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

George Sangster, Martin Collinson, Andreas J. Helbig, Alan G. Knox, David T. Parkin and Tony Prater

**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 Palearctic, *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

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.
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-
Distinct and lacks any great contrast. On *A. 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 loral 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 motting 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 (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.

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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 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 paraphyly, 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-
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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 subspecies 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.

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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 \textit{nimia} compared with \textit{crecca} may be caused by environmental influences.

Since Friedmann’s (1948) original paper, very little new information on \textit{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, \textit{nimia} was identical to \textit{crecca} (Johnson & Sorenson 1999). Using these data, the basis for recognising \textit{nimia} as a separate taxon is clearly weak and merits further study.

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

<table>
<thead>
<tr>
<th></th>
<th>Male</th>
<th>Female</th>
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<tbody>
<tr>
<td>Wing length</td>
<td></td>
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<tr>
<td>\textit{nimia}</td>
<td>182-204 (193.1)</td>
<td>185-189 (186.7)</td>
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<tr>
<td>\textit{crecca}</td>
<td>177-182 (179.3)</td>
<td>166-173 (172.0)</td>
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<td></td>
<td>174-187 (179.5)</td>
<td>167-182 (174.1)</td>
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<td></td>
<td>175-182 (178.0)</td>
<td>167-184 (176.4)</td>
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<tr>
<td>Tail length</td>
<td></td>
<td></td>
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<td>\textit{nimia}</td>
<td>65.1-76.0 (71.0)</td>
<td>65.6-66.6 (66.1)</td>
</tr>
<tr>
<td>\textit{crecca}</td>
<td>62.1-66.5 (63.7)</td>
<td>60.0-61.1 (60.6)</td>
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<tr>
<td></td>
<td>62.1-70.9 (65.3)</td>
<td>60.2-65.1 (62.6)</td>
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<td></td>
<td>61.4-64.7 (63.0)</td>
<td>58.3-66.0 (61.9)</td>
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<td>Exposed culmen</td>
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<td>34.2-36.1 (35.1)</td>
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<td>29.3-38.1 (35.6)</td>
<td>33.0-35.4 (34.0)</td>
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<td></td>
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<td>33.7-36.5 (35.5)</td>
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<td>Tarsus length</td>
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<tr>
<td>Middle-toe length without claw</td>
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