

The taxonomic status of Green-winged Teal *Anas carolinensis*

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ABSTRACT During the second half of the twentieth century, Green-winged Teal *Anas carolinensis* was almost universally treated as a subspecies of 'Common Teal'. Reassessment of morphological and behavioural differences between Green-winged Teal and Eurasian Teal *A. crecca*, together with molecular evidence regarding the phylogenetic relationships of Green-winged Teal, Eurasian Teal and Speckled Teal *A. flavirostris*, indicates that these taxa are best treated as separate species. The status of Green-winged Teal as a species can be justified under the Phylogenetic, Evolutionary and Biological Species Concepts. The basis for recognising *A. c. nimia* as a separate taxon is weak, but merits further study.

The Holarctic 'Common Teal' was until recently treated as a polytypic species, comprising three subspecies, *A. c. crecca* (Eurasian Teal, hereafter *crecca*) in the

Palaearctic, *A. c. nimia* (hereafter *nimia*) on the Aleutian Islands, and *A. c. carolinensis* (Green-winged Teal, hereafter *carolinensis*) elsewhere in the Nearctic. The treatment of

1. On behalf of the Association of European Rarities Committees and the British Ornithologists' Union Records Committee



crecca and *carolinensis* as conspecific dates back to the early part of the twentieth century, when the concept of polytypic species became predominant in ornithology (Hartert 1912-21; Witherby 1924; Peters 1931; Witherby *et al.* 1939). Most subsequent taxonomic publications (Delacour & Mayr 1945; Delacour 1956; AOU 1973; Johnsgard 1978, 1979; Madge & Burn 1988; del Hoyo *et al.* 1992; Johnson 1995) followed this treatment.

During the nineteenth century, *crecca* and *carolinensis* were treated as separate species (e.g. Gray 1871; Baird *et al.* 1884; Salvadori 1895). A number of recent authors have also adopted this stance (Stepanyan 1990; Livezey 1991, 1997; Gantlett *et al.* 1996; Johnson & Sorenson 1999; Sangster *et al.* 1999), although most of these have provided only brief statements on their reasons for doing so.

The Association of European Rarities Committees (AERC) and the British Ornithologists' Union Records Committee (BOURC) have decided, on the recommendations of their taxonomic advisory committees, to treat *crecca* and *carolinensis* as separate species. In this paper, which is written on behalf of the AERC and BOURC, we summarise the morphological, behavioural and molecular evidence for differentiation of *crecca* and *carolinensis*, and discuss the taxonomic status of *carolinensis* according to

the Phylogenetic (PSC), Evolutionary (ESC) and Biological Species Concepts (BSC).

Differentiation

Male plumage

Males of *crecca* and *carolinensis* are separable by a combination of plumage differences. These characters are well known and have been adequately described in the literature (Delacour 1956; Palmer 1976; Johnsgard 1978; Madge & Burn 1988; Millington 1998).

- *carolinensis* has a vertical white bar, or crescent, at the front of the flanks (absent from *crecca*)
- *crecca* has the inner webs of the long (outer) scapulars white, collectively forming a longitudinal white stripe above the flanks at rest; *carolinensis* lacks white on the scapulars
- *crecca* generally has conspicuous cream or pale buff lines separating the green from the rufous/chestnut parts of the head; in *carolinensis* these pale lines on the sides of the head are reduced or lacking
- *carolinensis* has fine (occasionally coarse) black vermiculations on the back and sides; in *crecca*, the mantle, scapulars and flanks are generally coarsely vermiculated black
- *carolinensis* has a deeper, more richly coloured wash on the breast than *crecca*



Arthur Morris/Windrush

115. Male Green-winged Teal *Anas carolinensis*, Jamaica Bay, New York, USA. The prominent vertical white bar at the front of the flanks, the absence of a white line above the flanks, and the inconspicuous pale lines on the sides of the head are the most obvious plumage characters separating male Green-winged from male Eurasian Teal *A. crecca*.



Tim Loseby

116. Male Eurasian Teal *Anas crecca*, Norfolk, April 1990.

Female plumage

Although females are 'almost identical' (Parkes 1958), it has long been known that the pale greater-covert bar, at the leading edge of the wing speculum, is richer in colour (brownish-buff or cinnamon-buff) in *carolinensis* than in *crecca* (Phillips 1923;

Schiøler 1925). Phillips (1923) stated that 90% of specimens can be identified to taxon by this character.

According to Millington (1998), the head pattern also appears different: 'Although there is much individual variation, the head pattern shown by [*crecca*] is largely indis-



Arthur Morris/Windrush

117. Female Green-winged Teals *Anas carolinensis*, Jamaica Bay, New York, USA. The individual on the right shows a relatively well-defined head pattern and finely mottled breast. The inner half of the greater-covert wingbar is a rich cinnamon-buff colour. The latter feature can also be seen on the folded wing of the individual to the left.

David Tipling/Windrush



118. Female Eurasian Teal *Anas crecca*. The head pattern of this individual is perhaps stronger than on many Eurasian (and therefore more similar to Green-winged Teal *A. carolinensis*), but the breast mottling is slightly bolder than on the Green-winged in plate 117.

tinct and lacks any great contrast. On [*carolinensis*], however, the head pattern can be really quite distinct, even vaguely recalling that of Garganey *A. querquedula*. The crown and eye-stripe may be dark brown, highlighting a pale supercilium, while a dark smudge on the ear-coverts may highlight an almost equally pale upper cheek stripe. At the same time, the loreal area may be very pale and clear of dark freckling, while the throat is often white.'

Other potential differences that have been proposed are: the colour of the bill (*carolinensis* appears to show far less pale coloration on the bill; Millington 1998); the 'tightness' of the mottling on the breast sides and fore-flanks (smaller, more compact patterning in *carolinensis*; Scott 1999); and the depth of the white tips of the outer secondaries (usually broader in *carolinensis*; Scott 1999). Given the fact that sample sizes are not specified, the taxonomic value of these purported differences remains unclear.

Molecular differentiation and phylogenetic relationships

A study based on mitochondrial DNA



Jonathan Leachy/WWT

119. Female Eurasian Teal *Anas crecca*, UK. Part of the greater-covert wingbar is washed cinnamon on this individual, demonstrating that there is some variability in this character. Compare with the Green-winged Teals *A. carolinensis* in plate 117.

(mtDNA) restriction fragments documented three distinct DNA sequences (haplotypes) in *crecca* from northeastern Russia and *carolinensis* from the state of Washington, USA (Zink *et al.* 1995). Two haplotypes were very divergent (3.6% sequence divergence). One of these haplotypes, however, was found both in northeastern Russia (n=1) and in the USA (n=1), suggesting either gene exchange between the continents or that this haplotype predates the divergence of *crecca* and *carolinensis*.

A phylogeny based on morphological characters grouped *crecca* and *carolinensis* as sister taxa, with Baikal Teal *A. formosa* being their closest relative (Livezey 1991). Behavioural and molecular comparisons (Johnsgard 1965; Johnson & Sorenson 1999), however, suggest that *crecca* and *carolinensis* are more closely related to the sexually monomorphic Speckled Teal *A. flavirostris* of South America. The molecular phylogeny of Johnson & Sorenson (1999) even suggests that *carolinensis* is more closely related to *A. flavirostris* (with 100% bootstrap statistical support) than to *crecca*. These authors also found that *crecca* and

carolinensis are genetically divergent, on the basis of cytochrome *b* and ND2 mtDNA sequences.

The paraphyletic relationship of *crecca* and *carolinensis*, which suggests that the common ancestor of *crecca* and *carolinensis* also gave rise to *flavirostris*, is unexpected. Thirty additional steps are required in the unweighted molecular data, however, to make these two species sister taxa (Johnson & Sorenson 1999). Statistical support for the inclusion of *crecca* in the *carolinensis/flavirostris* clade is less than 50% and, in a previous analysis of these data, *crecca* and *carolinensis* even turned up in different parts of the tree (Johnson & Sorenson 1998). The sister relationship between *A. flavirostris* and *carolinensis* is strongly supported, and indicates that the former evolved from birds colonising South America from the north (Johnson & Sorenson 1999).

Courtship behaviour

A detailed study by Laurie-Ahlberg & McKinney (1979) of the 'nod-swim' display of captive male teals has documented several quantitative differences in courtship behaviour between *crecca* and *carolinensis*.

The study found clear differences in the association between the 'nod-swim' and 'grunt-whistle' behaviours. In large courtship groups, about 30% of male *carolinensis* included nod-swim in their grunt-whistle displays, compared with only 3% for *crecca* males. The difference is highly significant statistically ($p < 0.01$). There are also differences in the frequency of the nod-swim display. Six *carolinensis* males performed nod-swim an average of 28.60 times (standard error 12.95) in 400 seconds. The mean value for 12 *crecca* males was 12.27 times (standard error 7.13) in the same time period. This difference is also highly significant ($p < 0.01$), and is largely due to the absence of nod-swim from the grunt-whistle behaviour of *crecca*. Removing composite behaviours from *carolinensis* still left 20.60 nod-swims (standard error 13.60) per 400 seconds, although this does not differ significantly from the rate for *crecca*. The independent nod-swim behaviour is usually given in response to the approach of another male. The difference between the two taxa implies a difference in the threshold of the nod-swim behaviour, and

this indeed seems to be the case. For *carolinensis*, 40% of approaches elicited a nod-swim response, significantly more than the 16% observed in *crecca* ($p < 0.01$).

Laurie-Ahlberg & McKinney (1979) summarised their results as follows: 'Despite the fact that nod-swimming appears to serve the same display functions in both races, striking quantitative differences are reported here: (1) The marked temporal association of nod-swimming with the grunt-whistle sequence in *carolinensis* is absent or greatly reduced in *crecca*. (2) Both the total nod-swim frequency and the frequency of independent nod-swimming are greater in *carolinensis* than in *crecca*. (3) The proportion of approaches followed by nod-swimming is greater in *carolinensis* than in *crecca*.'

Discussion

The case for lumping

Parkes (1955, 1958) discussed the taxonomic status of *carolinensis* in the context of the BSC. He argued that *crecca* and *carolinensis* should be treated at the level of subspecies because they are geographically discrete, the females are almost identical, and there are no behavioural differences between the two taxa. He also pointed out that, even though the occurrence of hybridisation is so common among ducks that it cannot be used as the sole basis for conspecificity, it is nevertheless interesting to note that some apparent hybrids between the two have been reported. Others who accepted *carolinensis* as a subspecies of *A. crecca* provided only brief justification for this view (Mayr & Short 1970; Beaman 1994).

The case for lumping seems to rest on (1) allopatry of breeding ranges, (2) similarity of females, (3) a lack of behavioural differences, and (4) the existence of intermediate, perhaps hybrid, individuals. None of these arguments is persuasive. First, geographical separation (allopatry) is not in itself sufficient evidence of conspecificity. What needs to be demonstrated is a lack of reproductive isolation (BSC), or a lack of diagnostic character states (PSC, ESC). Second, none of the current species concepts requires that *both* sexes should differ in external characters if a taxon is to be recognised as a species. Third, the supposed lack of behavioural differences is based on brief, anecdotal characterisations

of courtship behaviour (Cruickshank 1936) and is not supported by Laurie-Ahlberg & McKinney (1979), who instead found significant quantitative (though not qualitative) differences in three behavioural parameters. Finally, interspecific hybridisation by ducks is a common and widespread phenomenon. There is no reason to presume that reports of hybridisation are taxonomically more significant for teals than for other groups of ducks that are generally treated as species (e.g. Mallard *A. platyrhynchos*, [American] Black Duck *A. rubripes*, Pacific Black Duck *A. superciliosa*). Moreover, although males showing a combination of characters of *crecca* and *carolinensis* are known from Europe (Vinicombe 1994; Fraser *et al.* 1996), and from the USA in New England (Cruickshank 1936; Poole 1940; Palmer 1976) and the Pribilof Islands, Alaska (Mayr & Short 1970; Palmer 1999), these are not evidence of a lack of reproductive isolation. In Europe and New England, only one taxon normally occurs. In the Pribilof Islands, *carolinensis* is a (regular) vagrant, whereas *crecca* is an uncommon visitor (Palmer 1999). The degree of assortative mating cannot be assessed from these reports of intermediates, because in each of the areas vagrants generally do not have members of their own taxon available for mating. In conclusion, the case for lumping under the BSC is weak.

The case for splitting

The diagnostic plumage differences of male *crecca* and *carolinensis* are evidence of a separate evolutionary history, so that *crecca* and *carolinensis* can therefore be recognised as phylogenetic species (Cracraft 1983). The strong mtDNA support for a sister relationship between *carolinensis* and *A. flavirostris* with a more basal position for *crecca* is incompatible with the traditional view that *crecca* and *carolinensis* are conspecific and that *A. flavirostris* is a separate



Arthur Morris/Windrush

120. Eclipse male Green-winged Teal *Anas carolinensis*, Jamaica Bay, New York, USA. As on the female in plate 117, the inner part of the greater-covert wingbar of this eclipse male is deep cinnamon-buff in colour.

species. For a full understanding of the evolutionary history and biogeography of the complex, however, more information about mtDNA variation within the complex is desirable.

Under the ESC, *crecca* and *carolinensis* can be recognised as species because the differences in the plumage of male *crecca* and *carolinensis*, and the evidence for parphyly, suggest that these taxa represent separate population lineages, with their own 'evolutionary tendencies and historical fates' (Simpson 1961; Wiley 1978). Proponents of the ESC (Frost & Kluge 1994; Christofferson 1995; Mayden 1997) have suggested that it represents a theoretical (or primary) species concept and that the PSC is an operational (or secondary) species concept. These authors view the ESC and the PSC as complementary aspects of a single approach in which the PSC provides an operational criterion for the ESC. According to this interpreta-



121. Male Eurasian Teal *Anas crecca*, Minsmere, Suffolk.

tion, the evidence presented here in support of species status under the PSC also supports the treatment of *crecca* and *carolinensis* as evolutionary species.

Assessment of the taxonomic rank of *crecca* and *carolinensis* with the BSC is somewhat problematic because the breeding ranges of these taxa are allopatric. As mentioned earlier, reports of males showing a combination of the characters of *crecca* and *carolinensis* do not necessarily indicate a lack of reproductive isolation. As Mayr (1940) pointed out, the existence of a few hybrids does not immediately rule out species status under the BSC. Although *crecca* and *carolinensis* are not completely diagnosable by courtship behaviour, it is possible that the differences described in three aspects of courtship behaviour form a barrier to gene flow in the wild. In any case, the molecular evidence for a non-sister relationship of *crecca* and *carolinensis* strongly suggests that these taxa are best treated as separate species. Monophyly of polytypic species is not explicitly required by the BSC, but few systematists would intentionally recognise a taxon as a species when there is strong evidence that it represents a paraphyletic group of taxa.

In conclusion, *crecca* and *carolinensis* can be recognised as species under each of the three most popular species concepts. These taxa are therefore best treated as separate species: Eurasian Teal *A. crecca* and Green-winged Teal *A. carolinensis*.

The status of Anas crecca nimia

Friedmann (1948) described the populations on the Aleutian Islands as a separate sub-species *A. c. nimia*. Most subsequent authors have accepted this (Delacour 1956; Johnsgard 1978, 1979; Madge & Burn 1988; del Hoyo *et al.* 1992; Johnson 1995), although Delacour (1956) noted that it is a 'very slightly characterised sub-species [that] is hardly recognisable', while Gibson & Kessel (1997) treated *nimia* as a synonym of *crecca*.

Friedmann (1948) based his description of *nimia* solely on differences in average size from *crecca*. Friedmann's data are presented in table 1. In most measurements, *nimia* is larger on average than *crecca*. Except for wing length of females, however, *nimia* and *crecca* show overlapping ranges in all five biometric measurements.

Since the variances of Friedmann's measurements are not known, it is not clear whether the differences in average size between *nimia* and *crecca* are statistically significant. The lack of overlap in female wing lengths may have been caused by the small sample of *nimia*, of which only three females were examined. Delacour (1956) remarked that the various populations of *crecca* have a tendency to increase in size from west to east, in a continuous cline. Friedmann's measurements of *crecca* are consistent with this view. It is therefore possible that the populations on the Aleutian Islands are simply the end-point of this cline.

Table 1. Measurements (range, average) of *A. c. crecca* and *A. c. nimia* (taken from Friedmann 1948). All measurements in millimetres.

	Male	Female
Wing length		
<i>nimia</i> (13 males; 3 females)	182-204 (193.1)	185-189 (186.7)
<i>crecca</i> Kamchatka, Bering I (3 males); eastern Siberia (4 females)	177-182 (179.3)	166-173 (172.0)
<i>crecca</i> China, Japan, Korea (22 males); Japan, China, Burma, Thailand (17 females)	174-187 (179.5)	167-182 (174.1)
<i>crecca</i> Europe (3 males; 5 females)	175-182 (178.0)	167-184 (176.4)
Tail length		
<i>nimia</i> (13 males; 3 females)	65.1-76.0 (71.0)	65.6-66.6 (66.1)
<i>crecca</i> Kamchatka, Bering I (3 males); eastern Siberia (4 females)	62.1-66.5 (63.7)	60.0-61.1 (60.6)
<i>crecca</i> China, Japan, Korea (22 males); Japan, China, Burma, Thailand (17 females)	62.1-70.9 (65.3)	60.2-65.1 (62.6)
<i>crecca</i> Europe (3 males; 5 females)	61.4-64.7 (63.0)	58.3-66.0 (61.9)
Exposed culmen		
<i>nimia</i> (13 males; 3 females)	33.2-37.4 (35.8)	34.2-36.1 (35.1)
<i>crecca</i> Kamchatka, Bering I (3 males); eastern Siberia (4 females)	35.1-38.1 (36.8)	31.1-37.1 (34.2)
<i>crecca</i> China, Japan, Korea (22 males); Japan, China, Burma, Thailand (17 females)	29.3-38.1 (35.6)	33.0-35.4 (34.0)
<i>crecca</i> Europe (3 males; 5 females)	36.2-37.9 (37.1)	33.7-36.5 (35.5)
Tarsus length		
<i>nimia</i> (13 males; 3 females)	29.2-34.1 (31.4)	30.4-31.2 (30.9)
<i>crecca</i> Kamchatka, Bering I (3 males); eastern Siberia (4 females)	28.5-30.2 (29.6)	28.1-32.1 (29.4)
<i>crecca</i> China, Japan, Korea (22 males); Japan, China, Burma, Thailand (17 females)	28.1-31.1 (29.9)	27.2-30.1 (28.6)
<i>crecca</i> Europe (3 males; 5 females)	30.1-35.4 (31.9)	28.1-31.1 (29.3)
Middle-toe length without claw		
<i>nimia</i> (13 males; 3 females)	33.1-39.1 (35.7)	33.1-34.1 (33.8)
<i>crecca</i> Kamchatka, Bering I (3 males); eastern Siberia (4 females)	32.2-33.2 (32.8)	30.2-34.1 (32.8)
<i>crecca</i> China, Japan, Korea (22 males); Japan, China, Burma, Thailand (17 females)	31.1-36.4 (33.0)	28.1-34.1 (31.9)
<i>crecca</i> Europe (3 males; 5 females)	32.2-34.2 (33.2)	30.2-34.6 (32.3)

Variation in biometric characters is plastic and is subject to environmental induction (James 1983; Boag 1987). The influence of food during the nestling stage on the ensuing adult phenotype has been demonstrated for other Anatidae (Larsson & Forslund 1991; Larsson 1993; Leafloor *et al.* 1998). Consequently, the slightly larger average size of *nimia* compared with *crecca* may be caused by environmental influences.

Since Friedmann's (1948) original paper, very little new information on *nimia* has become available and its taxonomic status has not been re-examined. Palmer (1976) presented additional measurements, but these also lacked a measure of variance. In a comparison of 550 base pairs of the ND2 gene, *nimia* was identical to *crecca* (Johnson & Sorenson 1999). Using these data, the basis for recognising *nimia* as a separate taxon is clearly weak and merits further study.

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