

# Species limits within the genus *Melanitta*, the scoters

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Dan Powell

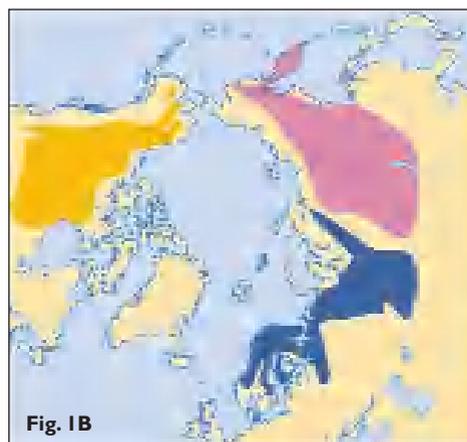
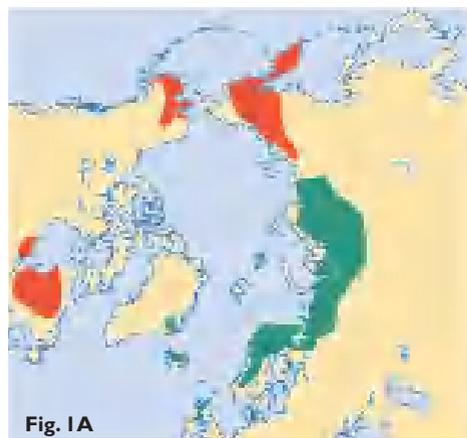
**ABSTRACT** As part of its reassessment of the taxonomy of birds on the British List, the BOURC Taxonomic Sub-committee has assessed all six recognised taxa of scoters *Melanitta* against its previously published Species Guidelines (Helbig et al. 2002). We consider that, on the basis of evidence currently available, at least five species should be recognised: Common Scoter *M. nigra*, Black Scoter *M. americana*, Velvet Scoter *M. fusca*, White-winged Scoter *M. deglandi* and Surf Scoter *M. perspicillata*. The taxonomic status of the Asian subspecies of White-winged Scoter (*stejnegeri*) is uncertain, owing to insufficient information on several aspects of its morphology and behaviour. Provisionally, we suggest that it is best treated as conspecific with *M. deglandi*.

### Introduction

Six taxa of scoters *Melanitta* are generally recognised within the seaduck tribe Mergini (Miller 1916; Vaurie 1965; Cramp & Simmons 1977; table 1). The Surf Scoter *M. perspicillata* is monotypic. The other taxa have traditionally been treated as two polytypic species by both the American and the British Ornithologists' Unions: Velvet (or White-winged) Scoter *M. fusca* with three races, *fusca*, *deglandi* (syn. *dixonii*) and *stejnegeri*; Common (or Black) Scoter *M. nigra* with two races, *nigra* and *americana*. All six taxa have also, in the past, been

regarded as separate species (BOU 1883, 1915; Dwight 1914).

For brevity, these taxa will henceforth be referred to by their subspecific names, i.e. *nigra* (Common or Eurasian Black Scoter), *americana* (American and East Asian Black Scoter), *fusca* (Velvet Scoter), *deglandi* (American White-winged Scoter), *stejnegeri* (Asian White-winged Scoter) and *perspicillata* (Surf Scoter). In Britain, *nigra* and *fusca* are widespread non-breeding and winter visitors, though small numbers of *nigra* breed in Scotland (Ogilvie *et al.* 2001). Two other forms, *americana* and *perspicillata*, are vagrants or scarce migrants in Britain (BOU 1992). At present, there are no accepted records of *stejnegeri* or *deglandi* in Britain, although both have occurred as vagrants elsewhere in the Western Palearctic (Garner *et al.* 2004).



**Fig. 1.** Approximate distribution of scoter taxa.

**1A.** The breeding ranges of Common Scoter *Melanitta nigra* (green) and Black Scoter *M. americana* (orange).

**1B.** The breeding ranges of Velvet Scoter *M. fusca* (blue), (Asian) White-winged Scoter *M. deglandi stejnegeri* (pink) and (American) White-winged Scoter *M. deglandi deglandi* (yellow).

**1C.** The breeding range of Surf Scoter *M. perspicillata* (green).

Table 1. Genus *Melanitta* (Boie 1822) (*Tageb. Reise Norwegen*, p. 301).

#### Subgenus *Melanitta* – White-marked Scoters

*M. perspicillata* (L. 1758) – Surf Scoter (*Syst. Nat.*, i, pp. 123–125).

*M. fusca* (L. 1758) – Velvet Scoter (*Syst. Nat.*, i, pp. 123–125).

*M. deglandi* (Bonaparte 1850) – White-winged Scoter (*Rev. Crit. Orn. Europe*, p. 118)

*M. d. stejnegeri* (Ridgway 1887) – White-winged Scoter (*Man. N. Am. Birds*, p. 112).

#### Subgenus *Oidemia* (Fleming 1822) (*Philos. Zool.*, ii, p. 260) – Black Scoters

*M. nigra* (L. 1758) – Eurasian Black Scoter, Common Scoter (*Syst. Nat.* i, pp. 123–125).

*M. americana* (Swainson 1832) – Black Scoter (*Faun. Bor. Amer.*, ii, p. 450).

### Problems of scoter taxonomy

Scoters have a broad Holarctic distribution (fig. 1; Appendix 1). Published literature does not define specifically whether the breeding ranges of *nigra* and *americana* or of *fusca* and *stejnegeri* overlap. However, there is little, if any, evidence that they do, and for the purposes of this assessment they are regarded as allopatric. It remains possible that they are to some extent parapatric (i.e. their ranges meet but do not significantly overlap). For example, a zone of near-parapatry has been described for *fusca* and *stejnegeri* in western Siberia (Rogacheva 1992).

As described below, Common/Black (*nigra* and *americana*), Velvet/White-winged (*fusca*, *deglandi* and *stejnegeri*) and Surf Scoters (*perspicillata*) differ in plumage and morphology in multiple diagnostic characteristics. They are divergent in ecology, and there are significant differences in their courtship displays and breeding behaviour. This is entirely normal for species that are, over parts of their range, sympatric. The three traditionally recognised species fulfil all requirements for specific status under any species concept.

Difficulties arise in the taxonomic treatment of the two sets of allopatric taxa: *nigra* and *americana* on the one hand and *fusca*, *deglandi* and *stejnegeri* on the other. In both cases, the taxa occupy non-overlapping ranges on both the breeding and (almost entirely) the wintering grounds. This is the problem: *nigra* and *americana* are clearly more similar to each other than they are to any other species, as are *fusca*, *deglandi* and *stejnegeri*, which underlies their traditional classification as subspecies. However, parapatric and allopatric sister species do not always show levels of divergence in multiple characters similar to those found between sympatric species, because there is no requirement for the ecological separation that characterises co-existing taxa (see Helbig *et al.* 2002). Consequently, in spite of their apparently smaller degrees of divergence, it is still possible that the 'subspecies' of *M. nigra* and *M. fusca* merit specific status.

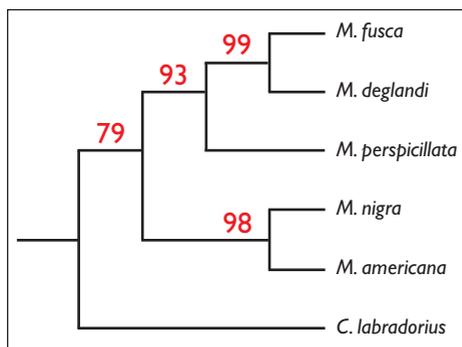
The remainder of this paper will assess the differences and similarities among the subspecies of Black/Common and Velvet/White-winged Scoters, in light of the differences among the accepted species in the genus *Melanitta*.

### Phylogeny of *Melanitta*

The pattern of a Holarctic distribution, in which closely related taxa are distributed allopatrically, is not unique to *Melanitta* but is also found to some extent in other seaduck, including *Somateria* (eiders) and *Bucephala* (goldeneyes and Bufflehead *B. albeola*; Livezey 1995). This suggests that splitting of seaduck lineages has resulted from relatively recent vicariance events: the Pacific basin and Northern Atlantic were probably isolated during Pleistocene glaciations, and these refugia seem to have been important areas for speciation. One can postulate that the extant scoter taxa are the result of the splitting of two ancestral lineages – a 'black' scoter and a 'white-marked' scoter – after isolation in two or three refugia during the glacial periods.

No molecular phylogenetic analyses have been performed. Livezey (1995) investigated Mergini phylogeny by cladistic analysis of 137 morphological characters; *nigra*, *americana*, *perspicillata*, *deglandi* (incl. *stejnegeri*) and *fusca* were included separately in the analysis. Relationships within *Melanitta* came out very clearly, albeit sometimes on the basis of very few characters, and a single most-parsimonious tree was resolved (fig. 2). This confirmed that *nigra* and *americana* are sister taxa (99% bootstrap support). They themselves comprise the sister group to other *Melanitta* taxa (93% support). Furthermore, *fusca* and *deglandi* are also sister taxa (98% support), more closely related to *perspicillata*. In this study, *stejnegeri* was not included as a separate taxon.

Evolutionary trends for body mass, sexual



**Fig. 2.** Scoter phylogeny, after Livezey (1995). A phylogeny of scoters *Melanitta*, part of a study of Mergini ducks based on 137 morphological characteristics. Branch lengths are arbitrary. The Labrador Duck *Camptorhynchus labradorius* was sister taxon to *Melanitta*. The numbers represent bootstrap statistical support for branch points.

dimorphism, clutch size and relative clutch mass across the Mergini were also examined. In all cases, *nigra* and *americana* showed identical trends; while *fusca* and *deglandi* showed clear divergence from *perspicillata*, and differed from each other on two counts (relative clutch mass and body mass). Livezey recommended the recognition of *deglandi* and *americana* at full species level, without further justification.

### Diagnosability

All the taxa within *Melanitta* are distinguishable from all other taxa in the genus on the basis of the colour, form and/or feathering of the bill (below). This applies to adult males and, in some cases, females.

#### *nigra* and *americana*

These two forms are currently classified together in subgenus *Oidemia*, which reflects the many shared features of morphology and plumage that distinguish *nigra* and *americana* from the other scoters (table 2).

Adult males are distinguishable on the basis of bill colour-pattern and shape (Dwight 1914; Dement'ev & Gladkov 1952; Cramp & Simmons 1977; Astins 1992). The bill of adult male *nigra* is largely black, with a swollen, black basal knob on the maxilla. Yellow coloration is normally restricted to a small area around the nostrils and along the culmen ridge. Examples

of *nigra* with larger amounts of yellow do occur, although they show the typical *nigra* bill shape (Garner 1989). In contrast, *americana* has a swollen, fully yellow bill-base. The nostrils are more elongated and closer to the bill tip on male *americana* than on male *nigra* (this may be a consequence of the different bill shape of the two taxa), and the bill of *americana* is shorter (*americana* mean 43.7 mm (42.0–45.5); *nigra* mean 47.5 mm (43.0–51.0)) (Dean 1989). Contrary to some reports, the nail overhangs the lower mandible no more in *americana* than it does in *nigra*, but it may be more arched.

In common with other scoters, the colouring of the bill base of both *nigra* and *americana* appears before the bill shape (Bent 1925), which may not be fully expressed until late in the second calendar-year (Alderfer 1992). Intermediate *nigra*-type birds with extensive yellow on the maxilla are probably immature male *nigra* (Cramp & Simmons 1977).

Females may also be distinguishable on bill shape or colour-pattern. Waring (1993) reported differences in head-and-bill profile between the two taxa. Adult female *nigra* may show small yellow markings around the nostrils, but these markings are reported to be more extensive in about 10% of female *americana*. The bill of female *americana* is shorter, on average (table 3). The differences reported in female bill shape and other plumage character-

**Table 2.** Features that distinguish the subgenera *Oidemia* and *Melanitta* (from Miller 1916, 1926; Brooks 1920; Bent 1925; Cramp & Simmons 1977).

Subgenus <i>Oidemia</i> ( <i>nigra</i> and <i>americana</i> )	Subgenus <i>Melanitta</i> ( <i>fusca</i> , <i>deglandi</i> , <i>stejnegeri</i> and <i>perspicillata</i> )
The outermost primary, P10, is heavily notched	P10 not heavily notched
P10 in adult male attenuated, shorter than P8	P10 longer than P8
16 tail feathers	14 tail feathers
Tail >2× tarsus length	Tail <2× tarsus length
Tail graduated for over half its length and rectrices pointed	Tail graduated for less than half its length; rectrices less pointed
Males have a simple tracheal structure lacking bullae	Bullae present in males
Bill small, commissure shorter than inner toe with claw	Bill larger, commissure longer than inner toe with claw
Outline of facial feathering nearly straight, not angled	Outline of facial feathering angled
Head and neck feathers are narrow, distal barbs converging at tip, giving striated effect	No modification of head and neck feathers
Silvery under-surface of primaries in both sexes	No silver wash to under-surface of primaries
Feet and nail of upper mandible black	Feet red, nail yellow, orange or red (males)
Adult male all black	Adult male not all black
Female/immature – capped head pattern without white patches	Female immature – white or off-white patches on head plumage
Iris brown in both sexes	Iris of males white

**Table 3.** Biometrics of Common Scoter *Melanitta nigra* and Black Scoter *M. americana*.

	<i>nigra</i> male	<i>americana</i> male	<i>nigra</i> female	<i>americana</i> female
Wing length (mm)	228–247	213–241	214–239	206–230
Tarsal length (mm)	43–54	45–49	41–46	42–45
Culmen length (mm)	43–51	40–47	40–48	39–44
Mass (g)	642–1,450	1,117.0±101.6	600–1,268	987.4±110.1

istics are not quantified, since individual variation is high; furthermore, they were not fully supported by a small series of skins at the NMS and Royal Museum, Edinburgh (MC pers. obs.).

Directly comparable data for the size and weight of *americana* and *nigra* are lacking, but there appear to be no diagnostic differences. Published data for *nigra* and *americana* from Bordage & Savard (1995), Dement'ev & Gladkov (1952) and Cramp & Simmons (1977) are summarised in table 3. Western and eastern populations of *americana* have not been compared morphometrically (Bordage & Savard 1995).

#### *fusca*, *deglandi* and *stejnegeri*

These three forms, together with *perspicillata*, form the subgenus *Melanitta*, sharing several characteristics that distinguish them from the subgenus *Oidemia* (table 2). Identification of adult male *fusca*, *deglandi* and *stejnegeri* is nor-

mally straightforward (Dwight 1914; Proctor & Pullan 1997). The main distinguishing features are the shape and colour of the bill, the size of the white eye-patch and the colour of the flanks.

#### Bill

The bill of *fusca* is yellow to yellow-orange, bordered by black along the small knob and the lower edges of the nostrils, cutting edges and (variably) the culmen, with a pinkish-orange nail. That of *deglandi* is a richer orange, becoming variably reddish laterally. On the lateral plate of the upper mandible, the distribution of red and yellow pigmentation is different between *deglandi* and *stejnegeri* (Garner *et al.* 2004). The bill of *deglandi* has yellow pigmentation bordering the black basal area of the bill, with red along the lower edge of the upper mandible, and a black rim on the lamellae; *stejnegeri* has red proximally, with yellow distally



David Tripling/Windrush

**85.** The brightly coloured bills of male scoters (as shown by this male Common Scoter *Melanitta nigra*) are in striking contrast to their predominantly black plumage, and accentuate the head movements made during courtship. Bill colour may also facilitate interspecific recognition.

along the lower edge of the upper mandible and usually no black rim.

The knob above the nostrils is, on average, larger on *deglandi* than on *fusca*, although the largest *fusca* knobs may approach those of *deglandi*. That of *stejnegeri* is yet more prominent, likened to the bow of a ship. Several of the photographs in Garner *et al.* (2004) suggest that the distinctive bill shape of *stejnegeri* is not always fully defined and may therefore overlap with the bill shape of *deglandi*. It is suggested that the 'less obvious' *stejnegeri* bills may belong to second- or third-year males, although there is no proof of this.

The bills of *stejnegeri* and *deglandi* also have more rounded nostrils than the bill of *fusca*. There is individual variation in all three taxa, and some overlap between the extremes of *deglandi* and *fusca* in bill form and colour. Note that *fusca* can show traces of a keratinous growth above the nostrils. As in other scoters, the bill colour of *deglandi* and *stejnegeri* develops before the final shape is fully attained.

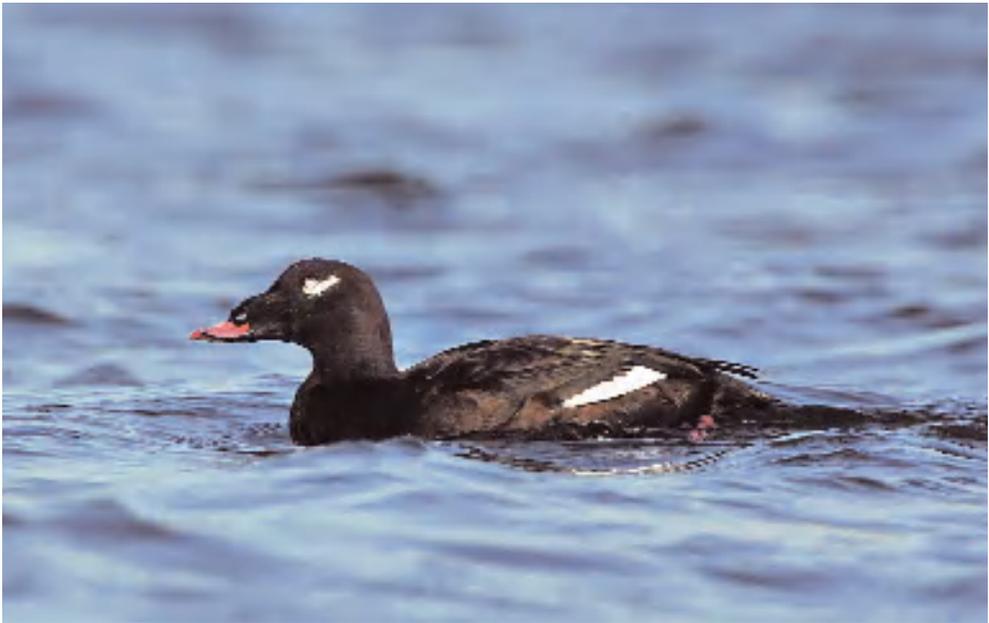
Females and immatures may also be identifiable (Garner 1999). Whereas female and juvenile *fusca* typically have a long bill, with a concave profile and little discernible basal knob, female and immature *deglandi* usually show traces of a knob (central culmen ridge), which

combines with a steeper culmen angle to make the bill look bulkier. The forehead of *deglandi* may also be steeper, giving this taxon a 'stepped' head profile, which can contrast markedly with the head shape of some *fusca*. In comparison with *deglandi*, female *stejnegeri* has a fuller, straighter forehead-and-bill profile, perhaps recalling Common Eider *Somateria mollissima*.

Feathering of the bill in relation to the nostrils is diagnostically different for all three taxa (Gardarsson 1997). There is individual variation, but in *deglandi* and *stejnegeri*, the feathering of the bill closely borders the proximal margin of their nostrils (1–4 mm), surrounding the bill base with a roughly square patch of feathering; this is in contrast to *fusca*, on which the bill feathering usually (but not always) stops 6–8 mm before the nostril. This is a reliable identification feature for all age- and sex-classes. Although feathers extend onto the culmen of *deglandi*, this is not the case for *stejnegeri*.

#### White subocular crescent of males

This is, on average, larger on *deglandi* and *stejnegeri* than on *fusca*, extending further behind the eye. There is possibly some overlap in this feature, but the extent has not been quantified. Garner (1999) reported an adult male *deglandi* with an eye crescent no more developed than on *fusca*.



Bob Steele

**86.** The brown flank feathering, the relatively long white subocular crescent, the stepped head-and-bill profile and the extensive red coloration of the bill all distinguish male White-winged Scoter *Melanitta deglandi* (this bird is of the American race *deglandi*) from Velvet Scoter *M. fusca*. Note also the round 'see-through' nostrils of *deglandi*, which are in contrast to the narrower, elliptical nostrils of *fusca*.

**Table 4.** Biometrics of Velvet Scoter *Melanitta fusca* and (American) White-winged Scoter *M. deglandi deglandi*.

	<i>fusca</i> male	<i>deglandi</i> male	<i>fusca</i> female	<i>deglandi</i> female
Wing length (mm)	269–293	271–298	250–271	256–285
Tarsal length (mm)	48–52	46–54	46–48	45–51
Culmen length (mm)	37–50	36–47	38–43	35–43
Tail length (mm)	75–89	69–87	67–78	73–88
Mass (g)	1,173–2,104	1,361–1,769	1,140–1,895	952–1,946

### Flanks

In both breeding and non-breeding plumages, male *deglandi* has dark brown flank feathers, tipped buffish, which contrast with the rest of the black upperparts. In breeding plumage, *fusca* and *stejnegeri* have glossy black flanks, these being less glossy, perhaps tinged brown, in non-breeding plumage. The base of all feathers is suffused brown (Cramp & Simmons 1977), so the flank colour of *deglandi* is the result of more extensive brown feather-bases.

### Measurements

Direct comparisons of measurements for the three taxa are not available, but comparing data in Cramp & Simmons (1977) with those in Brown & Frederickson (1997) for *fusca* and *deglandi* suggests that there are no diagnostic size differences (table 4).

### Moult

All scoters follow similar moult and plumage sequence strategies, and there are no differences between *americana* and *nigra*, nor among *fusca*, *deglandi* and *stejnegeri* (Dwight 1914; Bent 1925; Dement'ev & Gladkov 1952).

### Tracheal anatomy

Johnsgard (1961) investigated the taxonomic significance of tracheal anatomy in the Anatidae. The structure of the trachea and associated syrinx is a useful taxonomic tool for studies of waterfowl, although its value varies in different groups. Anatidae lack the complex syringeal musculature of songbirds, and therefore use differences in length, size and shape of the trachea and syrinx to produce specifically distinct vocalisations. Tracheal structure has been used to investigate the relationships of, for example, Harlequin Duck *Histrionicus histrionicus*, Bufflehead and Hooded Merganser

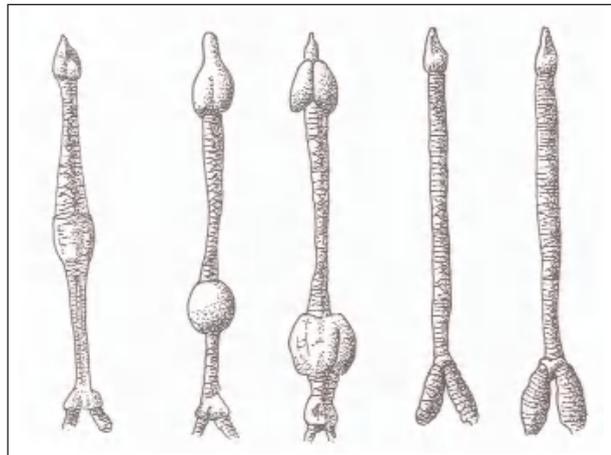
*Lophodytes cucullatus*. The tracheae of seaducks are the most variable among waterfowl, and those of the genus *Melanitta* are the most aberrant in their syringeal anatomy. They also show some of the greatest sexual dimorphism, suggesting a significant role for vocalisation in sexual display.

The tracheal structure of male *nigra* is simple, similar to that of females, and identical to that of male *americana* (Miller 1916, 1926). There are no bullae in males, and the bronchi are greatly enlarged (fig. 3).

Both Surf Scoter and white-winged taxa have tracheal bullae, although these are atypically small for Mergini. In *perspicillata*, the trachea is diagnostically different from that of all other scoters, but most similar to the trachea of *fusca* (Miller 1916, 1926). Perhaps significantly, *fusca* is clearly different from *deglandi* in the position of the tracheal enlargements (Miller 1926; fig. 3). There are no equivalent data for *stejnegeri*.

### Intestinal caeca

Miller (1926) reported on the length of intestinal caeca in the scoters. Those of both *nigra* and *americana* are greatly reduced com-



**Fig. 3.** The tracheal structure of (left to right) *Melanitta perspicillata*, *M. fusca*, *M. deglandi*, *M. nigra* and *M. americana*; from Miller (1916).

pared with the caecal length of other ducks, including other scoters. No caecal differences between these two taxa have been reported. Those of *perspicillata* are 80–123 mm long, based on a sample size of six males and one female. There is a suggestion that, on average, the caeca of *fusca* are longer (90–130 mm) than those of *deglandi* (67–100 mm) but the sample sizes are small and not taken from the same sources, and further work is required. Furthermore, caecal length varies seasonally, and until sex-, age- and season-matched samples are investigated, caecal length cannot be proposed as a taxonomically informative character.

### Courtship and copulation

In common with many other ducks, scoters have lengthy courtship displays, based upon a series of ritualised behaviours (modified or exaggerated comfort behaviours, alertness signals and aggressive/flight responses) that are performed predominantly by one or several males in the presence of a female (Cramp & Simmons 1977). There are separate displays associated with incitement to copulation. Courtship displays have been shown to be potentially important for specific recognition between closely related taxa: for example, Common Goldeneye *Bucephala clangula* and

Barrow's Goldeneye *B. islandica* have quite different courtship displays, in contrast to pre- and post-copulatory displays, which are similar (Myres 1959). Copulation displays are rather conservative in sea ducks and may be taxonomically informative (Myres 1959).

Directly comparable reports of the displays of all six taxa have not been published, so are described more fully in Appendix 2, based on Brooks (1920), Bent (1925), Gunn (1927), Boase (1949), Dement'ev & Gladkov (1952), Koskimies & Routamo (1953), Humphrey (1957), McKinney (1958), Myres (1959), Johnsgard (1965), Bengston (1966), Cramp & Simmons (1977), Bordage & Savard (1995) and Brown & Frederickson (1997). Several displays show variation within Mergini, which therefore may be useful for untangling phylogeny – these include pre-copulatory drinking by males, copulatory wing-flicks, post-copulatory rotations and 'steaming' (Appendix 2).

Comparisons of the three traditionally accepted species of Black/Common, Velvet/White-winged and Surf Scoters reveal specific and diagnostic differences in both their courtship and their copulation displays that may prevent hybridisation (Appendix 2). Any equivalent differences between the courtship and copulation displays of *nigra* and *americana*,



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**87.** Adult male Surf Scoter *Melanitta perspicillata* is unmistakable, but the outsize triangular bill with the square-cut edges also helps to distinguish females from the superficially similar female Velvet *M. fusca* and White-winged Scoters *M. deglandi*.

or among *fusca*, *deglandi* and *stejnegeri* would, therefore, have taxonomic significance. However, as noted in Appendix 2, there are very few, if any, described differences in the courtship and copulation behaviours between *nigra* and *americana* or among *fusca*, *deglandi* and *stejnegeri*.

The courtship vocalisations of *fusca* and *deglandi* are reported to be different (Cramp & Simmons 1977), but are poorly documented. In the course of our work on scoters, a potentially significant (but previously undescribed) difference between the courtship vocalisation of male *nigra* and that of *americana* has emerged. This difference is described fully elsewhere (Sangster in press). Briefly, the courtship call of male *nigra*, a repeated short 'phiu' lasting approximately 0.1 s, contrasts sharply with the longer call of *americana*.

#### Hybridisation and intergradation

Hybridisation involving the three universally recognised species of scoters is extremely rare. Hybridisation of *deglandi* × *perspicillata* has occurred, and *nigra* × Eurasian Wigeon *Anas penelope* has been reported. Additionally, *deglandi* has been reported to pair-bond with Common Eider, and *fusca* or *deglandi* × Common Goldeneye pairings are alleged

(Johnsgard 1965; Cramp & Simmons 1977; Gardarsson 1997). However, reproductive isolation between the three recognised scoter species is clearly efficient.

Since all forms show the proven potential for vagrancy, and the ranges of different taxa almost meet, the opportunity for their hybridisation probably occurs rather often. However, no intergrades of *nigra* and *americana* are known, and no hybridisation has been reported among *deglandi*, *stejnegeri* and *fusca*. The potential problems in identifying hybrids are one possible reason for this lack of reporting, along with the difficulties associated with subspecific identification of paired females.

#### Ecological differences, feeding habitat and food preferences for *Melanitta* taxa in sympatry and allopatry

##### Breeding behaviour and habitat

The nesting behaviour and habitat choice of breeding *americana* and *nigra*, and of *fusca*, *deglandi* and *stejnegeri* have not been explicitly compared previously. These details are contained in Appendix 3, based on Bent (1925), Dement'ev & Gladkov (1952), Koskimies & Routamo (1953), Bengston (1966), Cramp & Simmons (1977), Johnsgard (1978) and Kondratyev (1989).



Arthur Morris/Windrush

**88.** The Black Scoter *Melanitta americana* is colloquially known as the 'butterbill' by hunters in the USA because of the male's swollen yellow bill-base. This is visible at long range, so that even a vagrant among flocks of Common Scoters *M. nigra* stands out.

In summary, the nesting behaviours of the recognised species of scoter are not dissimilar and, when sufficient data exist, it appears that there is variation within taxa that is determined at least in part by the local environment. Minor differences that have been reported for nest-sites, egg sizes and colours between *nigra* and *americana* and among *fusca*, *deglandi* and *stejnegeri* are possibly to some extent due to biased reporting. Even if real, they may represent intra-taxon variation. In the absence of further information, it is concluded that there are no significant differences among the nesting behaviours of the two groups.

#### Winter habitat and diet

The diet of scoters has been studied primarily on the basis of stomach contents of hunted birds. It is perhaps to be expected that Black/Common Scoters, Velvet/White-winged Scoters and Surf Scoters would show different foraging strategies that reinforce niche separation. In fact, such differences have been difficult to establish. Mixed feeding flocks of two or three species of scoter occur during the winter on both sides of the Atlantic and Pacific Oceans, while separation into single-species flocks with different habitat choices is also frequent.

During the winter, *nigra* and *americana* avoid rough water, preferring shallow, open-sea conditions or estuaries (500–2,000 m from land), rather than broken rocky or island coasts (Brooks 1920; Dement'ev & Gladkov 1952; Cramp & Simmons 1977). On the Pacific coast, *americana* is usually segregated from *perspicillata* and *deglandi* (Bordage & Savard 1995). Shallow offshore waters are preferred by *nigra*, at a depth not more than 10–20 m; in one study, 81% of dives by *nigra* were within the depth range 2.2–3.7 m (Cramp & Simmons 1977). By comparison, *americana* can feed at depths of 13 m, but prefers to feed at depths of less than 7 m and may be found feeding among breakers in shallow water. There is no information on food selection for either taxon, but the implication is that they eat what is there! The diet of *nigra* was examined on medium and fine sandy sediment off the Belgian coast by Degraer *et al.* (1999). The polychaete *Lanice conchilega* community is of interest to *nigra* but Degraer *et al.* found no direct similarity between distribution of this food source and the distribution of flocks of wintering *nigra*.

There is no previously published comparison of recorded food items for all six taxa of scoter. This information is therefore summarised in Appendix 4, on the basis of Bent (1925), Dement'ev & Gladkov (1952), Cramp & Simmons (1977), Johnsgard (1978), Rogacheva (1992), Bordage & Savant (1995), Livezey (1995), Byrkjedal *et al.* (1997) and Brown & Frederickson (1997).

In summary, there are few directly comparable data. It seems as though ecological differences among the three traditionally accepted species of scoter, on both the wintering and the breeding grounds, are probably real, but variable and poorly defined – birds change their feeding habits depending on local conditions. When comparing *nigra* with *americana*, and *fusca* with *deglandi* or *stejnegeri*, it is not yet possible to pick out any consistent, biologically important differences in feeding ecology that may impact on their systematics. Indeed, they seem to be rather similar to each other, and the differences in ecology or food items that have been recorded can be explained either by latitudinal differences in habitat or available food species or by insufficient sampling. The evidence points to *nigra* and *americana* filling similar ecological niches, as do *fusca* and *deglandi*. There is no published evidence about the ecology and feeding strategies of the allopatric scoter taxa that suggests species-level differences.

#### Discussion

##### Taxonomic status of *nigra* and *americana* (Common/Black Scoters)

*Melanitta nigra nigra* and *M. n. americana* are allopatric sister taxa between which no hybridisation has been reported. Condition 4.2 of the species-defining criteria employed by the BOURC-TSC (Helbig *et al.* 2002) states that allopatric taxa may be treated as species if 'at least one character is fully diagnostic [i.e. enables either taxon to be identified with near-100% certainty], and the level of divergence is equivalent to that of the most closely related sympatric species'. On the basis of the differences in their bills, *nigra* and *americana* may be considered to fulfil this criterion, i.e. they are diagnosably distinct on the basis of the structure and colour pattern of the bill of adult males. Diagnosability is 100% on the basis of bill shape alone; but cannot be considered to be 100% on bill colour alone, since a small propor-

tion of *nigra* show an amount of yellow that approaches that of *americana*. It seems likely that *nigra* which show a large amount of yellow on the bill are subadult (second-calendar-year) birds, in which case diagnosability may be 100% for birds in their third calendar-year or older. In addition, there are population-level differences in the length of the bill (the means are different, but the ranges of bill lengths for each taxon overlap); and the shape of the nostrils of the two taxa are diagnostically distinct, but this may be a function of the different bill shapes, and thus cannot be regarded as an independent supporting character.

The two taxa do not show similar levels of divergence in any other physical character, as shown in table 5, nor, indeed, do they approach the overall level of differentiation seen between other closely related diving seaduck, such as Common and Barrow's Goldeneyes. Their claim to specific status would be strengthened if it could be shown that differences in the bill shape

and colour of the males were biologically significant and affected breeding performance or foraging strategy; and there is good reason to suspect that breeding performance may be affected by this character (Myres 1959). The brightly coloured bills of scoters probably function to accentuate the stereotyped head movements made during display – a form of sexual display relevant during pair formation. For duck species in which the males have brightly coloured plumage and iridescent specula, courtship movements are accentuated by movement of the head against the plumage background. Male scoters, with their unremarkable plumage, have produced an equivalent effect by developing extravagant bill structures and colours. There is no evidence that females formally assess the bills of potential mates, but it is reasonable to assume that this does occur and that it may be important for interspecific discrimination, an assumption that may be significant for *nigra* and *americana*.

**Table 5.** A pairwise comparison of significant and diagnostic differences among scoter taxa.

	<i>nigra</i> v <i>americana</i>	<i>nigra/americana</i> v <i>fusca/deglandi</i>	<i>fusca</i> v <i>deglandi/stejnegeri</i>	<i>deglandi</i> v <i>stejnegeri</i>	<i>fusca/deglandi/stejnegeri</i> v <i>perspicillata</i>
Bill dimensions/shape (male)	✓	✓	✓	✓	✓
Bill dimensions/shape (female)	✓?	✓	✓	nd	✓
Bill colour pattern (male)	✓	✓	✓	✓	✓
Bill colour pattern (female)	✓?	×	×	×	×
Nostril shape	✓	✓	✓	×	×
Shape of outer primary	×	✓	×	×	×
No. tail feathers	×	✓	×	×	×
Tail length	×	✓	×	nd	✓
Tracheal structure (males)	×	✓	✓	nd	✓
Facial feathering (a round bill)	×	✓	✓	✓	✓
Colour of primaries	×	✓	×	×	×
Plumage pattern (males)	×	✓	✓	✓	✓
Plumage pattern (females)	×	✓	×	×	✓
Iris colour (males)	×	✓	×	×	×
Iris colour (females)	×	×	×	×	×
Wing length (males)	×	✓	×	nd	✓
Wing length (females)	×	✓	×	nd	✓
Tarsal length (males)	×	×	×	nd	×
Tarsal length (females)	×	✓	×	nd	×
Moult timing	×	×	×	×	×
Courtship vocalisation	✓	✓	✓	nd	✓
Courtship display	×	✓	×	nd	✓
Copulation display	×	✓	×	nd	✓
Nesting ecology	×	✓	×	×	?
Habitat choice (summer)	×	✓	×	×	✓
Habitat choice (winter)	×	✓	×	×	✓

Key: ✓ consistent diagnostic differences reported in literature; × no consistent differences reliably reported; nd not determined – relevant data not found in literature.

There are diagnostic differences in the display calls of *nigra* and *americana* (Sangster in press), and these may serve to reinforce reproductive isolation between the two taxa. We advise caution at this time because, to the best of our knowledge, differences in call have never before been used as a primary line of evidence for defining species boundaries within ducks. Nevertheless, we include 'differences in call' as a further (potentially biologically relevant) feature by which it is possible to differentiate between the males of *nigra* and *americana*.

Clearly, the decision on the specific or subspecific status of *nigra* and *americana* is marginal and depends on the taxonomic criteria that are applied. Retention within one species could conceivably be justified under the Biological Species Concept, because reproductive isolation cannot be demonstrated for allopatric taxa. On the other hand, on current evidence of differences in sexual signals such as bill structure/colour and courtship vocalisations it is concluded that these diagnosable taxa form separate evolutionary lineages which are

unlikely to merge, thus justifying their splitting under Phylogenetic or Evolutionary Species Concepts. The treatment of these birds that is most consistent with Helbig *et al.* (2002) is to consider them as two monotypic species, *M. nigra* and *M. americana*.

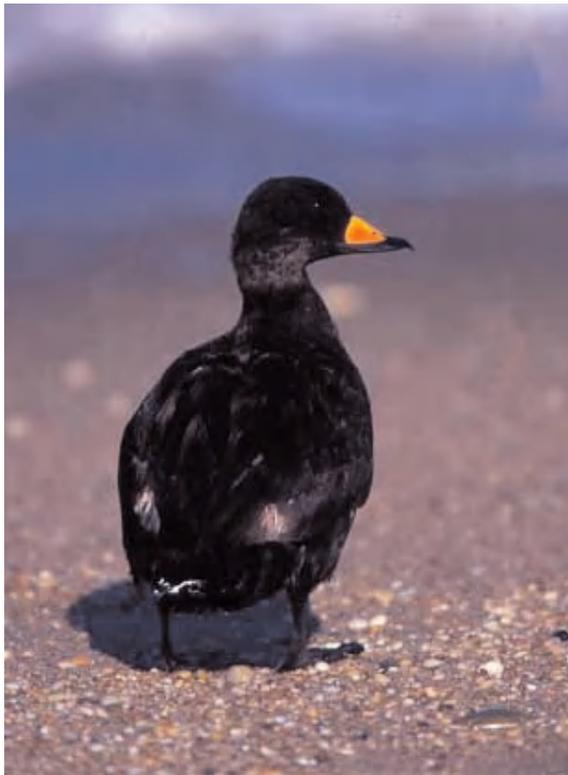
There is much yet to be discovered about *nigra* and *americana*. In particular, the occurrence and nature of any interaction between the two taxa around the River Lena may have implications for the decision to split them, but nothing is currently known about this. Further information about the possible assessment of male bill shape and colour for mate selection by females would also be valuable, as would a detailed molecular analysis. We intend to keep the taxonomic status of these birds under review in light of any emerging new evidence.

#### *Taxonomic status of fusca, deglandi and stejnegeri (Velvet/White-winged Scoters)*

*Melanitta fusca fusca*, *M. f. deglandi* and *M. f. stej-*

*negeri* are also diagnosably distinct. A pairwise comparison (*fusca* v *deglandi/stejnegeri*, *deglandi* v *stejnegeri* and *fusca/deglandi/stejnegeri* combined v *perispicillata*; table 5) suggests that the evidence for splitting these three taxa is more compelling than that for *nigra* and *americana*, since it involves more independent criteria. These include:

- *Bill shape (males)*: a stepped discontinuity in a continuously varying character. It is likely that there is near 100% diagnosability between *fusca* and *deglandi* on this feature alone, and 100% diagnosability between *deglandi* and *stejnegeri*.
- *Bill shape (females)*: there are differences, at the population level, among *fusca*, *deglandi* and *stejnegeri* possibly approaching a stepped discontinuity.
- *Bill colour pattern (males)*: there is close to 100% diagnosability between *fusca* and *deglandi*, and subtle but perhaps 100% diagnosable differences between *deglandi* and *stejnegeri*.
- *Nostril shape (males)*: probably 100% diagnosability between *fusca* and *deglandi*, in a continuously varying character. The taxa *deglandi* and *stejnegeri* are similar.



Arthur Morris/Windrush

**89.** This male Black Scoter *Melanitta americana* is probably in its second calendar-year, and shows how bill coloration develops before the bill shape is fully mature. Compare bill shape with that of the adult in plate 88.

- *Facial feathering around bill*: 100% diagnosability among all three taxa.
- *Male plumage*: a stepped discontinuity in the quantitative variation in flank colour between *deglandi* and both *fusca* and *stejnegeri*. Population differences (apparently different means, probably overlapping ranges) in extent of white eye-crescent between *fusca* and *deglandi*, not shown between *deglandi* and *stejnegeri*.
- *Tracheal structure*: apparent 100% diagnosability between *fusca* and *deglandi*, but equivalent data for *stejnegeri* are not presently available.
- *Voice (males)*: 100% differences reported between *fusca* and *deglandi*, possibly related to tracheal structure.

It is reasonable to suggest that *deglandi* and *fusca* should be treated as separate species under criterion 4.1 of Helbig *et al.* (2002), as allopatric taxa that are 'fully diagnosable in each of several discrete or continuously varying characters, related to different functional contexts'. Slightly more problematic is the question of whether to retain *stejnegeri* as conspecific with *deglandi*: *stejnegeri* is similar to *deglandi* in many respects and is the taxon for which there is the greatest amount of uncertain or missing data. On the basis of what is known – diagnosability on the basis of male bill shape and colour (a potentially reproductively important character), facial feathering (perhaps trivial), and male flank colour (perhaps trivial) – the argument for splitting *deglandi* and *stejnegeri* may appear to be almost as good as that for splitting *nigra* and *americana*. Given the lack of published information on *stejnegeri*, however, we conclude that further research into vocalisations and genetics is required; hence we provisionally retain *stejnegeri* as a subspecies of *M. deglandi*.

### Conclusion

For the purposes of the British List, it is suggested that the genus *Melanitta* is treated as comprising five species, four of which are on Category A:

- Common Scoter *Melanitta nigra*
- Black Scoter *M. americana*
- Velvet Scoter *M. fusca*
- Surf Scoter *M. perspicillata*

The extralimital White-winged Scoter *M. deglandi* is presently treated as polytypic, with subspecies *deglandi* and *stejnegeri*.

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### Appendix 1. Distribution of scoter taxa.

#### Common Scoter *Melanitta nigra*

Breeds Iceland, Scotland, Spitzbergen, N Europe and Asia to R. Khatanga, possibly further east. Winters off the coasts of W Europe and the Mediterranean, less regularly in the Black and Caspian Seas (Dement'ev & Gladkov 1952; Johnsgard 1978). A distinct moult migration is visible along the coasts of north-central Europe, although moult locations are partly unknown, sometimes far out at sea (Cramp & Simmons 1977).

#### Black Scoter *M. americana*

Breeds in N Asia (eastward from the Lena/Yana watershed to the Kamchatka Peninsula) and North America (Alaska/Canada – from Bristol Bay to Kotzebue Sound and Mt McKinley, sporadically east to Newfoundland). There are two, possibly disjunct, populations in North America: 1) coastal and alpine tundra of Alaska; and 2) N Quebec (Bordage & Savard 1995). Winters along the Asian and North American coasts of the Pacific, and along the Atlantic coast of North America (Dement'ev & Gladkov 1952; Johnsgard 1978). Southern limit of wintering area is at surface sea temperature greater than 10–11°C (Bordage & Savard 1995).

Apparently, *nigra* and *americana* replace one another abruptly on the lower Lena, but it is not known whether their ranges are in contact (Cramp & Simmons 1977). The eastern limit of *nigra* has been reported not to reach the R. Lena – stopping along

longitude 120°E in the Vilyuy basin (Rogacheva 1992). Near Lake Khantayskoye, *nigra* is common on small lakes in forests, with *fusca* (Rogacheva 1992), and is sympatric with *stejnegeri* in the Syurindinsk depression on upper reaches of R. Vilyuy (Rogacheva 1992). Southern limits of the breeding range of *nigra* in C Siberia follow the boundary between northern and middle taiga (Rogacheva 1992).

#### Surf Scoter *M. perspicillata*

Breeds in North America only, in Alaska, Yukon, Northwest Territories, south Hudson Bay, interior Quebec and Labrador. Winters on both coasts of North America and on the Great Lakes. Known from Russia – non-breeders are recorded on the Kommander Islands and Chukotskiy Peninsula (Dement'ev & Gladkov 1952).

#### (American) White-winged Scoter *M. (deglandi) deglandi*

Breeds in North America only, from NW Alaska to Hudson Bay, south to S Manitoba. Winters on both coasts of North America as far south as California and South Carolina. There are several records from the Kommander Islands and more than one record from Iceland (Gardarsson 1997).

(Asian) White-winged Scoter *M. deglandi stejnegeri*  
Breeds in E Asia, Altai to Kamchatka. The western limit of *stejnegeri* lies to the east of the R. Yenisey.

Occasional occurrences are reported on the lower Yenisey to Dudinka, but it is doubtful that it breeds there (Dement'ev & Gladkov 1952; Rogacheva 1992). It is a common gamebird on the upper Vilyuy. There is a possible discontinuity in this form's range in the southern part of the Angara area (Rogacheva 1992). Common, not abundant, on Anadyr and very patchily distributed throughout its range. Winters on the coasts of the W Pacific south to China (Dement'ev & Gladkov 1952).

#### **Velvet Scoter *M. fusca***

Breeds in N Europe and Asia, from Scandinavia to the R. Yenisey at least, perhaps to the mouth of the Khatanga. It occurs at the mouth of R. Yenisey (70°N) but is very rare (Rogacheva 1992). Common and ubiquitous in the extreme northern taiga zone and is partially sympatric with *nigra*. These two species make up the bulk of duck populations inhabiting the lakes of C Siberian open woodlands (Rogacheva 1992). Some of the reported sites in Russia may not represent permanent breeding areas (Dement'ev & Gladkov 1952). The eastern limit of its range is

assumed to lie in the upper reaches of R. Vilyuy. Only *stejnegeri* is found on the lower reaches; therefore it is possible, but not known, that the ranges of the two taxa meet (Cramp & Simmons 1977). Palmer (*Handbook of North American Birds*, Vol. 2, *Waterfowl*, 1976) indicates that their ranges are not known to meet, but non- or post-breeding *fusca* have been recorded in the gap between them. It is certainly possible that *fusca* breeds outside its main range (Rogacheva 1992). Isolated breeders are found in Turkey and Georgia. Winters from the neck of the Baltic Sea, into the North Sea and Atlantic Ocean. Smaller numbers winter in the Black, Mediterranean and Caspian Seas (Dement'ev & Gladkov 1952; Johnsgard 1978).

Thus *perspicillata* is confined to North America, where it is partially sympatric with *americana* and *deglandi*. In Europe and northwest Asia, *nigra* is sympatric with *fusca* west of the R. Yenisey, and with *stejnegeri* between the Yenisey and Lena rivers. In Asia, east of the Lena, *americana* is sympatric with *stejnegeri*.

#### **Appendix 2. Courtship and copulation displays of scoter taxa.**

Published accounts of courtship displays do not always allow for confident definition of known homologies within the Mergini. Clear differences are seen when the 'Common/Black', 'Velvet/White-winged' and Surf Scoters are compared with each other, but differences between *nigra* and *americana*, and among *fusca*, *deglandi* and *stejnegeri* are difficult to discern from the literature.

#### **Common Scoter *Melanitta nigra* and Black Scoter *M. americana***

Courtship displays have been well described, albeit independently, for both taxa. Observations of *nigra* (Gunn 1927; Boase 1949; Johnsgard 1965; Bengston 1966) in general correspond very closely with what is known for *americana* (McKinney 1958; Humphrey 1959).

A number of males gather round a smaller number (perhaps only one) of females. The calling males mob the female(s) and may attempt copulation (Boase 1949; Cramp & Simmons 1977). Overt aggressive chases between males are rare in both taxa (Gunn 1927; McKinney 1958).

Comparison of the elements of display reveals that both taxa exhibit a shared repertoire of stereotyped behaviours described in Cramp & Simmons (1977). The male display is built up from somewhat fixed sequences (Bengston 1966), which have been named as follows:

- 'Upward stretch' (Boase 1949) [= 'shake'] (McKinney 1958);
- 'Wing-flapping' (both taxa) [= 'obedience'] (Gunn 1927; Boase 1949) – note that during wing-flapping, both *nigra* and *americana* jerk their head

down as if the neck were broken, in contrast to other *Melanitta* species;

- 'Lateral head-shaking' – the most frequent display (Bengston 1966);
- 'Preening';
- 'Low rush' (Boase 1949);
- 'High rush' (Gunn 1927) probably the same as 'steaming' (McKinney 1958), and equivalent to 'steaming toward female' (Johnsgard 1965);
- 'Tail-snap';
- 'Water-flick';
- 'Short-flight' (Boase 1949);
- 'Bowing' (McKinney 1958).

The only described qualitative difference is a modified version of 'shake', without shaking (!) and termed 'body-up', that was explicitly not found by McKinney for *americana* but is described in Bengston (1966) for *nigra*.

The complete display for both taxa is a complex series of movements: courtship whistle (erect), tail-snap, low rush, water-flick, breast-preen, forward stretch, upward stretch, lateral head-shake. Bengston (1966) described head-shakes, bowing, tail-snap, low rush, short flight, shake, steaming with frequent wing-flapping and preening for *nigra*. Tail-snap is almost always followed by low rush, but low rush can be performed without prior tail-snap. Tail-snap and low rush are often left out of the display.

Humphrey (1957), describing *americana*, heard nothing like the 'teka teka' call which Gunn (1927) heard for *nigra*, although Brooks (1920) did describe a similar call for *americana*. Courtship calls of the males comprise a low, slurred, hooting pipe or plaintive whistling (Bengston 1966; Bordage & Savard 1995), shorter for *nigra* than for *americana*, as

described in main text and in Sangster (in press). Females of both taxa produce a low grating noise, like a door swinging on rusty hinges (Cramp & Simmons 1977; Bordage & Savard 1995).

Copulation behaviour also figures in pair courtship (Cramp & Simmons 1977). There are no described differences between *nigra* and *americana*. The female is not prone for long. Males generally perform an upward stretch, the female becomes prone and the male mounts immediately. After copulation, the male swims away while the female bathes. Copulation is not accompanied by a 'wing-shake' from the male, and differs in this respect from the behaviour of *fusca*.

**Velvet Scoter *M. fusca*, (American) White-winged Scoter *M. deglandi deglandi* and (Asian) White-winged Scoter *M. deglandi stejnegeri***

In contrast to the other scoters, courtship behaviour in this group is very similar to pre-copulatory behaviour. Monogamous pair-bonding starts in winter, with small groups of males actively quarrelling and displaying around a smaller number of females, often only one (Boase 1949). Pairing behaviour is similar in *deglandi* and *fusca* (Boase 1949; Dement'ev & Gladkov 1952; Koskimies & Routamo 1953; Myres 1959; Johnsgard 1965; Brown & Frederickson 1997) but that of *stejnegeri* has not been described fully. Ritualised behaviours within this group include:

Male swims around female with vertically raised head and half-opened quivering wings, accompanied by diving and splashing water.

- 'Underwater chases';
- 'Threat display' – similar to goldeneyes and *perspicillata*;
- 'Neck-erect-forward' (equivalent to similar displays seen in other scoters – see *perspicillata*);
- 'Ritualised (false) drinking'\*;
- 'Water-twitching'\*;
- 'Ritualised preening'\*;
- 'Crouching';
- 'Upward-stretch/shake' – as in other scoters;
- 'Wing-flapping' – as in other scoters;
- 'Skating' [= 'low rush?'] (Boase 1949);
- 'Short flight' (Boase 1949).

Those marked \* have been described as courtship displays but are probably primarily pre-copulatory.

Typically, the male swims after the female with 'neck-erect-forward', subsequently performing low rush, upward-shake, wing-flap, bowing, short flight. There is variation in the sequence and choice of behaviour units (Brown & Frederickson 1997). Courtship flights are much less frequent than in *nigra* but replaced by persistent underwater chases (Cramp & Simmons 1977). This group of scoters is rather silent, but vocal differences have been reported between the males of *fusca* and *deglandi* (consistent with the described differences in their tracheal bullae; see 'Tracheal anatomy' and fig. 3, p. 189). The

courtship call of *fusca* is a higher-pitched, double 'skryck', rather than the whistled double 'whur-er' of *deglandi*, which appears to have no *fusca* counterpart. Both taxa also make rather coarse purring and cackling noises (Dement'ev & Gladkov 1952; Cramp & Simmons 1977). The situation is made complicated by imprecise reporting, and there has been some confusion in the literature between vocal noises and those noises made by wing movement. Some extensive studies have detected no male vocalisations during courtship (Myres 1959; Brown & Frederickson 1997). Further investigation, preferably sonographic analysis, would be helpful. Females contribute few displays to courtship, and no differences are reported among the taxa (Cramp & Simmons 1977; Brown & Frederickson 1997).

Copulation has been described for *deglandi* in detail (Myres 1959), where, in contrast to other scoters, Bufflehead and goldeneyes, there is direct equivalence between courtship and copulation displays. Prior to copulation, both sexes perform false-drinking, and the male gives the water-twitch and preen-behind-wing displays. The female becomes prone shortly before the male mounts – similar to observed behaviour in *nigra/americana*. The male may give a vigorous double wing-shake (unlike *nigra*) as he dismounts, after which the birds swim away from each other.

**Surf Scoter *M. perspicillata***

Although not directly relevant to taxonomic treatment of the subspecies within Common/Black and Velvet/White-winged Scoters, it is emphasised that there are unique differences in the courtship and copulatory behaviours of *perspicillata* that distinguish this species from the other recognised species, as well as recognisable similarities and homologies with other Mergini.

During courtship, as with other scoters, a single female is surrounded by a few males, with much fighting and threatening behaviour between males. Males swim rapidly to and fro, keeping their head and neck erect, at intervals dipping the beak into the water. The female swims from one male to another (Bent 1925; Johnsgard 1965). The following displays have been reported:

- 'Threat display' much like that of *deglandi*;
- 'Crouch display' much like that of *deglandi*;
- 'Underwater chases' much like those of *deglandi*;
- 'Sentinel' pose [= neck-stretch of *nigral americana* and neck-erect-forwards of *deglandi/fusca*];
- 'Breast-scooping' [= combination of lateral head-shaking and breast-preening];
- 'Chest-rearing' – not found in other scoters, equivalent to rearing display of Steller's Eider *Polysticta stelleri* (Myres 1959);
- 'Fly away' [= *nigra/americana*];
- 'Short flight', similar to that seen in Steller's Eider and *Bucephala* spp. – when birds land, they may go into 'upward-wings-raised', as in *Bucephala*

(Myres 1959);

- 'Tail-raised', perhaps equivalent to tail-snap of *nigra/americana*;
- 'Head-turning', perhaps equivalent to lateral head-turning of eiders and goldeneyes.

The copulatory behaviour (Myres 1959) is similar to that seen in *deglandi* (cf. specific differences in

courtship behaviour), although the female is prone for more than two minutes – much longer than in the other scoters. The male does a water-twitch and preen-behind-wing, and may ritual-drink. The male mounts, and normally chest-rears as he dismounts (something not seen in *deglandi*).

### Appendix 3. Breeding habitat and behaviour of scoter taxa.

The presumed ancestral condition for breeding is fresh water. Subsequently, *deglandi* and *fusca* have shifted to significant use of brackish or salt water. Although *fusca*, *deglandi* and *stejnegeri* may be found in sympatry with other scoters in northern tundra, they are more strongly associated with woodland habitats, nesting in pine *Pinus* forests of Russia and zones of coniferous forest in Canada and Alaska, on shallow ponds with overgrown banks (Dement'ev & Gladkov 1952; Rogacheva 1992). Their ranges commonly extend to breeding areas on wooded shores and skerries along sea coasts. In general, *fusca*, *deglandi* and *stejnegeri* share the ability to nest far south of *nigra*, *americana* and *perspicillata*, with which they are partially sympatric, in both the Nearctic and the Palearctic. In addition, *deglandi* and *stejnegeri* are found sparingly at high altitude in the south of their ranges (Rogacheva 1992).

Both *nigra* and *americana* breed around freshwater bodies in arctic and subarctic tundra and northern taiga mossy bogs (Dement'ev & Gladkov 1952; Mc Kinney 1958; Cramp & Simmons 1977; Johnsgard 1978; Rogacheva 1992; Decarie *et al.* 1995). Although

not uncommon in suitable habitat, they are nowhere abundant and become less common in heavily wooded areas, in direct contrast to *fusca*, *deglandi* and *stejnegeri*. There seems to be more suitable habitat than birds to fill it (Johnsgard 1978). In the Nearctic, *perspicillata* occupies a similar range to *americana*, nesting around freshwater lakes, ponds and rivers within or beyond the northern tree limit (Bent 1925; Cramp & Simmons 1977; Johnsgard 1978).

### Common Scoter *Melanitta nigra* and Black Scoter *M. americana*

Nests are well dispersed at concealed sites in thick vegetation or under scrub, mostly near water. Aerial surveys of *nigra* and *perspicillata* in Quebec (Decarie *et al.* 1995) showed that Black Scoters were associated with the presence of ponds (<10 ha) with sedge and grass, in contrast to Surf Scoters, which were more often found on unvegetated medium-sized lakes (10–100 ha). In contrast to *fusca*, *nigra* males maintain a mobile territory around their female (Bengston 1966). In both *nigra* and *americana*, the male may desert the female for his moult migration at about the time incubation begins (Bengston 1966; Cramp & Simmons 1977), although in Scotland this is not nor-



Tim Loseby

**90.** The smooth, concave head-and-bill profile distinguishes this female Velvet Scoter *Melanitta fusca* from both female 'American' White-winged Scoter *M. d. deglandi*, which has a slightly stepped profile resembling that of the male, and female 'Asian' White-winged Scoter *M. d. stejnegeri*, which has a rather straight bill profile, perhaps recalling Common Eider *Somateria mollissima*.

mally the case (M. A. Ogilvie pers. comm.).

**Common Scoter** The nest is composed of dry vegetal remains with a down lining, well concealed in birch *Betula* or willow *Salix* scrub (Bengston 1966). There are 6–10 eggs (mean 6.8 in Ireland, 8.7 Iceland), pale greenish brown, cream to buff (Cramp & Simmons 1977), 59–72 × 42–46.5 mm, shell 0.315 mm thick. Incubation lasts 30–31 days with fledging at 45–50 days (Bent 1925; Dement'ev & Gladkov 1952; Cramp & Simmons 1977).

**Black Scoter** The nest is built on the ground near water, sometimes on the borders of a pond or on steep banks close to water, hidden by grasses or stunted bushes, with a downy lining (Dement'ev & Gladkov 1952). There are 8–10 eggs, pale yellowish-white (colour varies from light buff or pale pinkish buff to cartridge buff), 53.0–72.7 × 33.6–46.2 mm (mean 61.9 × 41.7 mm), shell 0.315 mm thick (Bent 1925; Dement'ev & Gladkov 1952). There may be individual and inter-population differences relating to local environmental conditions. Bordage & Savard (1995) gave egg sizes as 64.11 × 44.26 mm on average (range 62.63–65.37 × 44.04–44.59). Kondratyev (1989), describing a Russian population of *americana*, counted 5–7 eggs (mean 5.83), average 66.4 × 45.0 mm (range 62.5–72.3 × 41.5–46.3). There are no North American data on the incubation period.

**Velvet Scoter** *M. fusca*, (American) **White-winged Scoter** *M. deglandi deglandi* and (Asian) **White-winged Scoter** *M. deglandi stejnegeri*

These taxa tend to arrive late on territories, and may

wait for a month or more before the female lays (Johnsgard 1978). First breeding occurs in the third or fourth calendar-year (Cramp & Simmons 1977). The males defend a territory of variable size on the water, but usually leave as incubation starts. Some stay to defend the brood and female. The pair will hang around together in communal areas until the female starts sitting. Females tend to abandon the young before fledging, but remain to moult on the breeding grounds (Cramp & Simmons 1977; Johnsgard 1978).

**Velvet Scoter** Nests on damp lowland among sedges or grassy vegetation, right next to water of lake (or small pond) or up to 2–3 km away, under scrub or overhanging rock, in woods, or uses nestboxes – reports from different locations are extremely variable (Bent 1925; Dement'ev & Gladkov 1952). In the Gulf of Bothnia, the females usually select nest-sites under junipers *Juniperus* or other bushes, also broadleaved herbs, herb–shrub mixtures or boulders for nest cover (Johnsgard 1978). Near the coast, nesting may be associated with gulls (Laridae) and/or terns (Sternidae) (Cramp & Simmons 1977).

The female builds, using material within reach, and making a lining of dry grass and down. There are usually 6–10 eggs (up to 14), creamy white, 64.3–76.5 × 44.8–51.5 mm, mean 70.8 × 47.9. Incubation lasts about one month (Dement'ev & Gladkov 1952), specifically 27–28 days (Koskimies & Routamo 1953). Fledging occurs at 50–55 days, although the young are independent at 30–40 days (Cramp & Simmons 1977). Broods frequently unite and survival may depend on this (Dement'ev & Gladkov 1952; Cramp & Simmons 1977).



Arthur Morris/Windrush

**91.** The bill of an adult male White-winged Scoter *Melanitta deglandi* of the race *deglandi* has a broad, lateral black border outlining the bill, which is red distally and becomes yellow-orange close to the nostrils. This contrasts with the bill of the race *stejnegeri*, on which the black lateral border is less pronounced and the distal part of the bill is yellow, becoming red closest to the nostrils.

(*American*) *White-winged Scoter* Frequently nests far from water, the nest being covered by vegetation or between rocks, often in dense vegetation. The downy lining may be poor or profuse. There are 9–14 eggs of variable colour, dingy ochre/deep rich buff/pale pinkish buff/cartridge buff, mean 65.3 (55.4–72.5) × 45.7 (35.7–49.0) mm. Incubation lasts about one month (Bent 1925; Dement'ev & Gladkov 1952).

(*Asian*) *White-winged Scoter* Nests have been reported from the Altai, on open banks of lakes, close to water. In the Anadyr region, they are located on the high banks of rivers and lakes, hidden in bushes or grass, the lining of moss or dry grass, and brown-grey down. Typically 6–9 eggs (varies locally), pale straw ochre, 55.5–72.5 × 35.7–49.0 mm. Breeding dates vary according to local conditions and altitude.

#### Appendix 4. Food items of scoter taxa.

##### Common Scoter *Melanitta nigra* and Black Scoter *M. americana*

An indirect comparison of food items, taken separately for *nigra* and *americana* from data in Bent (1925), Dement'ev & Gladkov (1952), Cramp & Simmons (1977) and Bordage & Savard (1995) suggests that their diets, primarily molluscs and crustaceans during the winter and aquatic insects and other invertebrates during the summer, are qualitatively very similar.

*Common Scoter* *Mytilus edulis*++, *Cardium* spp. *Mya*, *Spisula*, other bivalves, *Nassa*, *Littorina*, *Hydrobia*, *Idotea*, *Gammarus*, *Carcinus*, echinoderms. In fresh water, *Anodonta*, *Lymnaea*, insects and larvae (dragonfly (Odonata) larvae, caddisflies (Trichoptera) and chironomids), annelids, small fish, roots and tubers.

*Black Scoter* *Mytilus* spp.++, *Mya*, *Spisula*, *Littorina*, gammarids, *Balanus*, etc. In fresh water, caddisflies (a major food item in the Anadyr region, 3.2% on American continent), amphipods, beetles (Coleoptera), Ephemeroptera and Nematoda.

##### Velvet Scoter *M. fusca*, (*American*) *White-winged Scoter* *M. deglandi* *deglandi* and (*Asian*) *White-winged Scoter* *M. deglandi* *stejnegeri*

The diet of *fusca* is similar to that of *nigra*, though more varied because *fusca* feeds in more variable conditions. At sea, *fusca* may be almost entirely molluscivorous (Dement'ev & Gladkov 1952). In Norway, *fusca* fed on sandy bottom, mainly on echinoderms, in association with Red-necked Grebes *Podiceps grisegena* (Byrkjedal *et al.* 1997). The food of *deglandi* varies widely in different localities (Bent 1925). Like *fusca*, it dives to submerged ledges at 5–20 m or more in search of molluscs (chiefly bivalves) and crus-

##### Surf Scoter *M. perspicillata*

As with courtship and copulatory behaviour, the nesting behaviour of the taxa under consideration bears comparison with the nesting behaviour of *perspicillata*. The nest may be either close to or some distance from water, well concealed among grass, under bushes or low branches (Bent 1925; Johnsgard 1978). The nest is a hollow consisting of dry debris, with much down (Dement'ev & Gladkov 1952). Between 5 and 7 (up to 9) eggs are laid, cartridge buff, pinkish or buffy white, pale yellowish, yellow-tinged or cream, mean 61.6 (58–67.5) × 43 (40.5–45) mm (Bent 1925). Brood merges may be common (unlike *nigra* and *americana*, but similar to *fusca* and *deglandi*). Males leave before hatching for moult migration. Females may leave before the young fledge (Johnsgard 1978).

taceans, also crayfish (Astacidae), fish, tadpoles (Amphibia), insect larvae, vegetable food, slugs and snails (Gastropoda) inland (Bent 1925). Like *fusca*, *deglandi* extensively chooses sandy or gravelly substrates as winter feeding areas. When it occurs in flocks with *americana* and *perspicillata*, *deglandi* tends to select larger food items (Brown & Frederickson 1997), using deeper feeding grounds further away from the shore. In these flocks, *americana* and *perspicillata* often feed together over different substrates from nearby *deglandi*.

*Velvet Scoter* *Mytilus edulis*++ (usually 5–20 mm, cf. <40 mm for *nigra*), cockles *Cardium*+, dogwhelks *Nassa*, *Mya*, *Macoma*, *Spisula*, *Mactra*, *Venus*, *Nucula*, *Astarte*, *Cyprina*, *Modiolaria*, *Leda*, *Solen*, *Tellina*, *Donax*, etc. rarely small fish, also plant remains. In fresh water, molluscs include *Bythinia*, *Valvata*, *Anodonta*, *Unio*, *Dreissena*, insects, annelids, fish, seeds, roots, etc. When food is scarce, *fusca* may eat roe and frogs (Ranidae). Juveniles concentrate on crustaceans, i.e. amphipods, also insect larvae.

(*American*) *White-winged Scoter* *Mytilus* spp.++, *Protothaca*, *Ostra*, *Pecten*, *Mercenaria*, *Thaus*, *Littorina*, *Yoldia*, *Nassarius*, *Ammodytes*, *Siliqua*.

(*Asian*) *White-winged Scoter* The diet of *stejnegeri* is not properly determined. This taxon has nearly the same habitat requirements as *fusca*. Caddisflies and stoneflies (Plectoptera) have been recorded as a food item in the Anadyr region.

##### Surf Scoter *M. perspicillata*

Primary food items vary seasonally as for other scoters (Bent 1925; Dement'ev & Gladkov 1952) and include molluscs, crustaceans, insects (caddisflies, dragonflies, *Dytiscus* diving beetles), also some fish, seeds and greenery of pondweeds *Potamogeton*.