The taxonomy and relationships of the northern swans

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The recent (1972) publication of the Wildfowl Trust's book *The Swans* has brought together an unprecedented array of information on all of the swans of the world, and makes it desirable to raise once again the question: how many species of northern swans are there, and what are their evolutionary relationships to one another? Delacour (1954) suggested the comprehensive vernacular name 'northern swans' to distinguish 'the various knobless white swans which breed in or near the Arctic parts of the northern hemisphere' from the Mute Swan (*Cygnus olor*) and the three southern hemisphere swans. The northern swans have generally (e.g. Stejneger, 1882; Wetmore, 1951; Vaurie, 1965) been regarded as constituting four separate species, although as early as 1832 Yarrell questioned whether the smaller North American (Whistling) swan should be regarded as specifically distinct from the comparable Eurasian (Bewick's) swan. Yarrell's observations on the Trumpeter Swan's tracheal anatomy did convince him that it should be regarded as a species distinct from both the Whooper Swan and from the two smaller northern swans. Later investigators who argued for the merger of the Whistling and Bewick's Swan, as well as for conspecificity of the Trumpeter and Whooper Swan, include Hartert (1920), Delacour & Mayr (1954), and Mayr & Short (1970). Thus, two different taxonomic approaches to the group have gradually emerged as shown in Table 1.

A fifth described form, *jankowskii*, is now believed to be invalid (Vaurie, 1965), as is a supposed Islandic race (*islandicus*) of the Whooper Swan.

Two major taxonomic questions are present. First, how many species of northern swans should be recognized in order best to illustrate their probable degree of phyletic distinction, and second, if fewer than four are to be recognized, what forms should be merged with what other forms?

The general criterion of species distinction in higher animals is that of reproductive isolation under natural conditions—i.e., failure to hybridize in nature. This criterion may be readily applied when the populations concerned have sympatric breeding areas, but becomes hypothetical when their breeding areas are allopatric. Contact in wintering areas may be insignificant if pairs are formed during migration or on breeding grounds and, once formed, are permanent.

Obviously the two North American populations are geographically isolated from the Eurasian ones, but what if any breeding sympatry occurs between the larger and smaller forms found on each continent? In North America, sympatry between the Whistling Swan and Trumpeter Swan is essentially absent, with one possible exception. Hansen *et al.* (1971) state that the breeding range of the Trumpeter Swan in western Alaska extends out into the tundra, which represents the typical breeding habitat of the Whistling Swan. However, the breeding contact between these two forms must at most be marginal, as indicated by King (1973). The wintering areas of the two North American populations are likewise almost wholly separate, with the only area of probable contact being the coastal region of British Columbia and Washington (cf. *The Swans*, pp. 42 and 46).

In Eurasia the situation is similar. The breeding ranges of the Bewick's Swan and Whooper Swan are almost entirely complementary (cf. *The Swans*, pp. 43 and 48; Dementiev & Gladkov, 1967). In a manner comparable to the situation in North America, the Bewick's Swan is limited to Arctic tundra breeding habitat, while the Whooper Swan occurs to the south in the forested zone, extending only locally into

Table 1. Two taxonomic approaches

	'Splitter' approach	*'Lumper' approach*
Whooper Swan	*Cygnus cygnus*	*Cygnus c. cygnus*
Trumpeter Swan	*Cygnus buccinator*	*Cygnus c. buccinator*
Whistling Swan	*Cygnus columbianus*	*Cygnus columbianus columbianus*
Bewick's Swan	*Cygnus bewickii*	*Cygnus columbianus bewickii*

tundra (Dementiev & Gladkov, 1967) or into willow scrub (Vaurie, 1965). Vaurie suggests that the ranges of the two may be in limited contact along river valleys south of the tundra limits, as for example the Yenisei at about 68° Latitude. The wintering ranges of the Bewick's and Whooper Swans overlap to a much greater degree than do those of the Trumpeter and Whistling Swans.

Thus, in general the breeding ranges of these forms show the complementary pattern typical of ecological races adapted to different habitats. Wild hybrids are not known, but overlapping mensural characters for nearly all traits would make such hybrids virtually impossible to recognize. In captivity no fewer than four of the six possible hybrid combinations among the four forms have been reported; at least one of these combinations (Whistling × Whooper) was 'probably fertile' (Gray, 1958).

Since the lack of definite breeding ground sympatry fails to provide an answer relative to reproductive isolation, one must look to specific anatomical or behavioural traits that might indicate levels of distinctness. These can be considered sequentially under the general headings of mensural characteristics (weights and measurements), colouration of bill and soft parts, voice and tracheal characteristics, and behavioural traits.

The four northern swans form a progressive series from small to large in the sequence Bewick's–Whistling–Whooper–Trumpeter. This series is contrary to Bergmann's rule and, like various populations of *Branta* and *Anser*, is evidently related to decreasing size (and associated decreasing periods of fledging) as an adaptation to arctic breeding. This association between breeding latitude and times to fledging has already been mentioned by Janet Kear (in *The Swans*, pp. 117–118).

Weights of adults generally exhibit some overlap in sample extremes, although average weights show a progressive series in each sex. A comparison of average adult weights (data from *The Swans*, p. 198) and average wing chord measurements (pp. 199–200) indicates that the Bewick's and Whistling Swans are very similar, as are the Whooper and Trumpeter Swans (Figure 1). According to Banko (1960, p. 64), there is a 2–3 lb overlap in minimum Trumpeter Swan and maximum Whistling Swan weights among females, while those of immature and adult males apparently to not overlap. Weight data in *The Swans* also indicate weight overlaps for Whistling and Trumpeter Swans but not for Whooper and Bewick's Swans.

Most authorities (e.g., Stejneger, 1882; Banko, 1960; Hansen *et al.*, 1971) suggest that the bill length, and especially the relative position of the nostrils, is the most useful criterion for separating the larger pair of swan taxa from their smaller counterparts. The smaller swans not only have shorter and slightly more concave culmens, but also their nostrils are located relatively closer to the tip of the bill. This relationship may be seen in a diagram (Figure 2) that plots the distance from the bill-tip to the anterior edge of the nostril, relative to the distance from the tip of the bill to the anterior edge of the eye (data from Stejneger, 1882). These plotted points also indicate a progressive variation, with most of the forms exhibiting consider-

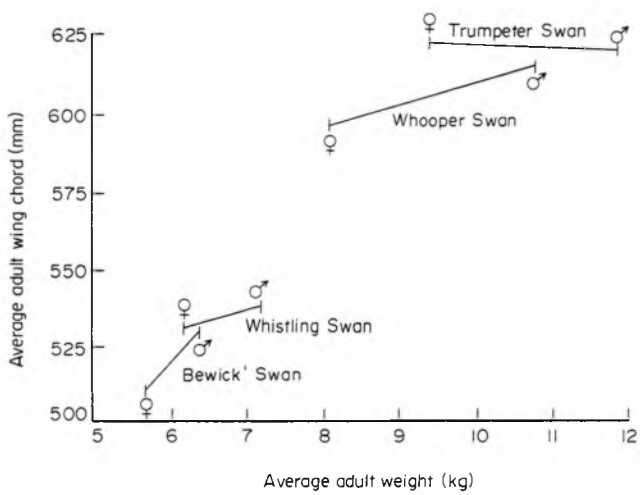

Figure 1. The relation between the average adult weight and average adult wing chord length in the four northern swans, as reported in *The Swans*.

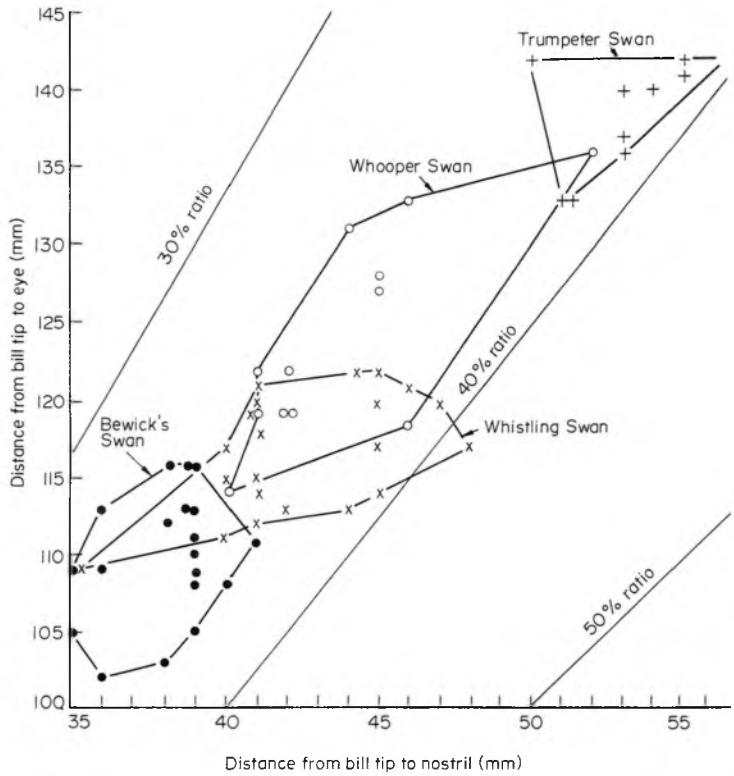

Figure 2. The relation between the distance from the bill-tip to the eye and the relative position of the nostril in adults (both sexes) of the four northern swans. Data from Stejneger (1882).

able overlap in this pair of measurements. It may be seen that, with increasing overall bill size, the distal part of the bill beyond the nostrils tends to become relatively longer than the proximal part. Hansen *et al.* (1971) observed that this same general relationship (body weight *v.* nostril-to-nail length) held for their sample of male Trumpeter Swans, but not for females. A similar progression of bill length relative to body size can be seen in these swans (Figure 3) and in various races of geese (e.g. *Anser fabalis*, *Branta canadensis*, etc.), and is clearly the result of allometric growth effects rather than the result of qualitative differences among the populations. Likewise, Boyd's comment (p. 22 of *The Swans*) that the most effective means of distinguishing Bewick's from Whooper Swans or Whistling from Trumpeter Swans is in their actual and relative neck lengths doubtless has the same explanation.

The colouration of the bill and soft parts is also deserving of mention. The standard 'field-guide' difference between Whistling and Trumpeter Swans is the presence of a yellow loreal mark on the former and its absence on the latter. The low reliability of this feature has been mentioned by Banko (1960) and by Hansen *et al.* (1971). Banko also noted that the presence of a reddish 'grinning streak' on the lower mandible is not limited to Trumpeter Swans. Tate (1966) reported that 30% of fifty-five adult-plumaged Whistling Swans she examined in California lacked the loreal mark, and that a pinkish or reddish colour was present on the lower mandible of all the Whistling Swans she examined. In the Bewick's and Whooper Swans the variable extension of yellow (below and beyond the nostrils in the Whooper) has been recognized as a useful fieldmark ever since Stejneger mentioned it in 1882. The enormous individual variation in this patterning among Bewick's Swans is now evident on the basis of the Wildfowl Trust's observations, but it does appear to provide a functional fieldmark separation of the two Old World forms. Yet few, if any, taxonomists would argue that it constitutes a species character, since logic would dictate that the two forms in greatest contact with one another should be the most dissimilar in their bill colouration, when the reverse is actually true. Lastly it might be mentioned

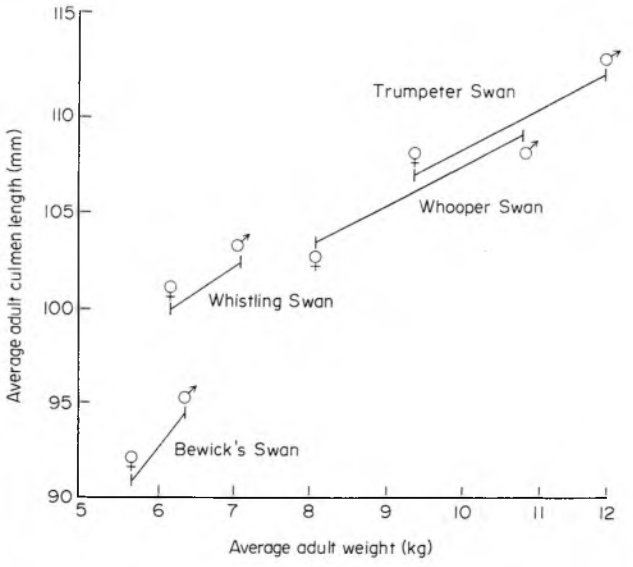

Figure 3. The relation between the average adult weight and the average adult culmen length for the four northern swans, as reported in *The Swans*.

that, contrary to Kortright (1943), the bill and foot colours of downy young and juvenile swans are virtually identical among the four forms (cf. p. 23 of *The Swans* and plate III of Delacour, 1954). Feathering on the foreheads of the downy young of the smaller swans is less extensive than in the larger ones, and as the birds mature the feather line on the forehead variably retracts. Stejneger (1882) mentioned that the Whistling Swan usually develops a pointed forehead line, while the Trumpeter Swan tends toward a rounded one, although he admitted seeing exceptions. Tate (1966) suggested that Whistling Swans might be recognized by their sparsely feathered brow-line, as opposed to the more continuously feathered brow of Trumpeter Swans. I have observed numerous exceptions to this, and believe that individual differences in exposure to abrasion probably account for these variations. Likewise, the number of tail feathers has long been recognized (Stejneger, 1882) as an unreliable and individually variable trait.

The voice and associated tracheal differences in these swans cannot be denied, and indeed is the basis for the vernacular name of three of the four populations. Yarrell (1832) initially recognized that the adult Trumpeter Swan has a unique dorsal protrusion of the sternum associated with a tracheal loop, and this feature has subsequently become the standard criterion for this form's identification. The other three swans also have extensive tracheal penetration of the sternum in a manner that is evidently progressive with age, and thus there is much individual variation in this trait (Schiøler, 1925; Tate, 1968). The dorsal projection of the Trumpeter Swan's trachea does appear to be constant, but Richard Banks (*in litt.*, 5 March, 1974) reported seeing two National Museum specimens of the Whistling Swan that show a slight dorsal bend in the trachea, forming a *buccinator*-like loop. He did not rule out the possibility that this was an artifact of drying. The possible resonating or other functions of the tracheal elongation achieved by sternal penetration are still being debated, but it is clear that the vocalizations of the four populations are qualitatively very similar, differing only in their fundamental frequencies and relative harmonic development (Johnsgard, 1972). As shown in Figure 4, the fundamental frequency differences show a progressive relation to body size and presumably also to tracheal length, although data are not yet available to test the predicted relationship between tracheal length and possible frequency modulation.

In terms of social behaviour patterns and displays, the four populations are extremely similar. All utilize a wing-waving triumph ceremony that is quite distinct from that of the Mute Swan, and all have virtually identical precopulatory and postcopulatory displays (Johnsgard, 1965; Kear, p. 83, in *The Swans*). Again, one might argue that on the basis of needs for reproductive isolation some differences in these patterns might have

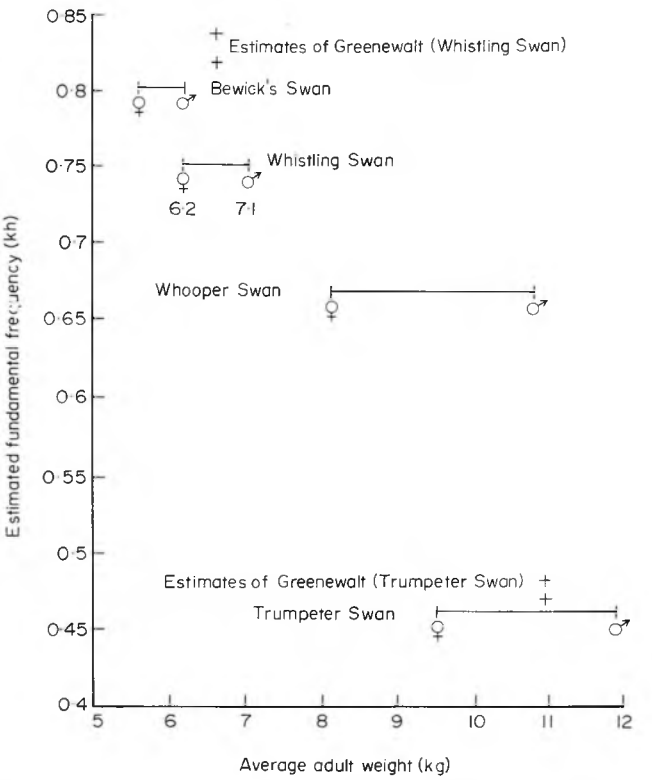

Figure 4. The relation between the average adult weight (as reported in *The Swans*) and the fundamental frequency of adult calls (sex unknown) for the four northern swans, as estimated by Johnsgard (1971) and Greenewalt (1968).

evolved if speciation between the geographically interacting populations had been completed.

In summary, the various anatomical and behavioural traits of these four populations tend to differ only in predictable quantitative ways that are associated with overall size differences, and these in turn are probably the result of ecological adaptation to differing habitats and breeding phenologies. Some of the criteria described above favour association of the two larger forms and the two smaller ones (e.g. wing chord and body weights), while others (such as degree of bill pigmentation) suggest affiliation between the two North American forms and the Eurasian ones. Yet others suggest a graded series without definite breaks. None, however, can be used to argue strongly that any single form is specifically distinct from any of the others. How then is the phylogeny of the members of this group to be explained and what is the most practical way of dealing with their taxonomy?

To account for the evolution of these four extant populations, one must accept one or the other of two general hypotheses. The first of these is to assume that a single ancestral northern swan was initially separated into arctic-tundra and temperate-zone breeding populations, either in North America or Eurasia. Each of these populations must then have spread out into comparable habitats of the other hemisphere. This would have been readily achieved in the case of the tundra-breeding populations where virtually no barriers to transhemispheric movements once existed, but is much more difficult to imagine for the temperate-latitude forms now represented by the Trumpeter and Whooper Swans. Ploeger (1971) believed that the Whistling and Bewick's Swans' ancestors had a circumpolar distribution prior to the Last Glacial, but were subsequently geographically isolated by glaciation, and have remained so until the present. Such an interpretation would favour the view that the Whistling and Bewick's Swans might best be considered subspecific replacement forms, and that the Trumpeter and Whooper Swans are less closely related to them than to one another, and also should be considered conspecific.

The second possibility is that a single northern hemisphere ancestral swan was initially split into Eurasian and North American components, each of which subsequently developed two populations, a larger form ecologically adapted to nesting in marshes or lakes of temperate grasslands or forests, and a smaller one adapted to breeding on arctic tundra. Presumably the boreal forest provided the initial barrier to their gene pools, but this habitat has been gradually colonized by the more southern populations and has resulted in limited secondary contact to timberline. Such a hypothesis would help to account for the similarities of bill pigmentation in the Old World and New World pairs of forms, and is also supported by parasitological evidence in the form of mallophagan similarities in the swan populations of the same hemisphere (Timmermann, 1964).

If one favours the first argument, then the 'lumper' taxonomy of Delacour & Mayr (1945), as shown in the beginning of this paper, might be the most logical one to follow. However, the second hypothesis would suggest either the recognition of a single Old World species (*cygnus* having priority over *bewickii*) and a New World species (*columbianus* having priority over *buccinator*), or even the more radical view that, inasmuch as geographic isolation prevents a test of reproductive isolation, only a single polytypic species should be recognized. I would support the latter position, and suggest the following technical and vernacular nomenclature:

Cygnus cygnus: Northern Swan
Cygnus cygnus cygnus (L.) 1758. Northern Whooper Swan
Cygnus cygnus columbianus (Ord) 1815. Northern Whistling Swan
Cygnus cygnus bewickii (Yarrell) 1830. Northern Bewick's Swan
Cygnus cygnus buccinator (Richardson) 1831. Northern Trumpeter Swan

This position would allow for acceptance of either of the speciation models described above. It would also emphasize the close anatomical relationships of all of the forms, rather than imply that we know more about the group's phylogeny than is actually the case. If this approach is unacceptable, then a retention of the 'splitter' approach of retaining four separate species would seem to be the most satisfactory interim solution.

References

Banko, W. 1960. The Trumpeter Swan. *North American Fauna No. 63:* U.S.F.W.S., Washington.
Delacour, J. 1954. *The Waterfowl of the World, Vol. I.* Country Life, London.
Delacour, J. & Mayr, E. 1945. The family Anatidae. *Wilson Bull.* 57:3–55.
Dementiev, G. P. & Gladkov, N. A. 1967. *Birds of the Soviet Union*, Vol. IV. Translated from Russian, Israel Program for Scientific Translations, Jerusalem.
Greenewalt, C. H. 1968. *Bird Song: Acoustics and Physiology.* Smithsonian Institution Press, Washington.
Gray, A. P. 1958. *Bird Hybrids.* Commonwealth Agricultural Bureaux, Survey.
Hansen, H. A., Shepheard, P. E. K., King, J. G. & Troyer, W. A. 1971. The Trumpeter Swan in Alaska. *Wildl. Monogr., Chestertown, No.* 26, 83 pp.
Hartert, E. 1920. Die Vögel der paläarktischen Fauna. Friedländer & Sohn, Berlin.
Johnsgard, P. A. 1965. *Handbook of Waterfowl Behavior.* Cornell University Press, Ithaca.
Johnsgard, P. A. 1972. Observations on sound production in the Anatidae. *Wildfowl*, 22:46–59.
King, J. G. 1973. The use of small airplanes to gather swan data in Alaska. *Wildfowl*, 24:15–20.
Kortright, F. H. 1943. *The Ducks, Geese and Swans of North America.* American Wildlife Institute, Washington.
Mayr, E. & Short, L. L. 1970. Species taxa of North American birds. *Nuttall Orn. Club, No.* 9, 127 pp.
Ploeger, P. L. 1968. Geographical differentiation in Arctic Anatidae as a result of isolation during the Last Glacial. *Ardea*, 56:1–159.
Schiøler, E. L. 1925. *Danmarks Fugle*, Vol. 1. Gyldendelske, Copenhagen.
Scott, P. and The Wildfowl Trust. 1972. *The Swans.* Michael Joseph, London.
Stejneger, L. 1882. Outlines of a monograph of the Cygninae. *Proc. U.S. Natn. Mus.* 5:147–221.
Tate, D. J. 1966. *Morphometric age and sex variation in the Whistling Swan* (Olor columbianus). M.Sc. thesis, University of Nebraska, Lincoln.
Timmermann, G. 1963. Fragen der Anatidensystematik in parasitologischer Sicht. *Proc. XIII Inter. Ornith. Congr.*, Vol. 1, pp. 189–197.
Vaurie, C. 1965. *The Birds of the Palearctic Fauna, Non Passeriformes.* H. F. & G. Witherby Ltd., London.
Wetmore, A. 1951. Observations on the genera of the waterfowl. *J. Wash. Acad. Sci.* 41:338–340.

Yarrell, W. 1832. Description of the organ of voice in a new species of wild swan (*Cygnus buccinator*, Richardson). *Trans. Linn. Soc. Lond.* 17: 1–4.

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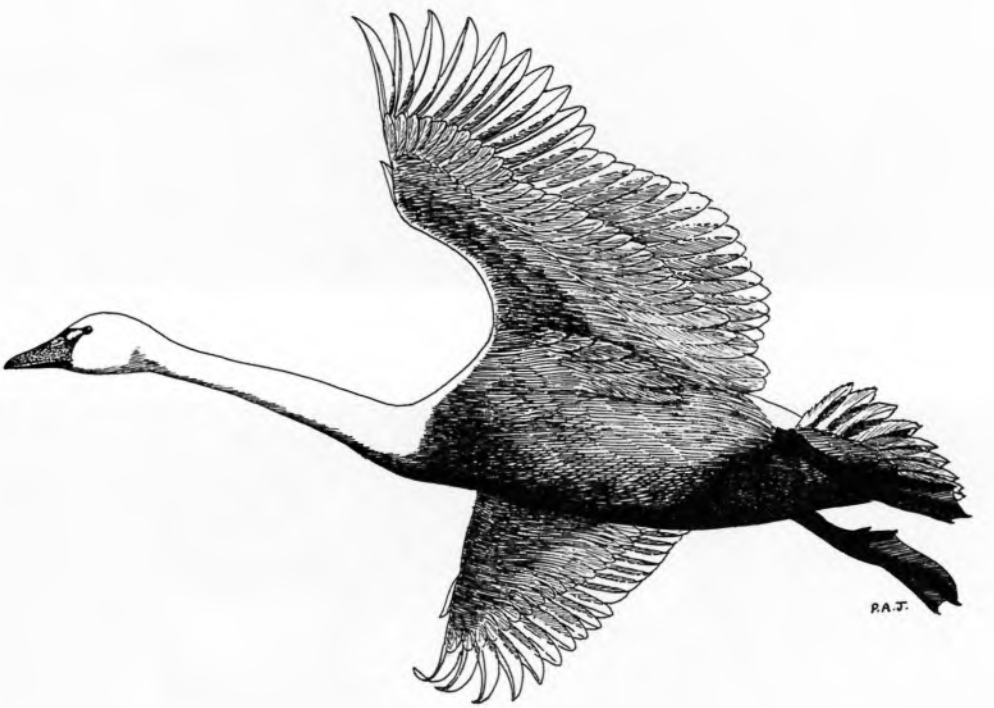

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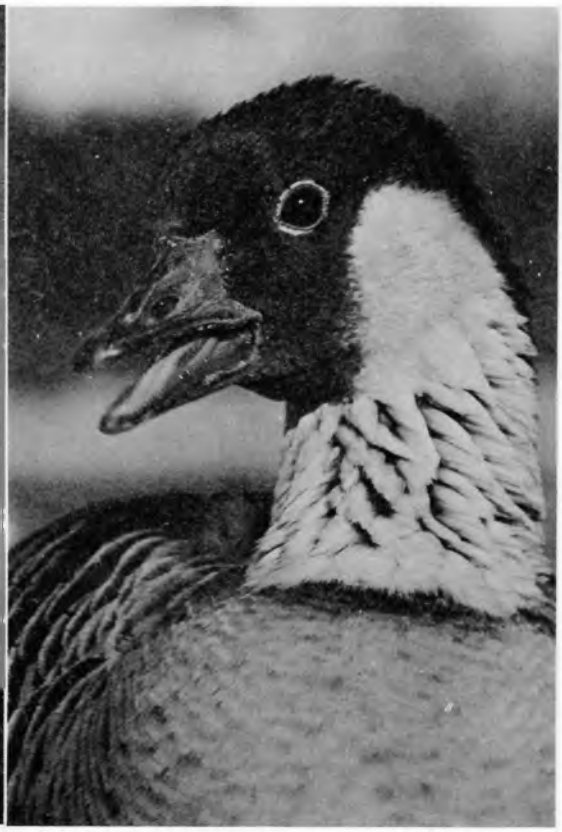

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Four portrait studies at Slimbridge

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