1998, hunters were allowed to enter the salt marsh and initiate shooting from 12:00, and shooting was permitted until 1½ hours after sunset. In 1999-2001, shooting was allowed from 1½ hours before to 1½ hours after sunset. Hunting always took place on Wednesdays, independent of weather, water level and presence/absence of waterfowl. The hunters always entered the salt marsh from the northwestern end of section B, and the hunters shot waterfowl, either when sitting without hides in low grass close to salt-pans or creeks, or when sitting close to reeds near the coast. Section C (129 ha) of the salt marsh remained shooting-free throughout the years 1990-2001. From 1991 onwards, shooting was prohibited in the open water refuge (1,249 ha) covering shallows, to the east, south and southeast of the salt marsh, including the islet and bays to the southeast (see Fig. 1). Unrestricted shooting took place from the reed beds along the north coast of the northern marsh (north of section C) independently of the experiment, and occurred on 15-25% of evenings, depending on year, and rarely involved more than 1-3 hunters (unpubl. data; K. Simonsen & M. Stolt, Nyord Jagtforening, pers. comm.).

Methods

The water level in 19 salt-pans/creeks was recorded 1-5 times/week by observation using a telescope from a 7 m high observation tower located at the north border of section C (see Fig. 1). The water level on the shallows

was determined 1-4 times/day on two fixed poles with scales.

To obtain information about the distribution and activity of hunters, each hunter denoted his location on a map, the number of shots fired, timing of arrival to and departure from the salt marsh, and timing of shooting. Furthermore, on 22 hunts, the timing of arrival and movements of the hunters and their dogs were observed from the tower, and the time of all shots fired was recorded.

Behavioural responses of the waterfowl to hunting were observed from the tower at one hunt in 1998, two hunts in 1999, 11 hunts in 2000 and eight hunts in 2001. Observations began when the first hunter entered the salt marsh, i.e. usually 1½ hours before sunset. Whenever a flock of geese, dabbling ducks or waders took flight, it was recorded (by noting or dictating to a tape recorder) whether or not the flock took flight because of disturbance stimuli, i.e. from walking hunters, running dogs, shots being fired or other causes. The sites at which flocks landed or the direction in which they disappeared was denoted on a map. The size of each flock taking flight was estimated, or individuals were counted, and the number of birds remaining on the salt marsh was counted whenever several flocks had taken flight.

To quantify the effect of hunting on the numbers of waterfowl returning on the days following each hunt, all waterfowl inside sections A-C were counted on the day of the hunt (but before the hunters entered the salt marsh) and on the first and second day after the hunt. To obtain information about longer-term effects, 14-34 supplementary counts were conducted annually during September-December 1998-2000. The waterfowl on the salt marsh (sections B-C) were counted from the tower, and the shallows were counted from a pier at the northern border of section A (see Fig. 1). Counts were conducted in the afternoon by use of a telescope (20-60x) and were always terminated before the hunters entered the salt marsh. The location of all waterfowl was plotted on detailed maps (1:6,000) made from aerial photographs, and the number of individuals foraging was recorded on most counts.

Data analyses

The number of individuals of each waterfowl species remaining inside the study area subsequent to disturbance from walking hunters, running dogs or shots was expressed as the proportion of the total number present on the shallow (section A) and on the salt marsh (sections B and C), respectively, before the hunters arrived at the salt marsh. For each species or group of species, we identified the series of events after which < 20% of the indi-

viduals remained in section A of the shallow and sections B and C on the salt marsh, respectively. We distinguished between the following series of events: (i) hunters had been walking and/or dogs had been running, (ii) hunters had been walking and/or dogs had been running, and the first two shots had been fired, (iii) the 3rd-7th shot had been fired, and (iv) more than seven shots had been fired. We distinguished between the period September 1998 - mid-September 2001 (referred to as 1998-2000) and the period mid-September 2001 - November 2001 (referred to as 2001) because the salt marsh was flooded in mid-September 2001, and this had a marked effect on subsequent numbers and distribution of waterfowl on the salt marsh.

The effect of shooting on the numbers returning after a hunt was analysed separately for the shallow (section A) and the southern salt marsh (section B+C). The northernmost area of the salt marsh (north of section C) was not included in the analyses, partly because of its distance to the shooting area and partly because of its low numbers of birds. Data from hunts that fulfilled the following criteria were included: 1) at least 30 individuals were present on the day of the hunt, 2) more than two shots were fired, 3) the temperature did not fall from above to below 0°C from the day of the hunt to the day after the hunt, 4) the water level did not decrease or increase by more than 20 cm from the day of the hunt to the day after the hunt. A species was included in the analyses if the above criteria were met for at least seven hunts. This and the above criteria were arbitrarily chosen, except for the water level and temperature criteria which were based on data about relationships between distributions of waterfowl and water level and temperature (Bregnballe et al. in press). In the shallows, the criteria were met for mute swan *Cygnus olor*, wigeon *Anas penelope* and mallard *A. platyrhynchos*, and in the salt marsh for greylag goose *Anser anser*, wigeon, teal *A. crecca*, mallard and lapwing *Vanellus vanellus*. Mute swan and lapwing were protected against hunting, whereas greylag goose, wigeon, teal and mallard had an open season from 1 September to 31 December.

A one-sided paired t-test was applied to test whether waterfowl numbers declined significantly from the day of the hunt (before the hunters entered the salt marsh) to the first and second day after the hunt. The number of waterfowl present on the first and second day after the hunt were thus tested against the number of individuals present 0-1 1/2 hours before the hunters entered the shooting area.

Results

Hunting effort

There were 9-13 hunters on the salt marsh in 40 hunts and 3-8 hunters in five hunts. The majority of hunters walked to their sites between 1 1/4 hours before sunset and 1/2 hour after sunset. The first shots were fired before 1/2 hour before sunset at 13 of the 14 hunts observed from the tower. At 12 of the hunts the first five shots were fired before 1/4 hour before sunset. The majority of shots (> 87%) were fired 1/4-1 hour after sunset, i.e. when dabbling duck flight activity was high. The total number of shots per hunt ranged from no shots during one hunt, over 1-2 shots during two hunts, 6-8 shots during five hunts, 11-40 shots during 18 hunts, 41-80 shots during 11 hunts, to 81-210 shots during eight hunts.

Behavioural responses to shooting

At the first shots, mute swans on the shallows swam from the shore towards deeper waters; in only one of 12 cases did 40-50% of the swans take flight because of shots (Table 1). The majority of dabbling ducks left section A of the shallows before the eighth shot, and they usually landed in the shallows around the islet south-east of the salt marsh or between the southern tip of the salt marsh and the islet, i.e. they usually moved < 3 km.

On the salt marsh, waterfowl usually responded to walking hunters and running dogs by taking flight when approached, but usually the waterfowl landed again on the salt marsh, though at a longer distance. During a few hunts, > 80% of the greylag geese and dabbling ducks left the hunting area (section B) and the adjoining section of salt marsh (section C) because of walking hunters and/or running dogs. On these days, the hunting area and its immediate surroundings (sections A-C) were emptied of waterfowl (except swans) before the onset of shooting. On most hunts, the majority of

Table 1. Number of hunts during which < 20% of the wildfowl remained on the shallow (section A) and the salt marsh (section B+C) after hunters and dogs had disturbed flocks of wildfowl or after 1-2, 3-7 or >7 shots had been fired during 1998-2000 and in 2001 (in parentheses).

Area/species	< 20% remained in the area after				> 20% remained throughout the hunt
	Activity of hunters and dogs	1-2 shots	3-7 shots	> 7 shots	
Shallow					
Mute swan				1	11
Dabbling ducks	2	4	5 (2)	1	1
Salt marsh					
Greylag goose	3	1	4	1 (1)	1 (2)
Dabbling ducks	2		8	(1)	1 (4)
Golden plover	1	1	1		(3)
Lapwing		1	2		(3)

Table 2. Mean number of wildfowl and range of numbers present on the shallow (section A) and on the salt marsh (section B+C) before hunters entered the area on the day of the hunt (N gives the number of hunts from which count data were included), and test statistics for paired t-tests comparing pre-hunting levels with numbers present on the first and second day after the hunts, respectively. Significant differences of one-tailed tests after Bonferroni correction are denoted with an asterisk.

Area/species	Number of individuals present before the hunt			Before vs the first day after the hunt		Before vs the second day after the hunt	
	Mean	Range	N	t	P	t	P
Shallow							
Mute swan	168	60- 377	12	1.89	0.086	1.61	0.139
Wigeon	132	30- 355	27	0.20	0.841	0.36	0.724
Mallard	172	35- 430	23	3.91	< 0.001*	0.50	0.621
Salt marsh							
Greylag goose	256	31- 996	23	0.42	0.676	0.03	0.975
Wigeon	599	55-1459	13	0.02	0.236	1.16	0.273
Teal	360	80- 845	17	1.31	0.984	0.51	0.619
Mallard	69	32- 94	8	3.67	0.008*	1.42	0.204
Lapwing	267	40- 705	9	1.72	0.124	1.57	0.161

geese and dabbling ducks left the hunting area and section C before the eighth shot.

In 2001, wigeon, teal, golden plover *Pluvialis aprinaria* and lapwing differed in their response compared to the previous three years. Thus, rather than leaving the salt marsh after having taken flight, wigeon, teal, golden plover and lapwing responded to the first shots by moving to the northern and northeastern part of section C where they remained and either resumed roosting (teal, golden plover and lapwing) or foraging (particularly wigeon) at 500-1,200 m distance from the shooting area.

When greylag geese left the salt marsh because of hunting disturbance, they usually flew at least 9 km to reach their night roost or the fields they often frequented before moving on to their night roost. Dabbling ducks disturbed on the salt marsh flew to the shallows to the southeast with most flocks landing around the islet, i.e. in the centre of the refuge. Golden plover and lapwing departed from the entire wetland area and flew south to areas located > 8 km from the salt marsh.

Numerical responses

The number of mallards present in section A on the shallows was significantly lower on the first day after hunt-

ing on the salt marsh than on the day of the hunt (Table 2) and declined in 19 out of 23 cases (Table 3). The numbers of mute swan and wigeon present on the shallows were not significantly affected by hunting (see Table 2), however, mute swan numbers were lower after nine hunts and higher after only three hunts (see Table 3).

Greylag geese, wigeon, teal and lapwing did not occur in significantly lower numbers on the salt marsh on the first or second day after the hunt than on the day of the hunt (see Table 2), but there was a significant decline in the number of mallards (see Table 2) with mallard numbers declining in seven out of eight hunts (see Table 3). Mallard numbers were also lower on the second day in six out of eight cases (see Table 3), but the decline was not significant (see Table 2). Lapwing numbers were lower on the first day after seven out of nine hunts than on the day of the hunt, but the declines were generally small (see Table 3).

Importance of prevailing conditions

The effect of hunting on wigeon and teal numbers on the salt marsh changed significantly from 1998-2000 to 2001. Wigeon numbers declined after six out of six hunts in 1998-2000, but in 2001 when the salt marsh became

Table 3. Number of hunts during which the numbers of wildfowl present on the shallow (section A) or on the salt marsh (section B+C) declined or increased from the day of the hunt to the following day.

Area/species	% decline				% increase			
	76-100	51-75	26-50	1-25	0-50	51-100	101-200	201-300
Shallow								
Mute swan		3	4	2	3			
Wigeon	5	3	2	2	6	5	3	1
Mallard	4	8	4	3	4			
Salt marsh								
Greylag goose	5	2	4	2	5	1	3	1
Wigeon	2		5		5	1	1	
Teal	3	3	3	2	3	3	1	
Mallard	5	2			1			
Mallard ¹	2	2		2				2
Lapwing	1		3	3	1	1		

¹ From the day of the hunt to the second day after the hunt.

extensively flooded early in autumn, wigeon numbers declined after only one out of seven hunts (Fisher's Exact Test: $P = 0.0047$). Teal numbers declined after 11 out of 12 hunts in 1998-2000 but after none out of six hunts in 2001 (Fisher's Exact Test: $P = 0.0004$).

Discussion

The wildfowl studied in our experiment showed behavioural as well as numerical responses to hunting activity on a section of salt marsh adjoining a shooting-free refuge. The wildfowl present inside the hunting area and in the two adjoining areas almost always responded to shooting by moving to neighbouring or more distant sites. The dabbling ducks took advantage of the proximity of the extensive shooting-free shallows which offered many alternative roosting sites. On the first day following hunting, mallard returned in reduced numbers on the shallows as well as on the salt marsh. This was also the case for wigeon and teal occurring on the salt marsh in 1998-2000. Greylag goose was, however, indifferent to intermittent shooting. Some greylag geese (5-32%, $N = 12$) left the salt marsh in between the termination of the count and the firing of the first shots and, therefore, not all the counted geese experienced that shooting took place on the southern section of salt marsh. Furthermore, many individuals (also of other species than greylag goose) abandoned the area at the first shots or, more rarely, soon after the hunters arrived. These early leaving individuals would not have experienced whether few or many shots were fired, unless they landed near to the area shot over.

The chances of detecting that some individuals abandon a site and postpone their return because they experience shooting, will vary among species depending on the turnover of individuals and their tendency to move among potential feeding and/or roosting sites from day to day. On specific parts of the shallows, wigeon numbers varied extensively from day to day because flocks were moving among foraging sites, mainly in response to changing water levels (Bregnballe et al. in press). Therefore, it is not unlikely that some of the individuals that appeared in section A on the shallows on the day after the hunt, may have been unaware that shooting had taken place on the previous evening (these individuals may have roosted or foraged far from the salt marsh when shooting took place). This may explain the absence of an effect of hunting on wigeon numbers on the shallows. At the other extreme, mallards were almost always roosting at a certain site on the coast of section A, and day-to-day fluctuations in numbers were normally low,

suggesting site faithfulness and a low turnover. We propose that the absence of arrival of new naive individuals on the days following shooting combined with a postponed return of the (or some of the) mallards normally present, gave rise to the decline in numbers on the first day after shooting.

The decision whether or not to return to a disturbed site is likely to be affected by the attractiveness of the site and the availability of equally attractive neighbouring sites. In 1998-2000, wigeon and teal mainly used the salt marsh as a roosting area during daytime with almost all birds occurring in the salt-pans and creeks. In these years, fewer birds returned on the first day after shooting than had been present on the day of the hunt. On the day subsequent to shooting, dabbling ducks were usually roosting on the shallows near the islet to the southeast of the salt marsh. This area of shallow water and sandbars may have functioned as an equally suitable roosting site as the salt-pans and creeks, i.e. the cost of not returning to the salt marsh on the following day may have been low because of its use mainly as a roosting site. The importance of the salt marsh as a foraging area was high in 2001 when the salt-pans and creeks were flooded, and the grass became partially flooded in early autumn (Bregnballe et al. in press). Therefore, leaving the salt marsh in 2001 probably meant leaving an attractive feeding area. In the autumn of 2001 wigeon and teal immediately returned to the salt marsh in numbers equal to those present prior to hunting. This shift in response in 2001 may reflect that the cost of not returning to the salt marsh subsequent to hunting was high in 2001 compared with the previous years. We interpret the shift in response as support for Houston, McNamara & Hutchinson's (1993) suggestion that the decision of individuals whether or not to return to a disturbed site depends on its value as a foraging site.

Management implications

The number of waterfowl exploiting the shot-over area and the neighbouring areas was not hampered by shooting in one section of the salt marsh at 1-3 weeks interval, except for the fact that some species returned in reduced numbers on the first day after a hunt. We found no indications that overall numbers nor the probability of returning to pre-hunting levels was lower when shooting occurred at an interval of one week rather than two or three weeks. In a German lake, Gerhard (1994) found that duck numbers usually returned to the original level within four days, occasionally even as soon as the following day. But Andersson (1977) studied the recovery of mallard on a Swedish lake where shooting was allowed one day each week, and he found that

mallards needed a respite of more than one week to reach pre-hunting levels. In Northwest Germany, mallard shooting took place at monthly intervals, and it took ca three weeks for numbers to recover (Jettka 1986). These differences in effects demonstrate that responses will vary between locations (and in some cases also within locations), depending on the prevailing local conditions (cf. Fox & Madsen 1997, Gill, Norris & Sutherland 2001, this study).

There is no doubt that the buffer against disturbance effects was high in our study area. All dabbling ducks had direct access to an adjacent refuge covering an extensive area of shallow waters offering many alternative roosting sites under most water level and wind conditions. Furthermore, the selected combination of temporal and spatial shooting regulation reduced the extension of shooting disturbance, both in time and space.

In our study seven shots appeared to be as disturbing as > 40 shots, i.e. the majority of waterfowl abandoned the area as soon as the first shots were fired. However, the dabbling ducks that flew to forage on the salt marsh at dusk may have been more reluctant to return on the nights following evenings when many shots were fired. Thus, on salt marshes in the northern part of the Wadden Sea, Jakobsen (1988) found ducks to be six times as abundant on nights following no shooting than on nights after shooting had taken place. Likewise, J. Thallund (in Meltofte 1994) found that night-time feeding activity of ducks outside a reserve decreased sharply during four successive evenings of hunting alternating with three days of no hunting.

We conclude that intermittent regulation of marsh shooting with an interval of at least one week offered a tool to ensure that waterfowl exploited the shot-over inshore zones and marshes outside the days when shooting took place, except for the day after the shooting. Temporal restrictions of shooting may thus be an applicable tool to manage marsh shooting in zones adjoining permanent shooting-free areas. However, it is predicted that responses will be more pronounced and last longer in areas where the turnover of individuals is low and the target species do not have easy access to adequate, alternative roosting sites nearby.

Acknowledgements - the experiments were funded by the Danish Environmental Research Programme under the topical centre Changing Landscapes in 1997-2000 and by the National Forest and Nature Agency in 2001. We thank the National Forest and Nature Agency for making the experiment possible through dispensations from reserve regulations. The study would not have been possible without the close collaboration of the local hunting club, local hunters and land owners.

Ebbe Bøgebjerg, Jens P. Hounisen, Per A. Kjær, Max Nitschke, Uffe Sørensen and John Faldborg are thanked for their participation in collecting data in the field. Thomas E. Holm is thanked for support with preparing the map. Tony Fox is thanked for commenting on the manuscript.

References

- Andersson, Å. 1977: Andjakten i Hullsjön. - Report, Skogshögskolan, Uppsala, 26 pp. (In Swedish).
- Bell, D.V. & Owen, M. 1990: Shooting disturbance - a review. - In: Matthews, G.V.T. (Ed.); Managing Waterfowl Populations, International Wetlands and Waterfowl Research Bureau Special Publication no. 12. IWRB, Slimbridge, UK, pp. 159-171.
- Bregnballe, T., Bøgebjerg, E. & Hounisen, J.P. in press: Regulering af jagt på vandfugle i kystzonen: Forsøg med datoregulering på Nyord. - Danmarks Miljøundersøgelser, Arbejdsrapport. (In Danish).
- Bregnballe, T., Madsen, J. & Rasmussen, P.A.F. 2004: Effects of temporal and spatial hunting control in waterbird reserves. - *Biological Conservation* 119: 93-104.
- Davidson, N.C. & Rothwell, P.I. 1993: Human disturbance to waterfowl on estuaries: conservation and coastal management implications of current knowledge. - *Wader Study Group Bulletin* 68: 97-105.
- Denny, M.J.H. 2001: Waterfowl disturbance: Effects of hunting in a coastal ecosystem. - PhD thesis, University of Sunderland, 166 pp.
- Evans, D.M. & Day, R.D. 2001: Does shooting disturbance affect diving ducks wintering on large shallow lakes? A case study on Lough Neagh, Northern Ireland. - *Biological Conservation* 98: 315-323.
- Fox, A.D. & Madsen, J. 1997: Behavioural and distributional effects of hunting disturbance on waterbirds in Europe: implications for refuge design. - *Journal of Applied Ecology* 34: 1-13.
- Gerhard, M. 1994: Ursachen und kurzfristige Auswirkungen von Störungen auf den Wasservogelbestandes Biebersteiner Weihers. - *Charadrius* 30: 70-76. (In German).
- Gill, J.A., Norris, K. & Sutherland, W.J. 2001: Why behavioural responses may not reflect the population consequences of human disturbance. - *Biological Conservation* 97: 265-268.
- Guillemain, M., Fritz, H. & Duncan, P. 2002: The importance of protected areas as nocturnal feeding grounds for dabbling ducks wintering in western France. - *Biological Conservation* 103: 183-198.
- Hill, D., Hockin, D., Price, D., Tucker, G., Morris, R. & Treweek, J. 1997: Bird disturbance: improving the quality and utility of disturbance research. - *Journal of Applied Ecology* 34: 275-288.
- Houston, A.I., McNamara, J.M. & Hutchinson, J.M.C. 1993: General results concerning the trade-off between gaining energy and avoiding predation. - *Philosophical Transactions*

- of the Royal Society of London B, Biological Sciences 341: 375-397.
- Jakobsen, B. 1988: Skumringsjagten på Skallingen. - In: Meltofte, H. (Ed.); Naturpejlinger. Skov- og Naturstyrelsen, Miljøministeriet, København, Denmark, pp. 162-166. (In Danish).
- Jettka, H. 1986: Jagdstreckenauswertung der Stockenten (*Anas platyrhynchos* L.) in einem Revier des Münsterlandes in Nordrhein-Westfalen. - Zeitschrift für Jagdwissenschaft 32: 90-96. (In German).
- Madsen, J. 1998a: Experimental refuges for migratory waterfowl in Danish wetlands. I. Baseline assessment of the disturbance effects of recreational activities. - Journal of Applied Ecology 35: 386-397.
- Madsen, J. 1998b: Experimental refuges for migratory waterfowl in Danish wetlands. II. Tests of hunting disturbance effects. - Journal of Applied Ecology 35: 398-417.
- Madsen, J. & Fox, A.D. 1995: Impacts of hunting disturbance on waterbirds - a review. - Wildlife Biology 1: 193-207.
- Meile, P. 1991: Die Bedeutung der "Gemeinschaftlichen Wasserjagd" für überwinternde Wasservögel am Ermantinger Becken. - Der Ornithologische Beobachter 88: 27-55. (In German).
- Meltofte, H. 1994: Registrering af jagten på Værnengene 1928-1990. - Dansk Ornitologisk Forenings Tidsskrift 88: 23-32. (In Danish).
- Väänänen, V-M. 2001: Hunting disturbance and the timing of autumn migration in *Anas* species. - Wildlife Biology 7: 3-9.
- Ziegler, G. & Hanke, W. 1988: Entwicklung von Stockenten (*Anas platyrhynchos*) - Beständen in der Häverner Marsch unter dem Einfluss der Jagd. - Die Vogelwelt 109: 118-124. (In German).