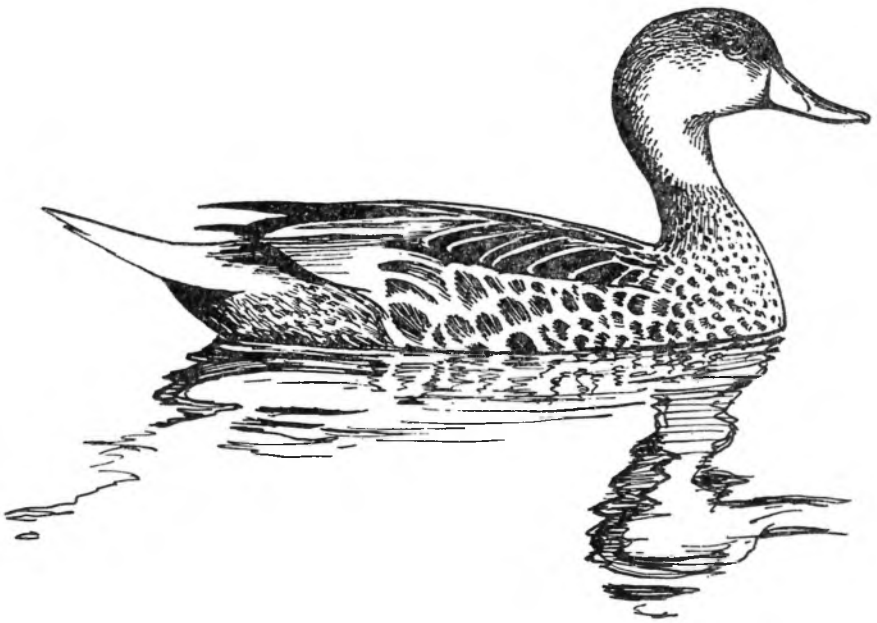

# The endemic ducks of remote islands

DAVID LACK

## Introduction

This paper is concerned with all those ducks which have formed distinctive subspecies restricted to one particular small and remote island or archipelago. Only dabbling ducks in the genus *Anas* are involved. Many species in this genus have an extremely wide range, but the average number of subspecies *per* species is as low as 1.9 for the 38 species recognised by Delacour (1954-64). Hence the fact that nearly all the ducks on remote small islands are separate subspecies means that, for ducks, they belong to relatively isolated populations. In contrast, on some of the archipelagos concerned, notably the Hawaiian Islands and Galapagos, various of the land birds are distinctive species or even genera. Ducks evidently wander widely and frequently, being helped by their powerful flight and their ability to settle on the sea.

## The islands and species concerned

The islands concerned, all either tropical or subantarctic, are set out in Table I, with the names and measurements of the resident forms of *Anas*. On large islands and on islands near continents many species of ducks coexist. For instance, 13 species, 7 in the genus *Anas*, breed regularly in Britain (Parslow 1967), 16 species, 6 in the genus *Anas*, in Iceland (F. Gudmundsson pers. com.), 8, 5 in the genus *Anas*, in the Falkland Islands (Cawkell and Hamilton 1961) and 7, with 2 more in the nineteenth century, 4 in the genus *Anas*, in New Zealand (Williams 1964). Some of the Falklands and New Zealand forms are endemic, not so those of British or Iceland. Although the various species of ducks look superficially alike, especially when seen together in a collection of living waterfowl, they have in fact evolved an adaptive radiation within the limits imposed by their aquatic life, and even the species of *Anas* evidently differ sufficiently in feeding habits for up to six to coexist in the same area (Olney 1965).

In contrast, on the remote small islands set out in Table I, only a single species of duck breeds, on Hawaii, Laysan, Washington (in the Line archipelago), the

**Table I. Ducks in the genus *Anas* on remote islands.**

| | | *male wing length in mm.* | *male culmen in mm.* | *female body weight in gm.* | *clutch* | *weight of egg in proportion to body weight* |
|---|---|---|---|---|---|---|
| TROPICAL ISLANDS | | | | | | |
| *A. platyrhynchos* MALLARD | | | | | | |
| *A. p. laysanensis* | LAYSAN | 201 | 39.5 | 450 | 5 | 10.9% |
| *A. p. wyvilliana* | HAWAII | 220 | 46 | 500 | 8 | 8.5% |
| nominate | northern | 265 | 53 | 1000 | 11 | 5.4% |
| *A. strepera* GADWALL | | | | | | |
| *A. p. couesi* | WASHINGTON (Line Is.) | 199 | 37 | — | — | — |
| nominate | northern | 271 | 41.5 | — | — | — |
| *A. bahamensis* BAHAMA PINTAIL | | | | | | |
| *A. b. galapagensis* | GALAPAGOS | 203 | 42.5 | — | — | — |
| nominate | S. America | 214 | 43 | — | — | — |
| *A. gibberifrons* GREY TEAL | | | | | | |
| *A. g. remissa* | RENNELL (Solomon Is.) | 187 | 33 | — | — | — |
| *A. g. gracilis* | Australasia | 202 | 39 | — | — | — |
| SUBANTARCTIC ISLANDS | | | | | | |
| *A. acuta* (NORTHERN) PINTAIL | | | | | | |
| *A. a. eatoni* | KERGUELEN & CROZETS | 218 | 32 | 450 | 4-5 | — |
| nominate | northern | 271 | 54 | 700 | 8 | — |
| *A. georgica* CHILEAN PINTAIL | | | | | | |
| *A. g. georgica* | SOUTH GEORGIA | 217 | 34 | 465 | 5 | 8.0% |
| *A. g. spinicauda* | S. America | 245 | 42 | 706 | 8 | 6.0% |
| *A. castanea* CHESTNUT TEAL | | | | | | |
| *A. c. aucklandica* | AUCKLANDS & CAMPBELLS | (136) | 40 | 400 | 3-4 | c.18.0% |
| *A. c. chlorotis* | New Zealand | 199 | 44 | 590 | 6 | 10.5% |
| *A. c. castanea* | Australia | 218 | 41.5 | 500 | 9 | 8.0% |

Notes: *A. s. couesi* is now extinct. Delacour (1954-64) admitted a separate subspecies near to *A. a. eatoni* on the Crozets and another near to *A. c. aucklandica* on Campbell Island, but these cannot be sustained. He also treated *A. aucklandica* (including the form *chlorotis* in New Zealand) as a separate species from *A. castanea*, but I have followed Frith (1967) in regarding them as conspecific.

These are the only breeding ducks on the islands concerned except for the Grey Duck *A. superciliosa*, of which the New Guinea-Polynesian form *A. s. pelewensis* (male wing 245 mm., culmen 20.5 mm. and female weight 670 gm.) breeds on Rennell, and the New Zealand form *A. s. superciliosa* (male wing 259 mm., culmen 51.5 mm. and female weight 1000 gm.) breeds on the Aucklands.

The measurements of male wing length and male culmen are the middle points between the extremes given by Delacour (1954-64) and the weights are from Lack (1968), assembled by J. Kear.

Galapagos, Kerguelen, the Crozets and South Georgia, and only two on Rennell and the Aucklands. The second species on the two latter islands is the Grey Duck *A. superciliosa*, which is not endemic on either, and which ranges widely over Polynesia, New Guinea and Australasia, and has recently colonised the only important subantarctic island, Macquarie, which does not have an endemic duck (Carrick 1957). *A. superciliosa* is decidedly larger than the other species with it on Rennell and the Aucklands (see note to Table I).

At least in Hawaii, Laysan, the Line islands and the Galapagos, the existence of only one resident species of duck is not due to the failure of other species to get there. Twelve other species, 8 in the genus *Anas*, have occurred in the Hawaiian archipelago, usually in winter, namely Pintail *Anas acuta* (regular), American Wigeon *A. americana*, Green-winged Teal *A. crecca*, Shoveler *A. clypeata* (regular), Blue-winged Teal *A. discors*, European Wigeon *A. penelope*, Northern Mallard *A. p. platyrhynchos* (the presumed ancestor of the resident endemic), Garganey *A. querquedula*, Lesser and/or European Scaup *Aythya affinis* and/or *A. marila*, Canvasback *A. valisineria*, Bufflehead *Bucephala albeola* and Ruddy Duck *Oxyura jamaicensis* (Udvardy 1961a, b; Clapp and Sibley 1967), while one migrant duck, *Anas discors*, is regular in the Galapagos (Leveque *et al.* 1966). That, despite these periodic visitors, there is only one resident species of duck in each of these archipelagos presumably means that there is an ecological niche for only one and that, once established. it can exclude the rest. The resident Gadwall *A. strepera* on Washington Island is now extinct, and it will be interesting to see whether one of the other six species of *Anas* recently recorded from the Line archipelago will become resident there.

The mainland species from which each of these island forms evolved are named in Table I. The only uncertain identification is that of the Laysan duck as a form of the Mallard *A. platyrhynchos*, but the Hawaiian form is intermediate between them in appearance, and some males of the latter have the characteristic plumage pattern of the northern race of the Mallard. The latter point suggests that the Hawaiian form is derived from the Northern Mallard, not the Mexican subspecies, as the latter lacks distinctive male plumage. The Laysan form could well be derived from the Hawaiian form, rather than from one of the continental forms independently.

Delacour (1954-64) followed other authors in treating the Auckland Island Teal as a separate species from the Australian Chestnut Teal *A. castanea*, but this is a purely taxonomic decision, and it is generally agreed that these two forms are closely related; following Frith (1967) they are here regarded as conspecific, together with the intermediate New Zealand Brown Teal, which is presumably the immediate ancestor of the Aucklands form. Each of these island ducks belongs to a species resident on the nearest mainland, except for the unlikely occurrence of the Northern Pintail *A. acuta* on Kerguelen and the Crozets, but this island form at times shows the male plumage pattern characteristic of *A. acuta*, so the identification can hardly be doubted. The Galapagos form of the Bahama Pintail *A. bahamensis* and the Rennell form of the Grey Teal *A. gibberifrons* are much less distinctive than the other island ducks discussed in this paper.

Perhaps the most striking point brought out by Table I is that, while there is only one endemic form on each of the archipelagos concerned, it is in each case derived from a different mainland species (except that both Laysan and adjacent Hawaii have the Mallard *A. platyrhynchos*). This state of affairs has perhaps arisen through the historical factor of which species happened to arrive and to become established first.

**Differences in ecology and feeding**

The continental species of *Anas*, including those from which the island forms were derived, live primarily in fresh waters and eat primarily vegetable matter, and all except one of the island forms do likewise. Most of them, however, appear to have a wider range of feeding habits than their respective mainland forms. Thus the *A. platyrhynchos* of Hawaii eats not only plant foods but many molluscs (Delacour 1954-64). The *A. acuta* of Kerguelen feeds mainly on inland waters and lagoons but also on the sea shore, and takes a much higher proportion of animal food, chiefly crustacea, than the mainland form (Paulian 1951; Milon and Jouanin 1953). The *A. georgica* of South Georgia likewise feeds partly on the shore and takes more animal food than the mainland form (Murphy 1936), and *A. castanea* of the Aucklands often feeds on the sea, in the areas of kelp (Oliver 1955). The exceptional form is *A. platyrhynchos* of

Laysan, which often swims, but which feeds almost entirely on land, on lepidopterous larvae, adult Diptera and other insects picked from the vegetation. Hence it has a different and more specialised niche than continental *A. platyrhynchos* (Warner 1963).

### Size and proportions

As also shown in Table I, the five island ducks for which the weight is known are much lighter than their presumed mainland ancestors, the reduction being to just under a half in the *A. platyrhynchos* of Laysan, to one-half in the *A. platyrhynchos* of Hawaii, and to two-thirds in the *A. georgica* of South Georgia and the *A. castanea* of the Aucklands. Similarly the wing of the insular form is in every case shorter than that of the presumed ancestor, the reduction being to two-thirds in *A. castanea* of the Aucklands, three-quarters in *A. platyrhynchos* of Laysan and *A. strepera* of Washington, four-fifths in *A. platyrhynchos* of Hawaii and *A. acuta* of Kerguelen, and 93-95% in *A. bahamensis* of Galapagos and *A. gibberifrons* of Rennell. The shorter wing length at least in part reflects the overall reduction in size already mentioned, except for a disproportionately short wing in the *A. castanea* of the Aucklands which is usually described as flightless (though Oliver (1955) has questioned this).

All these island ducks are about the same size. Their mean weights vary only between 400 and 500 grams (but several have not been weighed) and their mean wing lengths, omitting the flightless *A. castanea* of the Aucklands, vary only between 187 and 220 mm. Some forms have undergone a much greater proportionate reduction in size than others, but this is probably due, not to the length of time for which each has been isolated, but simply to the size of their respective ancestors. A medium-size *Anas* is evidently the most efficient kind of duck where it is the only resident species on a remote island, and this size has been evolved irrespective of the size of the ancestral form.

In most of these island ducks, the culmen and tarsus are smaller than in the mainland form, roughly in proportion to the overall reduction in size. However, the culmen is proportionately shorter in the *A. acuta* of Kerguelen than in the mainland form (0.15 of the wing length as compared with 0.20 in the mainland form), which might be adapted to this form's habit, already mentioned, of taking many small crustacea. Again, the Aucklands duck has a narrower beak than the Australian and New Zealand forms of *A. castanea*, but whether this is related to its diet is not known. The *A. platyrhynchos* of Laysan has, as might be expected from its terrestrial habits, a proportionately longer tarsus than the mainland form, the Hawaiian form being intermediate (the tarsus is 0.19 of the wing length in the Laysan, 0.17 in the Hawaiian, and 0.16 in the mainland form; measurements from Delacour (1954-64)).

### Colouring

The females of the island ducks have generally similar colouring to the females of their mainland ancestors, though sometimes with a minor difference in shade. In addition, the brightly coloured mirror or speculum on the wing is less glossy and/or has smaller white outer bars than in the respective mainland forms, in the *A. platyrhynchos* of Hawaii and Laysan, the *A. strepera* of Washington, the *A. castanea* of the Aucklands and probably the *A. georgica* of South Georgia. The speculum is thought to help in specific recognition, so it is probably less needed in island forms living away from other species than in mainland species living alongside several congeneric species. Sibley (1957) ascribed a similar function to the head markings of *A. bahamensis*, which are likewise less clear-cut in the Galapagos form than in that on the mainland, and the same applies to the Auckland Islands as compared with the New Zealand *A. castanea*.

The distinctive male plumage of many species of *Anas* is likewise attributed to the need for the female to select a male of her own species (e.g. Sibley 1957). Hence it is suggestive that while mainland *A. platyrhynchos*, *A. strepera*, *A. acuta* and *A. castanea* have distinctive male plumage, such plumage is entirely absent in both *A. platyrhynchos* of Laysan (though some males retain a curly tail) and in the single collected male of the *A. strepera* of Washington, while it is absent in many adult males of the *A. platyrhynchos* of Hawaii, the *A. acuta* of Kerguelen and the *A. castanea* of the Aucklands, while others have a dull version of the male plumage pattern. In the other species concerned, the male and female plumages are alike in the mainland form, so it is of no special significance that this also holds for the island form.

There is a general tendency for male birds to lose their distinctive plumage on remote islands, presumably because the reduced number of resident species means that specific recognition is less critical there (Mayr 1942; Lack 1947). The position is complicated in waterfowl, however, because most tropical ducks and many in the southern hemisphere, also lack distinctive male plumage. The reason is not known, but a similar reduction in distinctive male plumage is found in various passerine genera in the tropics compared with northern America (Hamilton 1961; Hamilton and Barth 1962).

**Breeding**

Also set out in Table I is another example of convergent evolution among the island ducks, their common tendency to have proportionately larger eggs and smaller clutches than the related mainland forms. The smaller clutch might be necessitated by the larger eggs, and the latter might be advantageous because the young are larger at hatching and so survive better if feeding conditions are less favourable than on the mainland. Ripley (1960) noted the unusually large eggs and ducklings of *A. platyrhynchos* of Laysan.

**Other island waterfowl**

To complete this account, two more endemic island forms of *Anas*, *A. theodori* on Mauritius and *A. pachyscelus* on Bermuda, perhaps also *Pachyanas chathamica* on the Chatham Islands, are known from subfossil remains but are now extinct (Howard in Delacour 1954-64). This author also listed various extinct island forms in other genera of Anatidae. The only other living anatid on a remote island is the Hawaiian Goose *Branta sandvicensis*, which is largely terrestrial and has specialised feeding habits (Miller 1937). It is probably derived from the Canada Goose *B. canadensis*.

**Discussion**

The ducks on small remote islands provide a striking parallel with the land birds of such islands discussed elsewhere (Lack 1969a). First, there is a big reduction in the number of resident species compared with the nearest mainland. Secondly, this cannot be attributed to difficulties of dispersal, since many ducks, in addition to the resident species, have been recorded on all the islands which have been frequently visited by ornithologists. The only reasonable explanation, as for the land birds on islands, is that many visiting species are prevented from establishing themselves through competition by the resident species. This is presumably because remote islands provide much more limited ecological opportunities than the mainland, so that a species with a broad niche is, in general, more efficient than a greater number with more specialised niches (*cf.* MacArthur and Levins 1967). Hence the adaptive radiation of the genus *Anas* on the continents goes into reverse, so to speak, on small and remote islands, and the end result is one medium-sized form with an unusually wide range of foods. In the same way, there are fewer species of Darwin's finches in the genus *Geospiza* on the small and remote than the large and central Galapagos islands, and some of these combine feeding niches filled by two separate species on the large central islands (Lack 1969b).

On small and remote islands, the niche for a duck is evidently filled most efficiently by a species of *Anas*, and, as just mentioned, this is of medium size, irrespective of the size of the presumed mainland ancestor. That the ancestral species is different on seven of the eight island groups concerned is presumably due to the historical accident of which species first colonised. That, nevertheless, all these species are of similar size is presumably due to convergent evolution.

The fact that two species of *Anas* coexist on Rennell and the Aucklands requires study; one is decidedly larger than the other, so they presumably differ sufficiently not to compete. There are parallels to this situation in land birds on islands, notably in White-eyes (Zosteropidae). Where ducks are exceptional is in having many species on certain larger islands, notably Iceland, and to a smaller extent the Falklands, both of which have relatively few land birds. Presumably the ecological opportunities for ducks are unusually favourable there; certainly this seems to be the case in Iceland. However, this suggestion needs testing by comparative measurements of the richness and diversity of the inland waters on the islands and on the adjoining continents, and until this has been done, the views put forward here are speculative.

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**Summary**

1. Eight endemic subspecies of ducks *Anas*, derived from seven mainland species, occur on remote tropical or subantarctic islands.
2. On most of these islands there is only one species, which is of medium size, irrespective of the size of the mainland form, and except in one case has a generalised diet. The males, and some of the females, tend to lose their specific recognition marks.
3. Many other species of ducks have reached the islands concerned, and they are presumably prevented from establishing themselves because, where ecological diversity is reduced, one species with a broader niche excludes a greater number of specialists.

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