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Feeding associations between Red-necked Grebes *Podiceps griseigena* and Velvet Scoters *Melanitta fusca* in winter

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Red-necked Grebes *Podiceps griseigena* wintering along the coast of Jæren, southwest Norway, were found to feed either solitarily or in close association with Velvet Scoters *Melanitta fusca* feeding on bottom prey (mainly echinoderms) dug out from the sandy substrate. By scuba diving at spots where both species were feeding, we found that stirring the sand caused polychaete worms to emerge from the substrate. Bottom samples showed that these worms (on average >1000 per m^2) vastly outnumbered other animal taxa living in the substrate and that polychaetes were probably the most likely prey of grebes associated with scoters. Food competition between the two species and/or kleptoparasitism by the grebes were probably not involved (no food-stealing attempts by the grebes toward scoters handling prey brought to the surface, no aggression by scoters toward grebes and no effect of the grebes on the time budget of the scoters). Red-necked Grebes associating with scoters were mainly first-year birds, and the frequency of association decreased from a maximum of nearly 60% of the grebes in November to *c.* 5% before spring departure in April. Grebes feeding solitarily hunted in a manner resembling divers (*Gavia*), and they brought fish to the surface significantly more often than grebes feeding with scoters. Solitary grebes spent less time feeding and more time preening and swimming than did grebes associating with scoters. The association appears to be a way naive birds could easily obtain prey. Skills needed to dive for more nutritious but agile fish are probably gradually acquired through the winter as more of the grebes adopt solitary feeding.

Birds frequently feed in mixed species flocks, often as a result of similar preferences for feeding habitat. Sometimes the feeding activity of one species makes food more available to other species, in which case heterospecific associations are formed more actively. Dabbling ducks may form feeding associations with swans, geese and American Coots *Fulica americana*, the feeding actions of which may bring to the surface food that is normally beyond the reach of the ducks (Bailey & Batt 1974, Knapton & Knudsen 1978). The startling of insects by grazing ungulates is utilized by feeding Cattle Egrets *Bubulcus ibis* and Yellow Wagtails *Motacilla flava*, resulting in both these species associating with cattle (Heatwole 1965, Källander 1993).

During midwinter monitoring of waterfowl along the coast of southwest Norway in the 1970s and 1980s, we found Red-necked Grebes *Podiceps griseigena* and Velvet Scoters *Melanitta fusca* occurred in close associations. Examining such associations in detail, we found them to be more than just an effect of similar habitat choice in the two species. Here we describe the pattern of association between the grebes and scoters and discuss the phenomenon in relation to food parasitism and commensalism.

STUDY AREA AND METHODS

The study was made on the coast of Jæren, a stretch of about 60 km of shallow water exposed to the North Sea with patches of sandy bottom partly colonized with Kelp *Laminaria* making up about a quarter of the coast. About 10,000 waterfowl of 20 species spend the winter there, amongst them 50 to 100 Red-necked Grebes (Byrkjedal & Eldøy 1980, 1984).

We conducted behavioural observations in a shallow bay, Solabukta, using the focal animal method (Altmann 1974) to examine the relationship between grebes and scoters. These observations were made on 11–12 December 1982, 27–28 October 1991, 23 January and 3–4 March 1992. Continuous observations, for as long as possible, of individual grebes and scoters were made from vantage points using a 20 to 45× telescope. When a focal bird disappeared from view, another individual was chosen. Observations on individual birds varied from 9 to 74 min. During these observations, we recorded the duration of different activities (feeding, preening, resting, locomotion, aggression and courtship), diving frequencies, duration of dives and estimated minimal horizontal distances moved during and

Table 1. *Synchrony of behaviour of Red-necked Grebes with accompanied Velvet Scoters, expressed as percentage of time spent in various activities by grebes during the time the scoters spent in a particular activity (data pooled from 5 sets of observations)*

	No. of minutes	Grebes			
		Feeding	Locomotion	Preening	Resting
Scoters					
Feeding	45	89%		5%	7%
Locomotion	10		100%		
Preening	37		16%	84%	
Resting	6			33%	67%

between dives. All timing was done with a stopwatch, and observations were dictated to a tape recorder or to a second observer. Distances were estimated using the body-length of the birds as a scale. Diving synchrony and individual distances between grebes and scoters were recorded in cases where they were close together, the association being apparent from the birds closely following one another.

Prey brought to the surface by any of the birds was identified if possible. In 1991–1992, special attention was paid to this aspect during about 10 h of observations of scoters. Scoters spent up to 2 min handling prey, frequently giving enough time for the prey to be identified in good light conditions.

In November 1993, 3 h were spent scuba diving to observe the relation between scoters and grebes under water as they fed together. In spite of a calm sea, particles suspended in the water prevented clear views, even though the birds were approached within 10 m.

To examine whether Red-necked Grebes associated with Velvet Scoters more often than expected by chance, a survey of waterfowl was made on 18–19 November 1984 along Solabukta and other stretches of the Jæren coast with a sandy bottom. Red-necked Grebes invariably fed over this bottom substrate in the area. Waterfowl seen on the sea surface were counted. Whenever Red-necked Grebes were encountered, their distance to the nearest waterfowl was estimated, and the grebes were watched for 5 min to determine whether they followed other waterfowl. Parts of the Jæren coast were searched for Red-necked Grebes between September and April in order to record the seasonal pattern in the grebes' associations with scoters.

Finding that Red-necked Grebes dived with Velvet Scoters searching for food and that the scoters surfaced with prey they had excavated from the bottom, we suspected that grebes fed on prey made available by the scoters. Capturing grebes for stomach samples failed, and we resorted to bottom samples in order to search for potential prey that grebes might use as food. During scuba diving in Solabukta on 15–16 November 1993, 17 bottom samples were taken. Bottom substrate (sand) samples were shovelled into nylon bags with 0.5-mm mesh; each sample was 17 × 20 cm and about 5 cm deep. The samples were taken at 1.5 to 3.7 m depth at places where scoters and grebes had just been feeding. The samples were sieved, and retained animals were transferred to 75% alcohol. The samples contained numerous polychaetes. In order to simulate the digging action of feeding scoters, a number of probes were made with a knife into the sandy bottom, and animals emerging were recorded.

In using statistics in comparing time budget percentages, we used arcsine transformations of the proportions (Zar 1984).

RESULTS

Behaviour of solitary grebes and grebes associated with scoters

During focal animal observations in Solabukta, Red-necked Grebes entered the bay at about 09.00 h to 09.30 h in a flock that had apparently been roosting further out at sea for the night. At that time, the Velvet Scoters had been feeding for some time and were dispersed over the bay. The grebes approached the scoters, and the flock dissolved as a number of the grebes each selected an individual scoter and dived together with it. Grebes which did not approach a scoter started to feed solitarily.

Among available waterfowl, Velvet Scoters were strongly preferred as partners by the Red-necked Grebes. On a stretch of coast sampled in mid-November 1984 (n = 454 waterfowl) 18 Red-necked Grebes were seen in association with other birds; 16 of these grebes (89%) were with Velvet Scoters, although this duck made up only 30% of the waterfowl (preferred by grebes to other waterfowl: $\chi^2_1 = 30.6$, $P < 0.001$). The remaining two Red-necked Grebes associated with Slavonian Grebes *Podiceps auritus*. The other available waterfowl, in addition to the Velvet Scoters, were Long-tailed Ducks *Clangula hyemalis* (21%), Eiders *Somateria mollissima* (11%), Common Scoters *Melanitta fusca* (10%), Slavonian Grebes (7%), Red-breasted Mergansers *Mergus serrator* (5%) and Razorbills *Alca torda* (5%).

Grebes associating with scoters synchronized their activities with those of the scoters (Table 1): when a scoter stopped feeding so did the grebe, but instead of seeking a new scoter which was actively feeding, the grebe continued its association with the original scoter. Grebes kept close to their chosen scoter, both while they were feeding (mean 1.2 m ± 1.0 s.d.; n = 47, 7 individual grebes) and when not feeding (mean 1.9 m ± 1.9 s.d., n = 22, 4 different individuals). In feeding associations, the grebe dived a few seconds after the scoter it accompanied (95% of 64 dives, simultaneous with the scoter in 3% and before the scoter in 2% of the dives). The grebe surfaced before the scoter in 93% of the cases.

Solitary grebes showed a food-searching behaviour similar to that of *Gavia* divers. Unlike grebes following scoters, they often peered under the sea surface while swimming. They

Table 2. *Frequencies and duration of dives and distances travelled by Red-necked Grebes feeding in association with Velvet Scoters and solitarily (data pooled from 11 associated and five solitary grebes)*

	Associated grebes			Solitary grebes				
	Mean	s.d.	*n*	Mean	s.d.	*n*	*t*	*P*
Dives per min	0.7	0.52	96	1.0	0.57	70	3.86	<0.001
Duration of dives (s)	46.0	7.78	55	39.3	12.78	48	3.23	<0.01
Horizontal distance under water (m)	2.8	2.03	41	27.7	18.06	50	8.69	<0.001
Horizontal distance on surface[a] (m)	1.2	0.75	16	4.6	7.90	40	1.69	n.s.

[a] Between dives.

dived less often than did grebes associated with scoters, stayed a shorter time under water, covered a much larger horizontal distance under water and swam a greater distance between dives (Table 2). Time budgets of associated and solitary grebes were different (Fig. 1). We found solitary grebes (n = 16 birds) spent, on average, 44% less time feeding than associated grebes (n = 14 birds, t = 3.88, P < 0.001) and almost two and three times as much time swimming and preening (t = 3.67 and 2.08, P < 0.001 and P < 0.05, respectively).

Solitary grebes brought fish to the surface significantly more often (10% of 77 dives) than did grebes associated with scoters (2% of 143 dives; Fisher's Exact Test, P = 0.018, Table 3).

Occurrence of association with age and season

Among the Red-necked Grebes seen in October and November, 13 birds were confidently identified as birds of the year and 22 as >1 year old (i.e. adults). Of the adults, 86% were solitary, while all of the first-year birds were with scoters (χ_1^2 = 24.5, P < 0.001).

In October–November, 45–60% of the grebes were associated with scoters (Fig. 2). From November, the frequency of association decreased through the winter (r_s = −0.94, P < 0.005), and before the spring migration in April, only a few birds (5%) were associated with scoters.

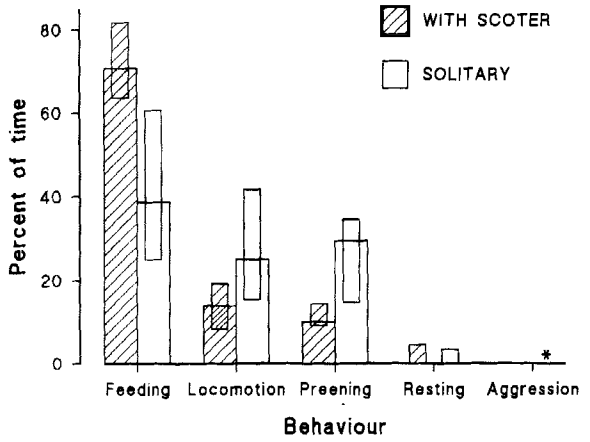

Figure 1. Time budgets of Red-necked Grebes with and without Velvet Scoter companions, shown as median and interquartile ranges for 14 grebes with scoters (204 bird-min) and for 16 solitary grebes (312 bird-min). * = behaviour recorded in <25% of the individuals.

Feeding behaviour of Velvet Scoters and their responses to grebes

The Velvet Scoters fed on sandy bottoms, where they dug for burrowing organisms (as shown by items brought to the surface). In 60% of 677 dives, scoters brought nothing to the surface; either no prey was caught, or the prey was swallowed under water. The following prey were brought to the surface: the sea urchin *Echiocardium flavescens* (70%), crabs (*Carcinus* sp., *Portunus* sp.) (10%), flounder (6%), *Asterias rubens* (4%), *Ammodytes* sp. (1%), *Dentalium entalis* (1%) and unidentified small prey (10%). The last were probably small bivalves, possibly the commonly occurring *Tellina* (see below), in which case 72% of what was brought to the surface represented bottom fauna. If all cases of surfacing without prey represented consumption of small bivalves living in the sand, a maximum of 92% of the prey items would be bottom fauna, requiring a digging search technique.

Table 3. *Fish prey brought to surface by Red-necked Grebes*

Prey	Grebes with scoters	Solitary grebes
Ammodytidae	3	2
Clupeidae		1
Spinachia spinachia		1
Cottidae		1
Fish not determined		3
Dives with no prey brought to surface	140 (98%)	69 (90%)

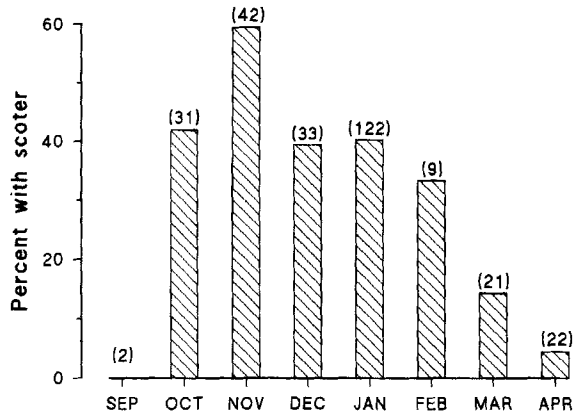

Figure 2. Seasonal occurrence of Red-necked Grebes associating with Velvet Scoters along the coast of Jæren, data pooled for 1981–1982 through 1993–1994. Numbers in parentheses are total number of Red-necked Grebes. (Note: Observation effort varied over the months, and total numbers do not accurately reflect seasonal occurrence of grebes).

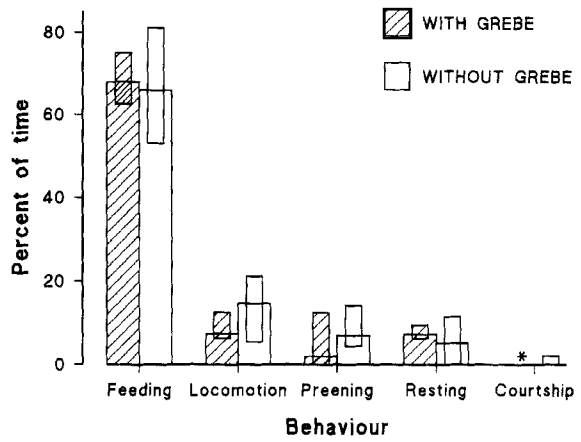

Figure 3. Time budget of Velvet Scoters with and without Red-necked Grebe companions, shown as median and interquartile ranges based on 10 scoters with and 20 scoters without grebes (135 and 593 bird-min, respectively). * = behaviour recorded in <25% of the individuals.

Neither during the time-budget observations on scoters and grebes in association nor in any other contexts that we watched them were any aggressive interactions detected between the two species. The presence of grebes did not have a significant effect on the time budget of the scoter (with *v* without grebe for each behaviour category: $t = 0.41–1.32$, n.s.; Fig. 3).

Samples of bottom fauna

In bottom samples from Solabukta, errant polychaetes (chiefly *Phyllodoce* sp.) made up 87% of the animals, and their average density exceeded 1000 worms per m² (Table 4). These worms were about 3–6 cm long. Bivalves, of which *Tellina tenuis* (3–11 mm long) made up 96%, had an average density of 69 animals per m². Small amphipods (4–7 mm long) occurred in a similar density, while the sea urchin *Echinocardium flavescens*, an important prey of Velvet Scoters, had a density of only 4 per m². One *Ammodytes tobianus* was also found in the samples.

Probes with a knife in the sandy bottom while scuba diving disturbed the polychaetes, which left the sand and swam into the water. In 10 probes, 1.2 animals emerged on average per probe (s.d. ± 1.55).

DISCUSSION

The study showed that wintering Red-necked Grebes frequently formed feeding associations with Velvet Scoters. The associations are more than random flocking, as Velvet Scoters are clearly preferred partners compared to other waterfowl. The grebes followed individual scoters, with which they synchronized their behaviour. The feeding behaviour and food differed between solitary and scoter-associated grebes. An affinity with Velvet Scoters by wintering Red-necked Grebes may be a widespread phenomenon; the species have been noted to occur together at Møre in western Norway (Folkestad 1978) and in Danish waters (Pihl 1995).

Among diving ducks in general, and certainly among waterfowl occurring along the coast of southwest Norway, Velvet Scoter are most likely to scoop and dig for food organisms in the bottom. Although they may feed extensively on epifauna, such as Mussels *Mytilus edulis* (Madsen 1954, Bagge *et al.* 1973), their broad bills make them well adapted to dig into soft bottom substrate (cf. prey reported by Stott & Olson 1973, Vermeer & Bourne 1984, Durinck *et al.* 1993). The present study shows that digging might be the chief mode of feeding employed by the scoters. Grebes diving along with individual scoters indicates that the grebes prob-

Table 4. *Estimated number of animals per m² in bottom samples (sandy bottom). Each sample was 0.068 m² and 6–8 cm into substrate and taken at Solabukta on 15–16 November 1993, at sites where grebes and scoters had recently been feeding*

Taxon	Density (*n*/m²)	s.d.	Range	Total animals
Polychaeta, Errantia[a]	1037	739	206–3000	1199
Gephyrea, *Golfingia* sp.	6	10.1	0–30	7
Bivalvia[b]	69	71.6	0–176	80
Gastropoda	1	3.5	0–15	1
Amphipoda	75	52.4	15–220	87
Mysidae	2	4.7	0–15	2
Echinocardium flavescens	4	6.2	0–15	4
Ammodytes tobianus	1	3.5	0–15	1

[a] *Phyllodoce* sp. = 81%.
[b] *Tellina tenuis* = 96%.

ably picked up food that became available as the scoters dug into the bottom. The likely options available to the grebes were kleptoparasitizing the scoter, picking morsels from prey disintegrating while mandibulated by the scoters (e.g. *Echinocardium*) and capturing prey disturbed from the bottom by the action of the scoter.

Presumably kleptoparasitism was not involved. Scoters were never seen to attack or show hostility toward the grebes or to try to avoid them. Time budgets (including time spent feeding) of scoters followed by grebes were not different from those of scoters feeding in the absence of grebes, indicating that the grebes had no major impact on the scoters' feeding. Moreover, grebes were never seen attempting to steal prey or pick morsels from prey brought to the surface by the scoters for handling. Echinoderms mandibulated by the scoters on the sea surface often disintegrated. This was an important prey group for the scoters and might have given the grebes ample opportunities to help themselves to pieces. Most likely, the grebes fed on organisms made available but not preyed upon by the scoters. Small bivalves (*Tellina*) were numerous in the bottom substrate, and a scooping action by the scoters might expose a number sufficient for the grebes to pick some. However, bivalves have not been found in the diet of Red-necked Grebes studied elsewhere in the nonbreeding season (Madsen 1957, Fjeldså 1982, Piersma 1988). Errant polychaetes are a more likely group of prey. They had a notably high abundance in the bottom samples, emerged actively out of the substrate when the latter was probed with a knife (presumably not dissimilar to the feeding action of scoters), and polychaetes have been found to be important food of wintering Red-necked Grebes in Danish waters (Fjeldså 1982). Polychaetes are rare or absent in the diet of Velvet Scoters (Madsen 1954, Stott & Olsson 1973, Bagge *et al.* 1973, Vermeer & Bourne 1984, Sanger & Jones 1984, Durrick *et al.* 1993). Also, small fish like gobies and bullheads (cottids), which often lay still on the bottom until closely approached, and *Ammodytes*, which regularly lie buried in the sand (Wheeler 1969), may be disturbed by the scoters. Observations on grebes showed that they surfaced with *Ammodytes* in a few cases after having dived along with scoters.

The method of feeding used by solitary grebes was the same as that used by divers, mergansers and auks diving for fish. Observations of prey brought to the surface indicate that solitary grebes took fish more often than did scoter-associated grebes. Fish are a more nutritious food than polychaetes. Fish (gadoids, clupeids, ammodytids) of 5–10 cm length yield about 5 to 65 kJ per prey (Harris & Hislop 1978), compared to only 0.1 to 0.2 kJ for a *c.* 10-cm-long polychaete (Pienkowski 1982). Energetically, one fish prey may be equal to 25 to 325 polychaetes. This may explain why solitary grebes spent less time feeding and more time in comfort activities (preening) than did scoter-associated grebes. Why should grebes associate with scoters? Presumably scoters make prey so easily available that they constitute an attractive food resource to the grebes even though the most commonly available prey, polychaetes, may be nutritionally less favourable. The birds associating with scoter are often birds of the year. These birds may have fed on insects in freshwater localities (Wobus 1964) before they reach the sea for the first time in their life. Polychaetes may be more similar to the prey they are used to, besides being easier to capture than more agile fish. The association of grebes with scoter diminishes over the winter; presumably the grebes gradually become more skilled at capturing fast-moving prey, enabling them to adopt the more demanding but energetically favourable pursuit of diving for fish. Among birds, time to learn foraging skills seems to be a common cause for differences in feeding between juveniles and adults (Marchetti & Price 1989).

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