Aggression is unlikely to drive Common Scoter *Melanitta nigra* progressive winter dispersal in Aalborg Bugt, Denmark

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Abstract

Common Scoter *Melanitta nigra* progressively disperse into deeper waters through the winter in Aalborg Bugt, Denmark, a pattern previously potentially attributed to density-dependent foraging due to prey depletion or changes in prey quality. An alternative explanation is that increasing intra-specific aggression or mate-guarding behaviour forces birds to spread out as winter progresses. To test this, scan sampling of Common Scoter behaviour was carried out along the Djursland coast during two winters (2024/25 and 2025/26). Of 2,892 individuals observed, none showed aggressive behaviour, and nearest-neighbour distances showed no consistent seasonal trend. These results provide no support for the social-spacing hypothesis and suggest that behavioural interactions are unlikely to contribute to the large-scale dispersal patterns documented in this region. Rather, they confirm that the species shows little winter territorial behaviour. This is likely because their benthic prey are continuously distributed (rather than patchy) in uniform habitat, so are not defensible, reducing incentives for aggressive spacing. The findings strengthen the inference that prey depletion, changes in prey quality or other density-dependent processes remain the most plausible mechanisms underlying winter redistribution in this species.

Key words: agonistic interactions, courtship, non-breeding density, offshore dispersal, winter redistribution.

Energetic constraints on sea ducks increase towards mid-winter as temperatures fall and daylength shortens. Continued exploitation of non-renewed finite food resources in the most easily accessible habitats (*e.g.* Common Scoter *Melanitta nigra* feeding on Atlantic Jackknife Clams *Ensis leei* that reproduce in early summer and early autumn; Phillipart *et al.* 2014; Kottsieper *et al.* 2019) likely intensifies competition for high-quality foraging sites as the winter progresses. In addition, pairing among scoter species (including Common Scoter) is thought to occur in winter (Carboneras & Kirwan 2020) so increasing defence of females (both to secure mating access and to secure feeding opportunities for them prior to breeding) might potentially also be expected

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to occur. Under such conditions, one might expect aggressive interactions to become more frequent later in the season. However, aggression may also be driven by short-term ecological factors, including local prey availability, flock density, disturbance, or weather conditions, which can vary markedly over hours or days.

Aerial surveys of Common Scoter in Danish and German marine areas showed that birds progressively spread out, dispersing over greater areas and into deeper waters as the non-breeding period continued (Fox *et al.* 2025). This pattern has been interpreted as being a response to density-dependent foraging pressures, caused by prey depletion and/or the arrival of additional birds. In the absence of evidence from repeated sampling of the food supply, those authors could not exclude other hypotheses to explain these consistent patterns across years and between two major wintering areas (the German Wadden Sea and the more sheltered less tidal Danish Aalborg Bugt) for the species. These included the hypothesis that intraspecific aggression and/or mate guarding increased as the winter progressed, forcing birds to spread out in late winter, resulting in the observed expansion in foraging range through the winter. Aggression inevitably influences spacing behaviour in several waterfowl species, including sea ducks, particularly during courtship or when defending profitable foraging patches (Eadie & Savard 2015). If Common Scoter exhibit similar seasonal increases in agonistic behaviour, this could provide a behavioural explanation for increasing winter dispersal. Here, this hypothesis is tested using scan sampling of Common Scoter behaviour in Aalborg Bugt over two winters, to determine whether there are seasonal changes in: (i) the proportion of Common Scoter within 1 m of each other, and (ii) levels of courtship and aggression that could contribute to observed declines in density.

Methods

Study area

Observations were conducted from seven observation points along the north coast of Djursland in eastern Jutland, Denmark between Hevring Strand (56.5226°N, 10.4420°E) and Gjerrild North Strand (56.5312°N, 10.8309°E, Fig. 1). The area forms the southern margin of Aalborg Bugt, one of the most important moulting and wintering areas for Common Scoter in Danish inshore waters (Nielsen *et al.* 2024; Fox *et al.* 2025), where the birds frequently feed close inshore over shallow (generally < 12 m), sandy (*i.e.* particle size 0.06–2.0 mm) bottom substrates (GEUS 2014; Lomholt *et al.* 2017; Allaart *et al.* 2026). Although interspersed with areas of mud and silt near river outflows and gravel in some areas, rocky substrates and stone reefs are rare and spatially highly restricted, resulting in relatively uniform sandy sea bottom substrates over very large areas of Aalborg Bugt, especially along the study area coastline. The coastal bivalve communities of the clean sandy substrates north of Djursland are apparently dominated by Atlantic Jackknife Clams (an invasive species but an important food source for Common Scoter elsewhere; Kottsieper *et al.* 2019; Schwemmer *et al.* 2019), although many other mollusc species

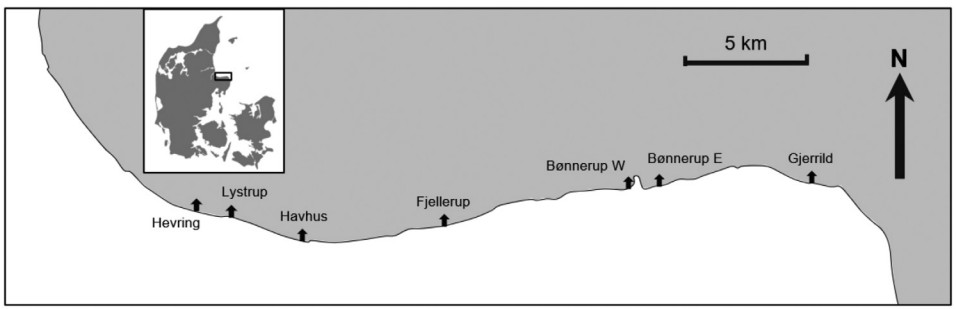


Figure 1. The location of the study area along the north coast of Djursland, eastern Jutland, Denmark (insert map), and the seven observation points (named) where scans of Common Scoter behaviour were made in winters 2024/2025 and 2025/2026 (main map).

such as the White Furrow Shell *Abra alba*, Icelandic Cyprine *Arctica islandica*, Common Basket-shell *Corbula gibba*, Bean-like Tellin *Tellina fabula*, Thin Tellin *T. tenuis* and *Thracia phaseolina* also occur (Gogina *et al.* 2016; Riemann *et al.* 2020). Some of which have also been identified in the diet of Common Scoter elsewhere (Fox 2003).

Activity budget sampling

Scan sampling was conducted primarily on still days, with Douglas sea states of 0–2 (*i.e.* flat calm to waves of 0.5 m "smooth" sea surface), to ensure maximum visibility and unambiguity in determining individual behaviours. Using a ×60 telescope, all identifiable Common Scoter within range were assigned to one of seven activity states. These were swim/loaf, preen, display, dive (when a bird was noted surfacing or submerging), aggression, sleep and other (all remaining behaviours). Scan sampling was chosen in preference to focal bird sampling to increase sample sizes but also to increase the probability of observing rare behaviours (Altmann 1974). Each bird was also recorded as being either < 1 m or ≥ 1 m of its nearest neighbour when encountered, as an index of local spacing, although this inevitably frequently included both members of a pair. To avoid pseudo-replication, only one scan was made per observation point per day, so birds were deliberately not re-sampled. Data were however gathered from as many separate vantage points along the coast as possible on a given date. Scans were initiated between 09:00 and 20:00 h on nine dates in both winters to avoid any diurnal bias. Percentage daily activity was calculated from data from all vantage points where the species was present and presented as means (± s.d.) of these discrete site-based observations. As the objective of this study was not only to describe seasonal changes in relative distribution (proximity) of the birds but to assess the role of aggression (which was not witnessed) in their dispersal, no statistical treatment was applied to the data.

Results

Scans showed that 63.7% of Common Scoter were swimming/loafing when encountered (74.4% in 2024/25; 51.8% in 2025/26; n = 1,130 and n = 712, Fig. 2),

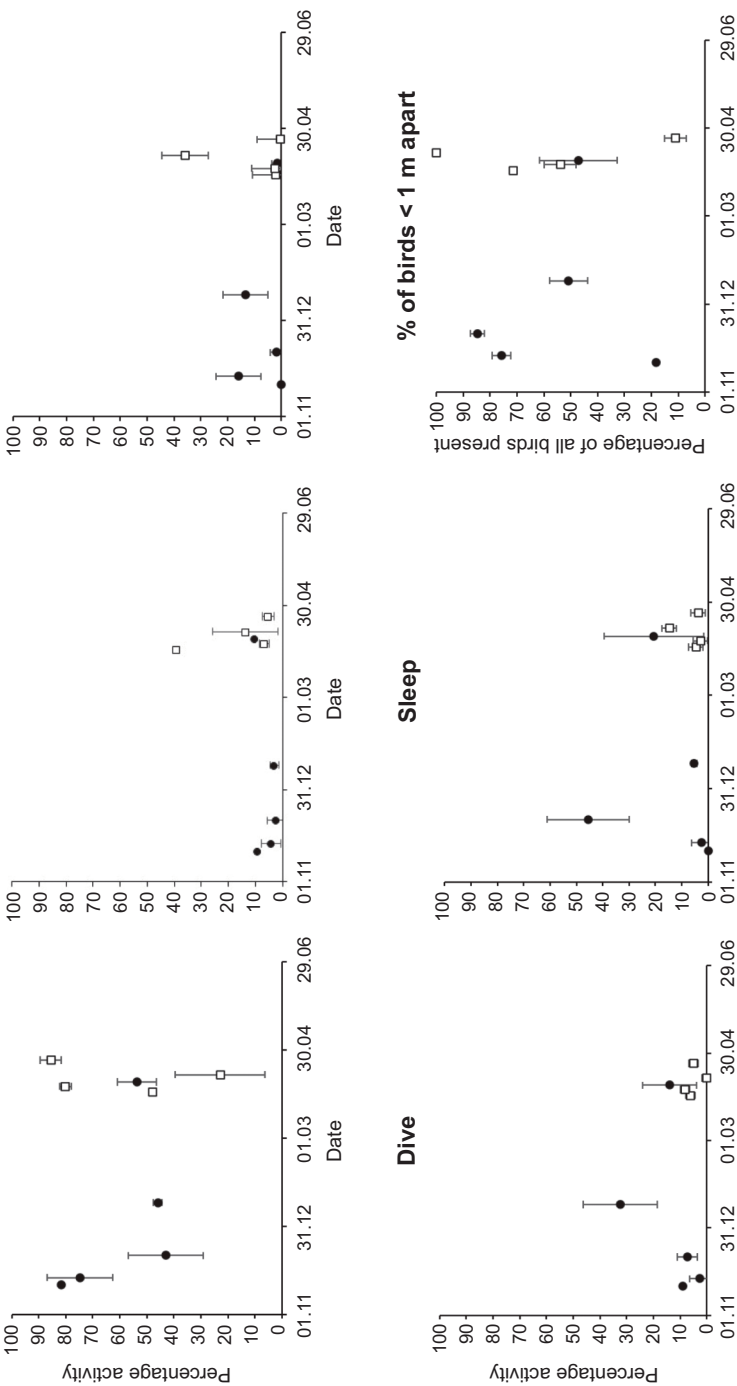


Figure 2. Behaviour plots of the five most frequently observed activity states recorded during behaviour scans of Common Scoter along the north coast of Djursland in winters 2024/2025 (open squares) and 2025/2026 (filled circles). Bottom right graph shows the percentage of all birds less than 1 m apart.

8.0% preening (10.1% in 2024/25; 5.6% in 2025/26; n = 154 and n = 77); 6.7% displaying (4.2% in 2024/25; 9.6% in 2025/26; n = 64 and n = 132), 12.7% diving (submerging/surfacing 5.6% in 2024/25; 20.5% in 2025/26; n = 85 and n = 282) and 8.9% sleeping (5.6% in 2024/25; 12.4% in 2025/26; n = 85 and n = 171). Crucially, no aggressive behaviour was recorded among the 2,892 individuals observed. Mean proportions of daily nearest-neighbour distances of < 1 m varied widely (ranging from zero to 100% within 1 m, Fig. 2), with no consistent seasonal pattern. Although courtship was observed regularly (but sporadically with no clear seasonal pattern), none involved major interactions that caused displacement, chasing or threat postures that resulted in a major displacement of participants in such activity.

Discussion

These observations provide no support for the hypothesis that increasing aggression contributes to the progressive dispersal of Common Scoter through the winter in Aalborg Bugt. Based on 2,892 behavioural observations spanning two winters, the complete absence of aggressive interactions indicates that agonistic behaviour is extremely rare among these birds during the non-breeding period, despite extensive opportunities to detect chases, displacement or threat postures. The absence of aggression is consistent with the species' ecology: Common Scoter can be extremely social in their foraging, showing synchronous diving, exploit uniformly distributed benthic prey in continuously even habitat, and exhibit limited territoriality in winter, all of which reduce incentives for aggressive spacing (Goudie & Ankney 1986). Sea ducks generally show low territoriality in winter because bivalve and benthic prey are frequently uniformly distributed (whether on sandy, gravelly or rocky substrates). As a result, their food resources are not easily defensible, reducing incentives for aggressive spacing in response to, for instance, highly patchy food resources.

Low levels of aggression have been reported previously in sea ducks. Goudie (1999) found < 1% agonistic behaviour in wintering scoters in British Columbia, attributing this to high flock synchrony and long-term pair-bonds (Robertson *et al.* 1998). The results presented here are very similar, although courtship activity was more frequent in Aalborg Bugt, consistent with generally described winter timing of courtship and pair-bond maintenance activity (Carboneras & Kirwan 2020). While courtship does not equate to aggression, in displaying groups, it may have been the case that defence of mates could result in group members being displaced away, but this was never observed to be the case. Importantly, despite encountering frequent courtship displays, none involved aggression or displacement, even in small aggregations where competition for mates resulting in displacement of some flock members might be expected. In contrast, whereas male Surf Scoters *Melanitta perspicillata* caught during moult in Canada likewise showed little aggression towards each other in the holding crates, adult females of the same species (caught at the first autumn staging area on departure from the breeding grounds) were highly aggressive and fought

with any conspecifics held in the same crate while males remained fairly docile (Scott Gilliland, pers. comm.). Aggression in scoters therefore may be highly species- and context-specific in nature.

The absence of aggression indicates that social-spacing is unlikely to drive the large-scale dispersal patterns documented by Fox *et al.* (2025). This strengthens the inference that density-dependent foraging processes, such as prey depletion, redistribution of birds arriving from other areas, or changes in prey quality/accessibility, remain the most plausible mechanisms behind the observed seasonal expansion into deeper waters.

One should be careful not to conclude too much from such a highly restricted set of data. Observations were restricted to calm weather and close inshore waters, which may bias the behavioural repertoire toward loafing and preening. Aggression, if present, might occur more frequently in deeper offshore feeding areas that were not sampled. Scan sampling is known to under-detect rare, brief behaviours, although the large sample size here makes it unlikely that frequent aggression went unnoticed. All observations were carried out in daylight, so nocturnal or crepuscular aggression cannot be excluded, although sea ducks typically show reduced social activity at night and Common Scoter specifically are known to fly from feeding areas to roost well away from daytime feeding areas (Patterson 2021). Finally, the study design was descriptive rather than inferential; while this is appropriate for a negative result, it limits the ability to quantify more subtle seasonal trends. Despite these caveats, the complete absence of aggression across two winters provides strong evidence that agonistic interactions are not a meaningful driver of winter dispersal in this population. It also underlines how little is known about the behaviours of non-breeding sea ducks that would certainly merit further research.

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