

Spatial and temporal patterns of foraging activity by breeding Common Scoters (*Melanitta nigra*) in Scotland

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Many populations of sea ducks have declined; poor foraging conditions in freshwater breeding habitats could be a contributory factor. The UK breeding population of Common Scoters (*Melanitta nigra*) declined by 63% between 1995 and 2007, prompting research which showed that lake use by breeding scoters was correlated with food abundance (large invertebrates) and accessibility (shallow water). Building on this earlier work, here we investigate scoter foraging activity at Scottish breeding lakes, in order to better understand declines and inform conservation measures. We hypothesised that foraging effort would (i) be concentrated in shallow water holding large invertebrates, (ii) differ between sexes, and (iii) vary through the season. We recorded scoter foraging activity during 208 *c.* one-hour watches, at 13 lakes over three years. Water depth and food abundance (invertebrates) were measured. Foraging was significantly associated with shallow water: areas within 10 m of lake shores, typically less than 0.9 m in depth, had 1.9 and 4.1 times more foraging use than expected by chance, for females and ducklings respectively. Where large invertebrates were relatively abundant, the association with shallow water was weaker, implying that abundant food facilitated foraging across a wider range of water depths. Contrary to expectations, males and females expended similar foraging effort on breeding lakes. We discuss various interpretations of this result, and recommend tracking studies to help resolve these. There was no evidence that foraging effort of pre-breeding females or broods varied seasonally. Our study highlights the value of shallow water and large invertebrates to breeding Common Scoters. Conservation action should therefore seek to protect and enhance these habitat elements, for example via management of water levels or fisheries.



1. Introduction

The ability of foraging birds to meet their nutritional needs can strongly affect breeding success and survival, and therefore, bird population trends (Newton 1998). Birds from a wide range of taxonomic groups increase their reproductive performance following food supplementation (Robb *et al.* 2008), via benefits at both the egg and chick stages (Rufino *et al.* 2014). Where food acquisition affects reproduction, natural selection should favour birds choosing profitable foraging locations (Sherry 2016). Preferred foraging locations can therefore reveal where food is most efficiently obtained (Flower *et al.* 2014), helping explain and confirm habitat associations at larger (home range) scales (Morrison *et al.* 2006).

Reliable information on habitat associations helps inform conservation actions (Bradbury *et al.* 2000). Reliability is improved if the patterns found in an initial study, are tested against those found in follow-up studies using different datasets and/or working at different spatial scales (Morrison *et al.* 2006). Robust habitat association information can be especially important to the design of effective conservation interventions. Meanwhile, sustained periods of elevated foraging effort (e.g., days or weeks) may indicate periods of food shortage (Lovette & Holmes 1995), which may affect population trends by reducing survival or reproductive output.

Waterfowl (Anatidae), like other birds with precocial young, have high nutritional demands in the breeding season, affecting breeding females (due to high clutch mass relative to body mass: Alisauskas & Ankney 1992), and chicks (to enable rapid growth rates: Sedinger 1992). Not only do precocial chicks have to feed themselves, they also face high risks of predation and chilling, which can be exacerbated by food shortage (Newton 1998). Hence, breeding season processes tend to strongly affect populations of bird species with precocial young (Sæther *et al.* 1996).

For migratory waterfowl, the nutritional requirements of breeding females could be met using resources acquired either during migration, or at breeding sites (“capital” and “income” breeders respectively: Jönsson 1997). If other factors (trends in body condition, prey choice and capture rate) are similar for males and females, and breed-

ing season foraging only happens at breeding sites, then female income breeders should spend more time foraging at breeding sites than males, reflecting their greater nutritional needs (Oppel *et al.* 2011, Arzel & Elmberg 2015). In sea ducks (Anatidae: Mergini), income breeding is the most commonly reported strategy (Alisauskas & Devink 2015). This pattern could apply in most ducks, but evidence is sparse for many species (Arzel *et al.* 2006) and mixed strategies could be commonplace (Drent *et al.* 2006).

Here, we investigate temporal and spatial patterns of foraging by breeding Common Scoters (*Melanitta nigra*) in Scotland. This population suffered a 63% decline over 25 years, down to only 52 pairs in 2007. Common Scoter is now a red-listed UK Bird of Conservation Concern (Eaton *et al.* 2015). Therefore, like other declining sea duck populations (Skov *et al.* 2011, Bowman *et al.* 2015), this population urgently requires conservation action. Like most sea ducks (Savard *et al.* 2015), Common Scoters winter at sea but breed in freshwater habitats, and forage mainly by diving. The breeding season diet of scoters includes a wide range of aquatic insects (e.g., caddisflies Trichoptera, mayflies Ephemeroptera, midges Diptera: Chironomidae) and other aquatic invertebrates (e.g., freshwater shrimps Amphipoda, water-fleas Cladocera) (Cramp & Simmons 1977, Bordage & Savard 1995, Brown & Frederickson 1997, Savard *et al.* 1998, Gardarsson & Einarsson 2002).

Typically there is much overlap in the reported diet of adults and ducklings, though some studies showed age-related differences in the relative importance of prey groups (e.g., Gardarsson & Einarsson 2002). Key factors influencing habitat use and breeding success in breeding ducks of boreal freshwaters are typically food resources and habitat structure (Holopainen *et al.* 2015). Food supply influences both habitat use (Lewis *et al.* 2015) and populations (Gardarsson & Einarsson 2004) of breeding scoters. Similarly, Hancock *et al.* (2016) found that lake use by breeding Common Scoters in Scotland was correlated with food abundance and accessibility, scoters occurring most often at lakes having relatively abundant large invertebrates and shallow water – this was interpreted as reflecting higher quality foraging habitat at such lakes.

However, no previous studies of breeding Common Scoters have investigated patterns in foraging activity, such as within-lake habitat use, or variation in foraging effort between the sexes, or through the season. Understanding these aspects of scoter ecology would inform conservation actions and help identify causes of population decline, as follows. Spatial foraging patterns could highlight key habitats which should be protected or enhanced. For example, habitats used by foraging scoters at a within-lake scale, might be similar to those associated with scoter occurrence at a whole-lake scale (Hancock *et al.* 2016), strengthening the evidence behind recommendations of that earlier study. Similarly, temporal foraging patterns might inform conservation actions by suggesting critical periods for foraging scoters, during which additional conservation measures (e.g., restrictions on human disturbance) could be put in place.

Critical periods for foraging can be indicated by raised foraging effort, as found by Hunter *et al.* (1994), studying ducklings subjected to experimental food reduction, and Žydelis & Richman (2015), studying adult sea ducks in late winter as food became depleted. Foraging patterns could also illuminate potential causes of population decline: for example, if foraging data suggests that these birds are capital breeders, then breeding performance might be affected by changes at sea (e.g., in spring staging areas) which reduce prey abundance or foraging success in that environment. Hence, in this situation, the geographical scope of conservation actions needed to support breeding performance by this population would not be limited to the breeding lakes.

In this study, we used foraging watches to understand habitat use by Common Scoters at the within-lake scale, and to investigate variation in foraging effort between the sexes and through the season. We build on our earlier work (Hancock *et al.* 2016) by exploiting a completely new dataset, comprised of 208, 1-hour foraging watches, spread across 13 study lakes and including over 41,000 “scoter minutes”. Specifically, we hypothesised that (i) within-lake habitat use would correlate with the foraging-related factors associated with whole-lake use in our earlier study: abundant large invertebrates and shallow water; (ii) females would spend more time foraging on breeding lakes

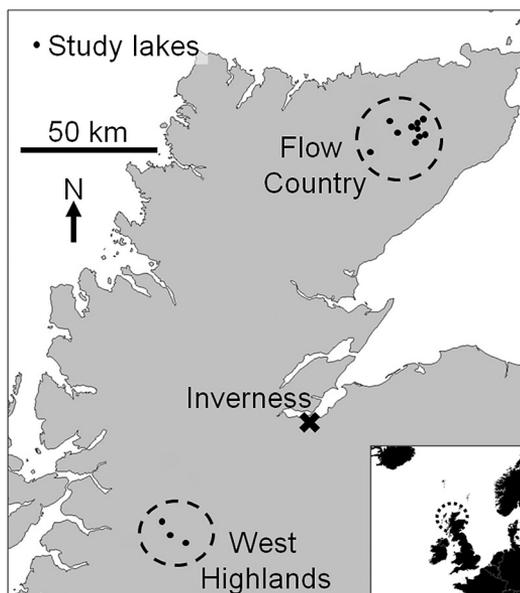


Fig. 1. The study lakes, within the two main regions still holding breeding Common Scoters in Britain, in northern Scotland. Inset: northern Scotland within north-west Europe.

than males, reflecting their additional nutritional needs and the commonly-reported pattern of “income” breeding by sea ducks; (iii) foraging effort would vary during the breeding season, reflecting seasonal variation in food abundance. Ultimately, we aimed to identify key habitats and processes affecting breeding Common Scoters, to better understand declines and inform conservation management.

2. Material and methods

2.1. Study areas, lake visits and habitat measurements

Our study areas included the two remaining concentrations of breeding Common Scoters in Britain (Balmer *et al.* 2013): the Scottish West Highlands and Flow Country (Fig. 1). Fieldwork took place between late April and mid-September over three breeding seasons: 2009, 2010 and 2011. There were three study lakes in the West Highlands and 10 in the Flow Country – all had recent, regular scoter breeding prior to the study.

Our approach was to include multiple lakes in

the study, in order that results might be of wider applicability. Necessarily this limited the detail of habitat characterisation possible at each lake. The small Flow Country lakes (2–40 ha, maximum depth typically ~2 m) usually held just one pair of scoters. They were surrounded by a relatively flat landscape comprising extensive blanket bog, forestry plantations, and areas of forestry undergoing restoration as bog (Lindsay *et al.* 1988, Hancock *et al.* 2018). The larger West Highlands lakes (300–1,300 ha, maximum depth typically ~10–15 m) sometimes held several pairs of scoters. These lakes were in a more mountainous landscape than the Flow Country – they occupied long, approximately parallel-sided glaciated valleys, containing moorland and forestry plantations. Like several other Scottish lakes used by scoters, all three West Highlands lakes were impounded in the 1950s for hydro-electricity generation (Miller 2002, Sample *et al.* 2015).

Lakes were nutrient-poor (phosphates 0.07–0.18 ppm) and acid to neutral (pH 4.5–7.2), with mean water surface temperatures of 5.2–16°C in late April / early May and 11–20 °C in late July / early August. Peat soils dominated most catchments, hence lake waters were typically strongly coloured and of low clarity (Secchi measurements averaging 1.7 m (range 0.76–3.4)). Fish present in study lakes included Brown Trout (*Salmo trutta*), which is native and present in most lakes in the Scottish scoter range, and Northern Pike (*Esox Lucius*), which is not native in the scoter range but widely introduced in the southern part of the range, including at our West Highlands study lakes (Maitland & Campbell 1992). This study was concurrent with the whole-lake study of Hancock *et al.* (2016), and our study lakes were the “key” sites of that study.

Sampling points (marked by small posts) were established at each lake. One point was located at random on the perimeter, and the others equally spaced around the perimeter, with a total of four or six points per lake in the Flow Country and West Highlands respectively. We chose this number of points per lake, in order to be able to complete each lake sampling visit in one day. The West Highlands lakes were large, but we were usually able to travel between points by boat, allowing six points to be sampled per day. The Flow Country lakes were smaller, but they were more remote and we

had to walk between points, allowing four points to be sampled per day. Had we sampled more points per lake, we would have had to reduce the number of lakes included in the study. This would have reduced our ability to generalise from our study to the wider Scottish scoter range, where breeding birds have occurred on at least 100 lakes (Underhill *et al.* 1998).

Habitat characteristics (water depth and invertebrate abundance) were measured at each point on three sampling visits per year: visit one in late April / early May (when scoters first arrive), visit two in June (the main incubation period), and visit three in late July / early August (during the brood-rearing period). All sampling points were sampled, regardless whether or not they were near to areas used by foraging scoters, in order to characterise the range of habitats available to foraging scoters within the study lakes (albeit at the scale of four or six locations per lake). We aimed to create two sets of habitat data: an early-season set for comparison with female foraging patterns prior to the brood period, and a late-season set for comparison with brood foraging patterns. Therefore, based on previous earliest brood records in the area, we defined two seasonal periods: pre- and post-hatch (before and after late June respectively). Habitat data from visits one and two, and visits two and three, were averaged to represent the pre- and post-hatch periods respectively.

At each sampling point, on each visit, water depth was measured 10 m from the shore. Thus, strictly speaking, we obtained a specific measure of littoral depth, rather than depth in general. Sampling was conducted by wading. Invertebrates were sampled using four different methods: pond-net sweeps under shoreline stones (Jackson 2005), pond-net sweeps across the water’s surface (Turner & Trexler 1997), soft sediment sampling using a Petit Ponar grab (Schloesser & Nalepa 2002), and colonisation traps, which invertebrates colonised between visits (Summers *et al.* 2011).

We sometimes had to wade some distance from the point to find suitable substrate types for the different sampling methods (e.g., fine sediments for grab sampling), but all sampling took place within 60 m of each sampling point, i.e., within an area of approximately 0.6 ha around each sampling point. Invertebrates were preserved in alcohol. Later, in the laboratory, their body lengths were measured

and they were identified to a higher taxon level (family for abundant groups, otherwise order or class) using Croft (1986). The body mass of each invertebrate was estimated using published length-weight regressions (see Hancock *et al.* 2016: Table S1). In our earlier study (Hancock *et al.* 2016) we found that lake use was correlated with a measure of large invertebrate abundance, rather than a broader measure of invertebrate biomass (including all invertebrates across the sampled body-size spectrum).

We therefore used the same large invertebrate measure in this study, calculated as follows. Firstly, the mass of the largest invertebrate in each sample was collated, and converted to a Z-score for that sampling method. Thus, data for the different sampling methods were converted to a common scale, with larger or smaller Z-values representing invertebrates that were relatively large or small, respectively, compared to the mean and range of variation of that particular sampling method. Secondly, these Z-scores were averaged by sampling point and visit, across all sampling methods, to give a combined measure of large invertebrate abundance, referred to henceforth simply as “large invertebrates”. These habitat data were the same as those used at the whole-lake scale by Hancock *et al.* (2016).

2.2. Foraging watches

Watches took place during both seasonal periods: pre- and post-hatch. For watches and later statistical analyses, we prioritised scoter life stages we expected to have high nutritional demands: females prior to incubation, and broods. In the pre-hatch period, we watched paired females and accompanying males, considering the breeding status of lone females to be uncertain (they could be non-breeders, failed breeders, breeding birds on incubation recess, or pre-incubation breeders without an accompanying male). In the post-hatch period, we watched broods, and any accompanying adult female(s).

Scoters were rare and mobile. Their occurrence at a particular lake was unpredictable. Some study lakes had little scoter use during the study period; broods were particularly rare. Therefore, in order to obtain meaningful samples of watches

from each lake in each year, we prioritised lakes with few watches already completed within that seasonal period. No watches took place within 24 hours of the previous watch at that lake. We observed between-lake movements by females (often) and broods (occasionally, also seen by Bordage & Savard 1995). Therefore, successive watches at one lake could be of different individual birds. However, given the rarity of the species in the area, it is also likely that different watches at a lake within a season would sometimes be of the same individual birds, especially if each bird tended to use a certain lake more than others.

We searched for scoters between first and last light, but because we needed adequate daylight for telescope use, relatively few watches took place close to dawn or dusk. Although sea ducks can forage throughout the 24-hour cycle under continuous daylight in the arctic summer (Oppel *et al.* 2011), in winter or at lower latitudes they are primarily diurnal foragers (Lewis *et al.* 2005, Żydelis & Richman 2015). Therefore, we considered that our diurnal studies would adequately measure foraging activity. Watches took place in all weather conditions allowing practicable data collection: only dense mist or gale-force winds were avoided.

Once scoter(s) had been located, the observer found a position a few hundred metres away where birds could be observed by telescope with minimal disturbance. Due to the remoteness of most sites, the birds were not used to humans being present – however, their behaviour suggested little disturbance when watched at this range. Birds were allowed to settle if visibly disturbed, then the watch commenced. Behaviour was recorded using Scan Sampling (Altmann 1974): once per minute, on the minute, the observer categorised the activity at that moment of each member of the focal scoter group. To record duckling size, as a measure of age, we estimated their waterline length as a proportion of that of an adult female.

A bird that had dived and was underwater was categorised as “foraging: underwater”. Other foraging-related behaviours were grouped as “foraging: at surface” – these mostly comprised “dive-pauses”, during which birds recovered between dives (though sometimes it was hard to distinguish a dive-pause from loafing or swimming). Other behaviours grouped in this category included occasional observations of birds on the surface with

their heads or bills underwater – sometimes they appeared to be feeding but other times they could have been looking underwater for predators or prey, cleaning their bills or drinking. Thus, these surface activities were not necessarily always foraging. Conversely, we assumed that diving would always be for foraging. Therefore, we defined “foraging activity” as the proportion of scans within a watch that were categorised as “foraging: underwater”. Similar studies often use this approach (e.g., Brown & Frederickson 1987, Goudie 1999, Lewis *et al.* 2007). A further benefit of this approach is that our results could also be useful in a very different context: correcting aerial surveys of diving birds for “availability bias” (e.g., Winiarski *et al.* 2014).

Other behaviour categories were alert/vigilant, swimming, calling/displaying, and “comfort” behaviours (preening, loafing, sleeping). At each scan, the observer estimated the distance between the focal bird(s) and the shore (Lesage *et al.* 2008), and noted which sampling point was nearest (using the posts marking these points). It was usually clear which sampling point was nearest to the focal scoter group. Each lake was divided into sectors defined using the sampling points: for each sampling point, the corresponding lake sector was the part of the lake nearest that point (Fig. S1). Because sampling points were evenly spaced around lake perimeters, sectors within a particular lake were similar in area, but not identical, due to the irregular shape of lakes. Because we typically observed scoters at considerable range (and, in the flat landscape of the Flow Country, a low viewpoint), it was hard to accurately place them on a map of the lake – however, we considered our mapping to be accurate at the scale of a whole lake sector. Similarly, we analysed distance-to-shore data in bins (0–5 m, 5–10 m, 10–50 m and over 50 m), and considered our distance-to-shore estimates of scoters reasonably accurate at the level of these bins. Nevertheless, the fact that these distance-to-shore estimates were simple visual estimates means that some observations will have been wrongly categorised, leading to some blurring of results between adjacent bins.

It could take some hours to reach remote breeding lakes, or search the larger lakes, before we found scoters to watch. Having found scoters, we wanted to ensure that each watch included a rea-

sonable period of foraging activity. Previous studies have shown that breeding scoters may spend periods of up to 30–40 minutes loafing or preening, between foraging bouts (Brown & Frederickson 1997). We therefore aimed for each watch to last one hour, a standard period used in some other studies (e.g., Lewis *et al.* 2007). However, birds sometimes disappeared from view. If they were later re-located, the watch was extended to give approximately one full hour of observation. But sometimes birds could not be re-located, or flew from the lake, preventing a full hour’s observation. Any watches of less than 15 minutes were removed from the dataset.

2.3. Data analysis

Spatially, at the lake-sector level, we examined foraging activity in relation to water depth and abundance of large invertebrates. Temporally, at the lake-year level, we examined seasonal variation in foraging activity. Each analysis included data from two scoter “life-stages”: pre-incubation females, and broods. For each life-stage, there might be multiple watches at one lake-sector or within one lake-year. Such multiple watches would not represent true replicates, because in many cases they would be of the same individual birds, observed on different occasions. We addressed this issue by combining such multiple watches into a single, mean value for that lake-sector or lake-year.

For spatial analyses, we averaged data across all available watches for a given life-stage and lake-sector, and analysed data at this level. There were 58 lake-sectors (10 Flow Country lakes with four sectors, three West Highlands lakes with six sectors) and two scoter life-stages, hence for this analysis, sample size (N) was 116, with correlation within lake-sector (for the two scoter life-stages) and within lake (for the different lake-sectors). Similarly, for temporal analyses, we combined data across all available watches for a given life-stage and lake-year and analysed data at this level. There were 39 lake-years (13 lakes in three years) and two scoter life-stages, hence $N=78$, with correlation within lake (for the two scoter life stages) and within year (for the different lakes). Analyses were performed using generalised linear mixed

Table 1 Study sample sizes: the numbers of watches, their dates and lengths, and the numbers of scoters present.

	Scoter category	
	Females, accompanied by males ¹	Broods
Number of watches	93	115
Watch date ²	23 May (21 Apr–22 Jun)	1 Aug (4 Jul–20 Sep)
Watch length, minutes ²	58 (18–126)	63 (17–151)
Mean number of scoters in view during watch (no. one-minute scans / watch length) ²		
Adult females	1.33 (0.07–4.82)	0.60 (0.00–1.50) ³
Adult males	1.46 (0.38–4.92)	(absent)
Ducklings	(absent)	3.05 (0.33–8.00)

1) Assumed to be breeding females at the pre-incubation stage.

2) Means and ranges at the watch level.

3) Adult attendance fell as ducklings grew (females accompanied broods during 100%, 77%, 89% and 23% of watches of ducklings sized up to 25%, 26–50%, 51–75%, and over 75% of female waterline length respectively, $N = 22, 52, 19$ and 22).

models (GLMMs), fitted with the GLIMMIX procedure in SAS (Stroup 2013, SAS 2014).

To analyse the spatial pattern of foraging activity, we fitted one GLMM (Table S1), in which the response (y) variable was the mean number of underwater foraging scans per watch for a given lake-sector and life-stage. We used a Poisson error structure and log link. The explanatory (x) variables of interest were two habitat variables: water depth and large-invertebrate abundance, and their interaction. The proportion of lake area covered by that sector, and the mean total number of scans per watch at that lake, were included as covariates, to account for within-lake differences in lake-sector area, and between-lake differences in mean watch length.

We included scoter life-stage as a two-level fixed effect, to account for overall differences in foraging activity between life-stages. Lake and lake-sector were included as random effects, to model correlation between multiple observations at these two levels. Interpretation focussed on whether either habitat variable or their interaction was significantly associated with the amount of foraging activity at a lake-sector.

To analyse the temporal pattern of foraging activity, we first determined its seasonal trend, for each combination of lake-year and scoter life-stage where at least two watches were available. At the watch level, for each lake-year and life stage, we regressed the percentage of scans comprising foraging activity, against watch date. Posi-

tive or negative slope estimates from these regressions indicated that foraging activity tended to rise or fall with date, respectively. Slope estimates were then used as the response (y) variable in a GLMM (Table S1), which had a normal error structure and identity link. The explanatory variables were scoter life-stage, year and their interaction. Lake and year were included as random effects, to model correlation between multiple observations at these levels. This two-stage approach to temporal analysis is considered robust, where, as here, it is appropriate to weight each subject equally, despite them having different numbers of repeat measurements (Brown & Prescott 2015). Interpretation focussed on whether mean seasonal trends in foraging activity differed from zero (across all years, or in any one year) or between years or scoter life-stages.

3. Results

We made 595 lake visits, totalling 1,366 hours. These resulted in 208 watches totalling 41,219 scoter-minutes, approximately equally split between pre-incubation females and broods (Table 1). On average, 16 watches were completed per lake, but this varied considerably: three lakes where scoters were rarely found had fewer than five watches, while four had over 20.

Plotting the distribution of scoter foraging in relation to distance from shore (Fig. 2) suggested

Fig. 2. Foraging scoters use near-shore, shallower areas within lakes more than would be expected from their area: comparing proportions of lake area and foraging activity at different distances from the lake shore (means and standard errors, averaging at the lake level). These data were collected during foraging watches, in the form of visual distance-to-shore estimates of foraging scoters. The typical depths in these zones (horizontal axis – italics) were estimated later from lake sampling data.

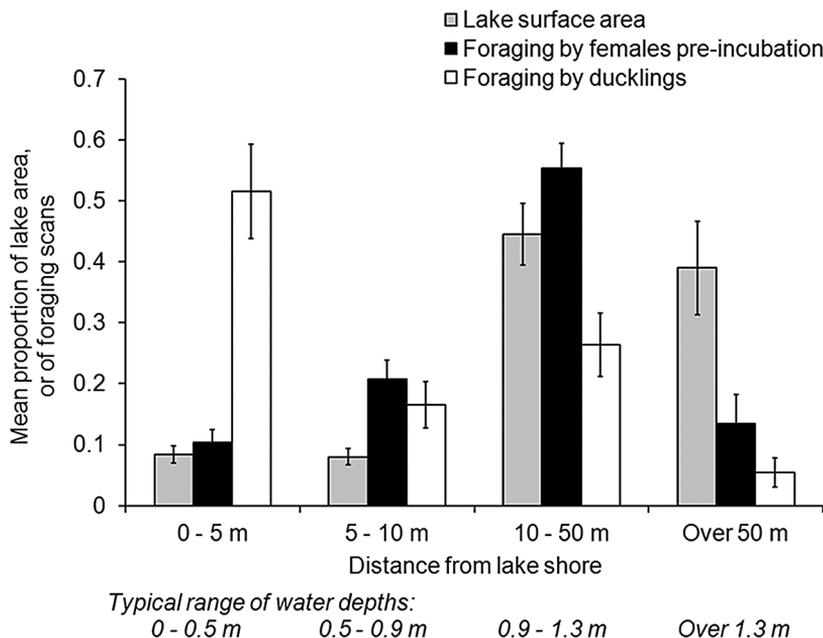


Table 2 Analysis of the spatial pattern of foraging behaviour. Parameters from a model (GLMM) of the mean number of foraging scans by lake sector, vs. two habitat variables: large invertebrate abundance, water depth and their interaction. Other fixed effects were included in the model to account for variation associated with scans per watch, lake-sector size and scoter life stage. Random effects modelled the effect of lake and lake-sector, and adjusted the results for over-dispersion. The model used a Poisson error structure and log_e link.

Effect	Estimate	Standard error	P	Test alpha value ¹
Fixed effects				
Intercept	1.435	0.461		
Mean number of scans per watch, all activities	0.00238	0.00127	0.0629	–
Proportion of the lake covered by this lake sector	1.670	1.695	0.3290	–
Scoter life stage (female pre-incubation, or brood)			0.1104	–
Water depth index	-0.396	0.136	0.0046	0.05
Large invertebrate abundance	0.118	0.142	0.4097	0.05
Water depth index × large invertebrate abundance	0.501	0.167	0.0034	0.05
Means of categorical fixed effect variables				
Scoter life stage:				
Female pre-incubation	1.746	0.178		
Duckling	2.109	0.167		
Random effects (covariance estimates)				
Lake	0.000	0.000		
Lake-sector	0.449	0.151		
Over-dispersion parameter	4.238	0.797		

1) Hypothesis tests were restricted to the two habitat effects (water depth, invertebrate abundance) and their interaction.

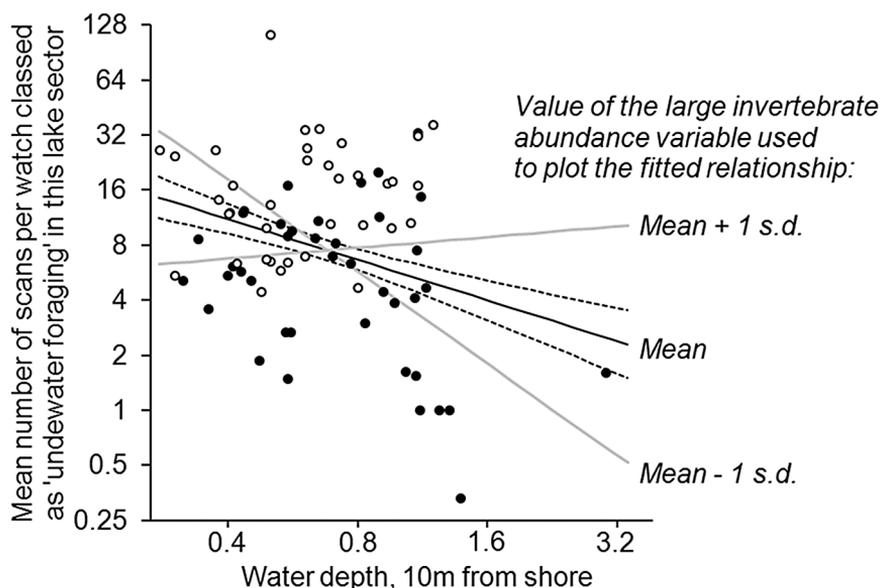


Fig. 3. Foraging scoters were strongly associated with lake sectors having shallower water: the fitted relationship between water depth and foraging activity. Points show the raw data at the level of lake sector, separated by scoter life stage (black circles: females pre-incubation, open circles: broods). The black line shows the fitted relationship (and standard errors), compensating for differences in lake sector size and mean total number of scans per watch, averaged across both scoter life stages, with large invertebrate abundance set at its mean value. The grey lines show the fitted relationship with large invertebrate abundance set at the mean value \pm standard deviation. Note the log scale on both axes. Note that water depth was measured as the depth, 10 m from the shore, at a central point in each lake sector. Thus, strictly, this is a measure of littoral depth rather than depth in general.

greater use of shallow water areas. Most foraging took place within 50 m of lake shores, where depths were typically less than 1.3 m: these areas held 87% and 95% of female and duckling foraging scans respectively, despite only comprising 61% of lake areas. Statistical analysis supported the association with shallow water: lake-sectors having shallower littoral zones had significantly more foraging than other lake-sectors (Table 2). Fitted foraging activity was over four times greater at the shallowest lake sectors than at the deepest (depths around 0.3 m and 3 m respectively, 10 m from shore) (Fig. 3), where large invertebrate abundance was around average values (around 7.3, 3.2, 2.0 and 1.1 mg for stone sweeps, colonisation traps, sediment grabs and surface sweeps respectively).

The association between foraging scoters and shallow water interacted strongly with large invertebrate abundance (Table 2): where large in-

vertebrates were more abundant, the association with shallow water was weaker (Fig. 3). If the largest invertebrate per sample averaged about 0.8 standard deviations above the mean, the fitted depth relationship became flat, implying no effect of water depth on foraging activity for this scenario. This would mean the largest invertebrate per sample being around 12, 7.1, 4.1 and 2.3 mg for stone sweeps, colonisation traps, sediment grabs and surface sweeps respectively. Conversely, a scenario where the largest invertebrate per sample was smaller than average, implied a stronger fitted association between foraging scoters and shallow water (Fig. 3). Thus, overall, scoter foraging activity was concentrated in shallow water, but where large invertebrates were relatively abundant, a wider range of water depths were used.

Pre-incubation females averaged 41% (lake-level standard error 4.8) of their time foraging underwater – values for accompanying males were

Fig. 4. Time-activity budgets by seasonal period and scoter life-stage, averaged at the lake level. (a) Females and accompanying males, prior to incubation: males and females spend similar amounts of time foraging in the pre-incubation period. (b) Broods of ducklings, and accompanying females (if present).

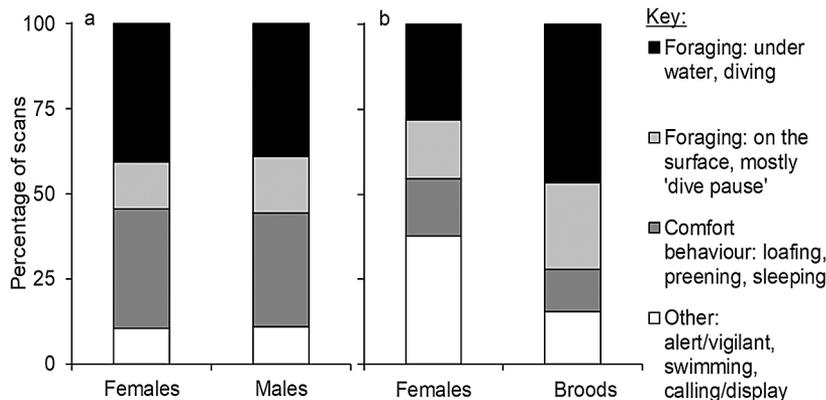


Table 3 Analysis of the seasonal pattern of foraging behaviour. Parameters from a model (GLMM) which had as a response (y) variable, the trend of foraging effort against date, by lake, scoter life stage and year. Positive or negative values of y would thus indicate that foraging effort increased or decreased over time, respectively.

Effect	Estimate	Standard error	P values		
			Significance of:		
			Each effect in the model	Difference from zero	Test alpha value ¹
Fixed effects					
Intercept	1.60	3.45			
Scoter life stage			0.401		0.006
Year			0.022		0.004
Scoter life stage × Year			0.775		0.050
Means of categorical fixed effect variables					
Scoter life stage					
Female pre-incubation	1.23	1.22		0.344	0.005
Brood	-0.88	1.20		0.491	0.007
Year					
2009	1.25	0.47		0.028	0.004
2010	-1.44	1.77		0.449	0.006
2011	0.72	1.75		0.696	0.013
Scoter life stage × Year					
Females, 2009	2.65	0.74		0.016	0.004
Broods, 2009	-0.16	0.39		0.698	0.017
Females, 2010	-0.56	0.50		0.288	0.005
Broods, 2010	-2.32	3.45		0.532	0.008
Females, 2011	1.60	3.45		0.662	0.010
Broods, 2011	-0.16	0.39		0.699	0.025
Random effects (covariance estimates)					
Lake	0.00	0.67			
Year	0.00	0.00			
Scoter life stage × Year ²	0.00 to 148	1.21 to 80			

1) Because 14 tests were conducted, we used alpha levels that were adjusted using the sequential Bonferroni method.

2) Heterogeneous variance between different Scoter life stage × Year groups was modelled by including a separate random effect for the residuals of each group; the range of these six values is given here.

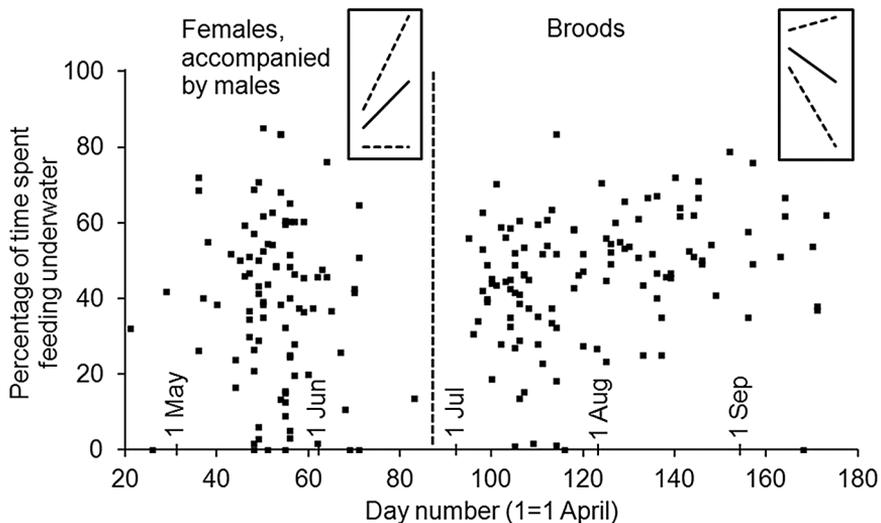


Fig. 5. Within-season patterns in scoter foraging activity: neither females nor broods show a clear trend in foraging effort as the season progresses. The individual data points (each representing one watch) are indicated by black squares. The fitted mean slopes of foraging effort vs. date (\pm one standard error), for a nominal 10-day period, are plotted as inset graphs.

similar (39%, s.e. 4.2) (Fig. 4). Males and females often dived together. A paired *t*-test at the whole lake scale confirmed that foraging effort did not differ significantly between the sexes ($P=0.51$, $N=12$ lakes, based on 93 watches). Ducklings averaged 46% of their time foraging (s.e. 3.2) but adult females accompanying them, notably less (28%, s.e. 3.7) (Fig. 4).

We found no significant within-season trend in foraging activity, either across all years or within any year, either for females pre-incubation or for ducklings (Table 3: estimated fixed effect means, i.e., estimates of seasonal trends in foraging activity, do not differ significantly from zero, Fig. 5). Within-season trends in foraging activity did not differ between scoter life-stages or years, or show any interaction between year and life-stage (Table 3: fixed effects have no significant effect on the response variable). However, data were quite sparse: two of the 13 study lakes had insufficient data, and we were only able to estimate seasonal trends for 23 and 16 of the 33 remaining possible lake-years, for females and broods respectively.

There was relatively little change in large invertebrate abundance between early and later parts of the season (Fig. S2). The largest invertebrate per sample averaged around 6.6 mg in the pre-hatch

period, and only about 20% lower, around 5.3 mg, in the post-hatch period. Four insect orders contributed 76–77% of large invertebrate biomass: dragonflies and damselflies (Odonata), caddisflies (Trichoptera), beetles (Coleoptera) and mayflies (Ephemeroptera): all have been recorded in scoter diet (Introduction). Odonata and Trichoptera declined in abundance during the season, but Coleoptera increased (Fig. S2a). Meanwhile, Ephemeroptera showed little change in seasonal abundance at the order level, but within the order, some families decreased while others increased (Fig. S2b).

4. Discussion

4.1. Within-lake foraging habitat use

Foraging scoters were strongly associated with those parts of lakes where the littoral zone was shallower. Water depth might affect foraging, either by affecting the prey resource, or its availability to scoters. For diving birds, diving to greater depth is more energetically costly (Shepard *et al.*, 2009). Thus, if prey abundance and ease of capture did not vary with depth, greater use of shallow wa-

ter might be expected. However, lake-bed habitats and associated invertebrates usually vary markedly with depth (Moss 2010). In our lakes, typical invertebrates of shallow, stony littoral zones were caddisflies (Trichoptera), mayflies (Ephemeroptera) and aquatic beetles (Coleoptera). Meanwhile, the soft sediments of deeper lake-bed habitats often held bloodworms (larval Diptera: Chironomidae) and pea mussels (Mollusca: Sphaeriidae). Scoters have been found to feed on all these invertebrate groups, suggesting they can take prey from a variety of depths or substrates. Shallow water allows more light to reach the lake bed, and light is a key determinant of productivity in lakes similar to those of our study (Karlsson *et al.* 2009). Light penetration allows macrophytes to grow and these can support large invertebrates like dragonflies and damselflies (Odonata) (Weatherhead & James 2001).

Thus, shallow water could provide more productive habitats with more varied habitat structure, leading to abundant invertebrate life. However, we found an association between foraging scoters and shallow water in a model that also included (and hence controlled for) a measure of large invertebrate abundance. This suggests that shallow water use reflected factors other than prey abundance, such as prey type, or the relatively low energetic cost of diving to the lake-bed in shallow water. Like Tierney (2001), we found some evidence that broods showed a stronger association with near-shore, shallow areas than adults (Fig. 2), suggesting some age differences in prey type or the capacity to dive to depth.

Although shallow water foraging has been reported in other breeding scoter studies (Brown & Frederickson 1997, Lesage *et al.* 2008), some studies report breeding scoters commonly foraging in water up to 3.5 m deep (Bengtson 1971, Tierney 2001). At sea, scoters typically forage in water 1–15 m deep (Fox 2003, Kaiser *et al.* 2006, Lewis *et al.* 2007). The energetic costs of deeper diving may be worthwhile where food is abundant, of high quality, or easily captured. Scoters and other diving ducks sometimes prefer larger food items where a range of sizes are available (Hamilton *et al.* 1994, Leopold *et al.* 2007), suggesting that more energetically costly, deep-water foraging may become more profitable where larger prey occur. Our results support this idea: use of deeper

water became more likely where larger invertebrates were more abundant.

Foraging habitat choice could be influenced by factors unrelated to foraging. Near-shore, shallow water areas may hold greater risks of mammalian predator attack (Lewis *et al.* 2005). Meanwhile, water depth may affect risk of attack by aquatic predators such as Northern Pike (*Esox Lucius*) (present in the West Highlands and known to attack and eat ducklings: Maitland & Campbell 1992) or Black-throated Divers (or loons) (*Gavia arctica*), which we observed attacking scoters (Supplementary material: Appendix 1). Northern Pike may spend less time in shallowest parts of lakes, than in deeper areas: Rogers (1998) found, at two study lakes, that mean spring and summer water column depths used by tracked Northern Pike were in the range 2–3 m, Kobler *et al.* (2008) found, at one study lake, that mean distance to shore of tracked Northern Pike in summer was 51.4 m (s.e. 8.3), with larger pike tending to spend more time further from the shore than smaller pike.

In relation to divers or loons (Gaviidae), Sperry (1987), Kirkham & Johnson (1988) and Morton & Pereyra (2011) describe multiple loon attacks on wildfowl in North America. Similar to our observations, they noted that attacks often came from below, which would require water deep enough for a diving loon to approach undetected, and when attacked, females with broods often sought refuge on the shore, implying that broods nearer the shore would be able to escape more quickly from loon attack. Sperry (1987) further suggested that Common Goldeneye (*Bucephala clangula*) would be more vulnerable to loon attack than other ducks in their study area, because they tended to frequent deeper parts of lakes. The greater vulnerability of ducklings to predation or attack, compared to adult scoters, might provide an alternative explanation as to why near-shore, shallow water foraging was more pronounced in ducklings (Fig. 2).

4.2. Comparing female and male foraging effort

Pre-incubation females and accompanying males expended similar foraging effort: the expected greater energetic demand of females (for egg-lay-

ing) was not reflected in greater observed foraging effort at breeding lakes. This result was unexpected, and contrasts with some other studies of ducks shortly prior to nesting (e.g., Oppel *et al.* 2011, Arzel & Elmberg 2015) which found that females spent more time foraging, when compared to males at the same sites over the same time periods. Our results could be explained in three different ways, which we discuss below.

Firstly, female Common Scoters in our region may be “capital breeders”, supporting their additional nutritional needs from bodily reserves acquired at (probably marine) spring staging areas. In this case, we would expect female scoters at our study sites to show a more marked tendency to lose body mass during the breeding season, than accompanying males. Other studies of different scoter species have suggested both income and capital strategies may be used in different populations or regions, based on comparing male and female foraging effort on the breeding grounds, and investigating other factors like diet and body composition (Brown & Frederickson 1987, Alisauskas & Ankney 1992, Savard *et al.* 1998). Evidence increasingly suggests that, rather than an income-capital dichotomy, there can be a range of strategies between these extremes, including by the same species in different breeding areas (Drent *et al.* 2006).

Secondly, scoters may visit coastal areas to forage during the breeding season itself, our study lakes being only 13–26 km from the sea. Alisauskas & Devink (2015) suggested that such strategies may be more common than is usually supposed. In this case, we would expect that female scoters breeding at our study sites would forage more intensively than males at nearby marine sites, in order to acquire the necessary resources for breeding.

Thirdly, although we observed similar apparent foraging effort (underwater time) by males and females, it is possible that females could acquire more food than males, with similar time budgets, by taking more or larger prey when under water. Bengtson (1971) found sex differences in the freshwater diet of breeding Common Scoters, from stomach contents of birds drowned in fishing nets. Females had taken relatively more Chironomids, and males more fish eggs. Similarly, Tschakofske (2010) found sex differences in the

diet of moulting Surf Scoters (*M. perspicillata*), females taking relatively more crustaceans. Males in breeding pairs might sometimes dive alongside females for social rather than foraging reasons, resulting in similar time budgets but differing food intake: synchronous diving by sea ducks at sea may have a partly social explanation (Żydelis & Richman 2015).

To distinguish between these interpretations, miniature tracking devices fitted to birds offer increasing potential. Location tracking devices (e.g., Kang *et al.* 2016) could be used to identify spring staging areas, or to determine if marine areas are used during the breeding season. Female and male time budgets could be measured in such areas using foraging watches. Dive loggers (e.g., Chimienti *et al.* 2017) could be used to compare underwater foraging behaviour of males and females, diving together at their breeding lakes. Tracking studies would therefore be a key element of future studies of Scottish breeding scoters. They would also be of great value in clarifying movement patterns around the breeding grounds during the season by individual scoters, an area about which little is known (Introduction). At the within-lake scale, scoter tracking information could usefully be complemented by hydro-acoustic surveys of lake bathymetry, to give a much more detailed picture of associations with lake depth than was possible in this study.

Overall, in terms of scoter conservation, the first two of the above interpretations would imply that scoter breeding performance at these freshwater lakes could be affected by marine sites, either spring staging areas, or coastal areas near to the breeding grounds. As for many duck populations (Arzel *et al.* 2006), the staging sites of Scottish breeding Common Scoters are poorly known, and similarly, coastal areas near to breeding sites have not been systematically surveyed for scoters during the breeding season. However, if any key marine areas were identified, for example using tracking studies, then they could be protected from disturbance or harmful development. As exemplified by sea ducks feeding on eggs of spring spawning Pacific Herring (*Clupea pallasii*) (Lewis *et al.* 2007), marine areas can offer rich spring foraging opportunities. In Scotland, former west coast populations of spring spawning Atlantic Herring (*Clupea harengus*) are showing some early signs

of recovery (SPFA 2018). These areas are near to some Scottish breeding sites – however, nothing is known of whether spring herring spawn is, or once was, an important food resource for Scottish breeding scoters.

Comparing our scoter foraging effort estimates with two other breeding-season scoter studies (Fig. S3) showed that adult female values were similar across studies (falling within our standard errors), but male foraging effort was somewhat lower (by 9% and 34%) in the other two studies. Unlike our study, where most lakes only held one or two pairs, these other studies (Brown & Fredericksen 1987, Partridge & Smith 1988) took place at large lakes holding many scoter pairs, where male scoters may spend relatively more time mate-guarding, and hence less time foraging.

4.3. Within-season trends in foraging effort

We found no clear tendency for foraging effort to vary through the season, for either pre-incubation females or broods. Thus there was no evidence of a seasonal pattern in foraging effort that might result from food being harder to obtain in particular parts of the season. Some potential prey groups decreased in abundance over the season, but others increased, resulting in relatively little change in overall abundance (albeit this was measured at a coarse temporal scale).

If foraging scoters were feeding on a wide range of prey groups in these lakes, as the literature shows they can (Introduction), they may be relatively unaffected by changes in abundance of particular groups. Common Scoters in Iceland (Bengtson 1971) and other wildfowl (Krapu & Reineke 1992) can feed on a succession of different invertebrate groups during the breeding season. The closely-related Black Scoter (*M. americana*) is one of the most generalist American sea ducks in terms of diet and foraging strategies (Žydelis & Richman 2015). This could include taking a wide range of prey types, with differing phenologies, during the breeding season.

Many freshwater prey groups show greater species diversity at lower latitudes (Heino 2009), suggesting that temperate regions like our study area could support a more diverse prey base than boreal or arctic regions. For example, despite be-

ing about 60% larger than the UK, Norway holds fewer species within six of the seven major aquatic insect groups considered by Heino (2009). Hence, overall, Common Scoters in our study lakes may be taking a wide range of invertebrate species, with a range of different phenologies. This may reduce their vulnerability to changes in the timing of abundance of particular invertebrate species. Mean foraging effort in our relatively southerly study area did not differ consistently from that observed in more northerly breeding scoter studies (Fig. S3).

4.4. Conclusions and implications for scoter conservation

Our results show, unexpectedly, that female and male scoters spend similar proportions of their time underwater, apparently foraging, while at breeding lakes in the pre-nesting period. We suggest three alternative interpretations for this result: (i) female scoters are capital breeders, bringing bodily resources from marine staging areas; (ii) female scoters feed at sea during the breeding season itself, to a greater extent than males; (iii) at breeding lakes, females have a higher feeding rate while under water, compared to males. We recommend that tracking studies are carried out, to clarify which of these interpretation(s) apply. The first two of these interpretations would mean that breeding females support their extra nutritional needs from resources gathered away from the breeding lakes. This would then imply that conservation actions to help breeding performance in this population should also encompass relevant marine areas.

We found no significant variation in foraging effort through the season, for pre-breeding females, or for broods. Compared to boreal regions, temperate regions like Scotland may support a more diverse prey resource for birds like scoters (Heino 2009), which may help buffer them against seasonal changes in abundance of particular prey species or groups.

Our results highlight the importance of shallow water for foraging scoters, and suggest that abundant large prey may help scoters forage successfully in a wider range of water depths. This foraging study therefore provides a fine-scale, mechanistic explanation for patterns of whole-

lake use found previously (Hancock *et al.* 2016). Habitat use by breeding Common Scoters, at both the within-lake and between-lake scales, therefore appears to relate strongly to prey availability, as is common for sea ducks in marine environments (Žydelis & Richman 2015). Thus, our results strengthen the evidence supporting the conservation interventions suggested previously for breeding Common Scoters in Scotland (Hancock *et al.* 2016), as follows. At lakes allowing some control over water levels, such as those used for hydroelectricity generation, conservation measures should aim to maximise the area of shallow water. At lakes where Brown Trout (*Salmo trutta*) may reduce large invertebrate abundance (Hancock *et al.* 2016), reducing trout numbers (e.g., by increasing angling) could increase prey availability, allowing scoters to forage over a wider range of depths. Both techniques should lead to an increased area of suitable foraging habitat and hence offer significant potential in helping reverse population declines.

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Mustalintujen ravinnonhankinta-käyttötymisen vaihtelu Skotlannissa

Monet merialueiden sorsapopulaatiot ovat vähentyneet. Tähän voi osaltaan vaikuttaa huono ravintotilanne lisääntymisalueilla sisävesissä. Mustalintujen pesimäpopulaatio Iso-Britanniassa on vähentynyt 63 % vuosina 1995–2007. Aiemmat tutkimukset osoittivat, että järvien ravintotilanne

(suuret selkärangattomat ravintokohteet) ja ravinnon saavutettavuus (matalat vedet) korreloivat positiivisesti pesivien mustalintujen määrän kanssa.

Tässä tutkimuksessa selvitettiin mustalintujen ruokailuaktiivisuutta skotlantilaisissa järvissä, tavoitteena ymmärtää paremmin populaatioiden vähenemisen syitä ja tukea suojelutoimia. Ennustamme, että (i) ravinnonetsintäaktiivisuus olisi suurimmillaan matalissa vesissä, jossa on eniten suuria selkärangattomia ravintokohteita, (ii) koiraat ja naaraat eroavat ravinnonetsinnässä, ja (iii) ravinnonetsintä muuttuu pesimäkauden edetessä. Mustalintujen ruokailua seurattiin 208 tunnin jaksossa, 13 järvellä kolmen vuoden tutkimusjakson aikana. Lisäksi mitattiin veden syvyys ja selkärangattoimien ravintoeläinten määrä.

Mustalintujen ruokailu oli merkittävästi keskittynyt matalaan veteen: mustalintunaaraat ja poikaset ruokailivat 1,9 ja 4,1 kertaa todennäköisemmin 10 metrin etäisyydellä rannasta ja alle 0,9 metrin syvyisillä rannoilla, kuin sattumalta voitaisiin odottaa. Alueilla, jolla suurten selkärangattomien määrä oli yleisesti suurempi, matalia alueita käytettiin suhteellisesti vähemmän – tämä viittaa siihen että kun ravinto on runsasta, veden syvyydellä ei ole niin suurta merkitystä. Vastoin odotuksia, koiraat ja naaraat käyttivät yhtä paljon aikaa ravinnonetsintään. Yksilöiden seuranta tutkimukset voivat valottaa tätä tulosta. Naaraiden tai poikuiden ravinnonetsintäkäyttäytyminen ei muuttunut pesimäkauden edetessä. Tutkimus korostaa matalien vesialueiden ja suurten selkärangattomien merkitystä mustalintujen ravinnossa: suojelutoimet pitäisi siten keskittää näihin elinympäristöihin, esimerkiksi veden korkeuksien ja kalastuksen säätelyllä.

References

- Alisauskas, R.T. & Ankney, C.D. 1992: The cost of egg laying and its relationship to nutrient reserves in waterfowl. — In *Ecology and Management of Breeding Waterfowl* (eds. Batt *et al.*): 30–61. University of Minnesota Press, Minneapolis.
- Alisauskas, R.T. & Devink, J.-M. 2015: Breeding costs, nutrient reserves, and cross-seasonal effects: dealing with deficits in sea ducks. — In *Ecology and Conservation of North American Sea Ducks* (eds. Savard *et al.*): 125–168. CRC Press, Boca Raton.
- Altmann, J. 1974: Observational study of behaviour: sampling methods. — *Behaviour* 49: 227–267.

- Arzel, C. & Elmberg, J. 2015: Time use and foraging behaviour in pre-breeding dabbling ducks *Anas* spp. in sub-arctic Norway. — *Journal of Ornithology* 156:499–513.
- Arzel, C., Elmberg, J. & Guilleman, M. 2006: Ecology of spring-migrating Anatidae: a review. — *Journal of Ornithology* 147: 167–184.
- Balmer, D.E., Gillings, S., Caffney, B.J., Swann, R.L., Downie, I.S. & Fuller, R.J. 2013: Bird Atlas 2007–11: the breeding and wintering birds of Britain and Ireland. — BTO Books, Thetford.
- Bengtson, S.-A. 1971: Food and feeding of diving ducks breeding at Lake Mývatn, Iceland. — *Ornis Fennica* 48: 77–92.
- Bordage, D. & Savard, J.-P.L. 1995: Black scoter *Melanitta nigra*. In *The Birds of North America* no. 177 (eds. Poole, A. & Gill, F.): 1–20. — *Birds of North America*, Philadelphia.
- Bowman, T.D., Silverman, E.D., Gilliland, S.G. & Leirness, J.B. 2015: Status and trends of North American sea ducks. — In *Ecology and Conservation of North American Sea Ducks* (eds. Savard et al.): 1–28. CRC Press, Boca Raton.
- Bradbury, R.B., Kyrkos, A., Morris, A.J., Clark, S.C., Perkins, A.J. & Wilson, J.D. 2000: Habitat associations and breeding success of yellowhammers on lowland farmland. — *Journal of Applied Ecology* 37: 789–805.
- Brown, P.W. & Frederickson, L.H. 1987: Time budget and incubation behaviour of breeding white-winged scoters. — *Wilson Bulletin* 99: 50–55.
- Brown, P.W. & Frederickson L.H. 1997: White-winged scoter *Melanitta deglandi*. In *The Birds of North America* no. 274 (eds. Poole A. & Gill F.): 1–28. — *Birds of North America*, Philadelphia.
- Brown, H. & Prescott, R. 2015: *Applied Mixed Models in Medicine*. — Wiley, Chichester.
- Chimienti, M., Cornulier, T., Owen, E., Bolton, M., Davies, I.M., Travis, J.M.J. & Scott, B.E. 2017: Taking movement data to new depths: Inferring prey availability and patch profitability from seabird foraging behaviour. — *Ecology and Evolution* 7: 10252–10265.
- Cramp, S. & Simmons, K.E.L. (eds). 1977: *The Birds of the Western Palearctic*, Vol.1. — OUP, Oxford.
- Croft, P.S. 1986: A key to the major groups of British freshwater invertebrates. — *Field Studies* 6: 531–579.
- Drent, R.H., Fox, A.D. & Stahl, J. 2006: Travelling to breed. *Journal of Ornithology* 147: 122–134.
- Eaton, M., Aebischer, N., Brown, A., Hearn, R., Lock, L., Musgrove, A., Noble, D., Stroud, D. & Gregory R. 2015: *Birds of Conservation Concern 4: the population status of birds in the UK, Channel Islands and Isle of Man*. — *British Birds* 108: 708–746.
- Flower, C.E., Long, L.C., Knight, K.S., Rebbeck, J., Brown, J.S., Gonzalez-Meler, M.A. & Whelan, C.J. 2014: Native bark-foraging birds preferentially forage in infected ash (*Fraxinus* spp.) and prove effective predators of the invasive emerald ash borer (*Agrilus planipennis* Fairmaire). — *Forest Ecology & Management* 313: 300–306.
- Fox, A.D. 2003: Diet and habitat use of scoters *Melanitta* in the Western Palearctic – a brief overview. — *Wildfowl* 54: 163–182.
- Gardarsson, A. & Einarsson, A. 2002: The food relations of waterbirds of Lake Myvatn, Iceland. — *Verhandlungen des Internationalen Verein Limnologie* 28: 754–763.
- Gardarsson, A. & Einarsson, A. 2004: Resource limitation of diving ducks at Myvatn: food limits production. — *Aquatic Ecology* 38: 285–295.
- Goudie, R.I. 1999: Behaviour of harlequin ducks and three species of scoters wintering in the Queen Charlotte Islands, British Columbia. — In *Behaviour and Ecology of Sea Ducks*, Canadian Wildlife Service Occasional Papers no. 100 (eds. Goudie, R.I., Peterson, M.R. & Robertson, G.J.): 6–13. — Canadian Wildlife Service, Ottawa.
- Hamilton, D.J., Ankney, C.D. & Bailey, R.C. 1994: Predation of zebra mussels by diving ducks: an enclosure study. — *Ecology* 75: 521–531.
- Hancock, M.H., Robson, H.J., Smith, T.D. & Douse, A. 2016: Correlates of lake use by breeding Common Scoters in Scotland. — *Aquatic Conservation: Marine and Freshwater Ecosystems* 26: 749–760.
- Hancock, M.H., Klein, D., Andersen, R. & Cowie, N.R. 2018: Vegetation response to restoration management of a blanket bog damaged by drainage and afforestation. — *Applied Vegetation Science* 21: 167–178.
- Heino, J. 2009: Biodiversity of aquatic insects: spatial gradients and environmental correlates of assemblage-level measures at large scales. — *Freshwater Reviews* 2: 1–29.
- Holopainen, S., Arzel, C., Dessborn, L., Elmberg, J., Gunnarsson, G., Nummi, P., Pöysä, H. & Sjöberg K. 2015: Habitat use in ducks breeding in boreal freshwater wetlands: a review. *European Journal of Wildlife Research* 61: 339–363.
- Hunter, M.L., Witham, J.W. & Dow H. 1984: Effects of carbaryl-induced depression in invertebrate abundance on the growth and behaviour of American black duck and mallard ducklings. *Canadian Journal of Zoology* 62: 452–456.
- Jackson, D.B. 2005: Environmental correlates of lake occupancy and chick survival of black-throated divers *Gavia arctica* in Scotland. — *Bird Study* 52: 225–236.
- Jönsson, K.I. 1997: Capital and income breeding as alternative tactics of resource use in reproduction. — *Oikos* 78: 57–66.
- Kaiser, M.J., Galandi, M., Showler, D.A., Elliott, R.W., Caldwell, R.W.G., Rees, E.I.S., Stillman, R.A. & Sutherland, W.J. 2006: Distribution and behaviour of Common Scoter *Melanitta nigra* relative to prey resources and environmental parameters. — *Ibis* 148: 110–128.
- Kang, T., Kang, Y.-M., Jeong, W., Moon, O.-K., Yoon, H.,

- Choi, J. & Lee, H. 2016: Spring migration of mallards (*Anas platyrhynchos*) tracked with wild-trackers in East Asia. — *Journal of Asia-Pacific Biodiversity* 9: 323–327.
- Karlsson, J., Byström, P., Ask, J., Ask, P., Persson, L. & Jansson, M. 2009: Light limitation of nutrient-poor lake ecosystems. — *Nature* 460: 506–510.
- Kirkham, I.R. & Johnson, S.R. 1988: Interspecific aggression in loons. — *Journal of Field Ornithology* 59: 3–6.
- Kobler, A., Klefoth, T., Wolter, C., Fredrich, F. & Arlinghaus, R. 2008: Contrasting pike (*Esox lucius* L.) movement and habitat choice between summer and winter in a small lake. — *Hydrobiologia* 601:17–27.
- Krapu, G.L. & Reinecke, K.J. 1992: Foraging ecology and nutrition. — In *Ecology and Management of Breeding Waterfowl* (eds. Batt *et al.*): 1–29. University of Minnesota Press, Minneapolis.
- Leopold, M.F., Spannenburg, P.C., Verdaat, H.J.P. & Kats, R.K.H. 2007: Identification and size estimation of *Spirula subtruncata* and *Ensis americanus* from shell fragments in stomachs and faeces of common eiders *Somateria mollissima* and Common Scoters *Melanitta nigra*. — In *Common eiders Somateria mollissima* in the Netherlands (ed. Kats, R.K.H.): 63–86. — Rijksuniversiteit Groningen, Groningen.
- Lesage, L., Reed, A. & Savard, J.-P.L. 2008: Duckling survival and use of space by surf scoter (*Melanitta perspicillata*) broods. — *Ecoscience* 15: 81–88.
- Lewis, T.L., Esler, D., Boyd, W.S. & Zydels, R. 2005: Nocturnal foraging behaviour of wintering surf scoters and white-winged scoters. — *The Condor* 107: 637–647.
- Lewis, T.L., Esler, D. & Boyd, W.S. 2007. Foraging behaviors of surf scoters and white-winged scoters during spawning of Pacific herring. — *The Condor* 109: 216–222.
- Lewis, T.L., Lindberg, M.S., Schmutz, J.A., Bertram, M.R. & Dubour A.J. 2015: Species richness and distribution of boreal waterfowl broods in relation to nesting and brood rearing habitats. — *Journal of Wildlife Management* 79: 296–310.
- Lindsay, R.A., Charman, D.J., Everingham, F., O'Reilly, R.M., Palmer, M.A., Rowell, T.A. & Stroud, D.A. 1988: The Flow Country. The Peatlands of Caithness and Sutherland. — Nature Conservancy Council, Peterborough.
- Lovette, I.J. & Holmes, R.T. 1995: Foraging behaviour of American redstarts in breeding and wintering habitats: implications for relative food availability. — *The Condor* 97: 782–791.
- Maitland, P.S. & Campbell, R.N. 1992: *Freshwater Fishes of the British Isles*. — HarperCollins, London.
- Miller, J. 2002: *The Dam Builders: Power from the Glens*. — Birlin, Edinburgh.
- Morrison, M.L., Marcot, B.G. & Mannan, R.W. 2006: *Wildlife-Habitat Relationships: Concepts and Applications*. — Island Press, Washington DC.
- Morton, M. & Pereyra, M.E. 2011: Additional Data and Perspectives on Interspecific Aggression in the Common Loon, *Gavia immer*. — *Canadian Field Naturalist* 125: 61–62.
- Moss, B.R. 2010: *Ecology of Freshwaters: a View for the Twenty-First Century*. — Wiley-Blackwell, Oxford.
- Newton, I. 1998: *Population Limitation in Birds*. — Academic Press, London.
- Oppel, S., Powell, A.N. & Butler, M.G. 2011: King Eider foraging effort during the pre-laying period in Alaska. — *The Condor* 113: 52–60.
- Partridge, K. & Smith, K. 1988: Common Scoters: the Lough Erne decline in an all-Ireland context. — RSPB, Sandy.
- Robb, G.N., McDonald, G.A., Chamberlain, D.E. & Bearhop, S. 2008: Food for thought: supplementary feeding as a driver of change in avian populations. — *Frontiers in Ecology & Environment* 6: 476–484.
- Rogers, K.B. 1998: *Habitat Use by Largemouth Bass and Northern Pike on the Rocky Mountain Arsenal, Colorado*. — Colorado State University Fort Collins, Colorado (PhD Thesis).
- Rufino, L., Salo, P., Koivisto, E., Banks, P.B. & Korpi-mäki, E. 2014: Reproductive responses of birds to experimental food supplementation: a meta-analysis. — *Frontiers in Zoology* 11(80): 1–13.
- Sæther, B.-E., Ringsby, T.H. & Røskaft, R. 1996: Life history variation, population processes and priorities in species conservation: towards a reunion of research paradigms. — *Oikos* 77: 217–226.
- Sample, J.E., Duncan, N., Ferguson, M. & Cooksley, S. 2015: Scotland's hydropower: Current capacity, future potential and the possible impacts of climate change. — *Renewable and Sustainable Energy Reviews* 52: 111–122.
- SAS 2014: SAS/STAT version 9.4. — SAS Institute Inc., Cary, NC.
- Savard, J.-P.L., Bordage, D. & Reed, A. 1998: Surf scoter *Melanitta perspicillata*. In *The Birds of North America* no. 363 (eds. Poole, A. & Gill, F.): 1–28. — Birds of North America, Philadelphia.
- Savard, J.-P.L., Derksen, D.V., Esler, D. & Eadie, J.M. (eds.) 2015: *Ecology and Conservation of North American Sea Ducks*. — CRC Press, Boca Raton.
- Schloesser, D.W. & Nalepa, T.F. 2002: Comparison of five benthic samplers to collect burrowing mayfly nymphs (*Hexagenia* spp.: Ephemeroptera: Ephemeridae) in sediments of the Laurentian Great Lakes. — *Journal of the North American Benthological Society* 21: 487–501.
- Sedinger, J.S. 1992: *Ecology of pre fledging waterfowl*. — In *Ecology and Management of Breeding Waterfowl* (eds. Batt *et al.*): 109–127. University of Minnesota Press, Minneapolis.
- Shepard, E.L.C., Wilson, R.P., Quintana, F., Laich, A.G. & Forman, D.W. 2009: Pushed for time or saving on fuel: fine-scale energy budgets shed light on currencies in a diving bird. *Proceedings of the Royal Society B* 276: 3149–3155.

- Sherry, T.W. 2016: Avian food and foraging. — In Handbook of Bird Biology (eds. Lovette, I.J. & Fitzpatrick, J.W.): 265–310. — Wiley, Chichester.
- Skov, H., Heinänen, S., Žydelis, R., Bellebaum, J., Bzoma, S., Dagys, M., Durinck, J., Garthe, S., Grishanov, G., Hario, M., Kieckbusch, J.J., Kube, J., Kuresoo, A., Larsson, K., Luigujó, L., Meissner, W., Nehls, N.W., Nilsson, L., Petersen, I.K., Roos, M.M., Pihl, S., Sonntag, N., Stock, A., Stipniece, A. & Wahl, J. 2011: Waterbird Populations and Pressures in the Baltic Sea. — Nordic Council of Ministers, Copenhagen.
- Sperry, M.L. 1987: Common Loon attacks on waterfowl. — Journal of Field Ornithology 58: 201–205.
- SPFA (Scottish Pelagic Fishermen's Association). 2018: News – Searching for winter / spring spawning Western Herring. www.scottishpelagic.co.uk/searching-for-winter-spring-spawning-western-herring.
- Stroup, W.W. 2013. Generalized Linear Mixed Models. Modern Concepts, Methods and Applications. — CRC Press, Boca Raton.
- Summers, R.W., Mavor, R., Hogg, S. & Harriman, R. 2011: Lake characteristics and their selection by breeding Slavonian Grebes *Podiceps auritus* in Scotland. — Bird Study 58: 349 – 356.
- Tschaekofske, H.J. 2010: Prey selection and its relationship to habitat and foraging strategy of molting White-winged (*Melanitta fusca*) and Surf Scoters (*M. perspicillata*) in Puget Sound, WA, and the Strait of Georgia, BC. — Dissertation, Evergreen State College, Olympia, Washington.
- Tierney, D. 2001: The biology of Common Scoter *Melanitta nigra* breeding on Irish loughs – population, behavioural and feeding ecology. — Dissertation, National University of Ireland, Galway.
- Turner, A.M. & Trexler, J.C. 1997: Sampling aquatic invertebrates from marshes: evaluating the options. — Journal of the North American Benthological Society 16: 694 – 709.
- Underhill, M., Gittings, T., Callaghan, D.A., Hughes, B., Kirby, J.S. & Delany, S. 1998: Status and distribution of breeding Common Scoters *Melanitta nigra nigra* in Britain and Ireland in 1995. — Bird Study, 45: 146–156.
- Weatherhead, M.A. & James, M.R. 2001: Distribution of macroinvertebrates in relation to physical and biological variables in the littoral zone of nine New Zealand lakes. — Hydrobiologia 462 115–129.
- Winiarski, K.J., Burt, M.L., Rexstad, E., Miller, D.L., Trocki, C.L., Paton, P.W.C. & McWilliams SR. 2014: Integrating aerial and ship surveys of marine birds into a combined density surface model: A case study of wintering Common Loons. — The Condor 116: 149–161.
- Žydelis, R., Richman, S.E. 2015: Foraging behaviour, ecology, and energetics of sea ducks. — In Ecology and Conservation of North American Sea Ducks (eds. Savard *et al.*): 241–266. CRC Press, Boca Raton.

Online supplementary material

- Appendix 1: Supplementary results: Observations of scoters disturbed by predators
- Supplementary Table S1: Overview of the variables and units of analysis used in statistical models
- Fig. S1: A schematic map of a fictitious study lake with four sampling points, showing the lake area and the four lake sectors
- Fig. S2: The abundance of large invertebrates in the early and late parts of the breeding season
- Fig. S3: Comparing the foraging time budgets of scoters between this study and other studies