THE DISTRIBUTION AND TAXONOMY OF OYSTERCATCHERS

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ABSTRACT

Basic information on the distribution of members of the genus *Haematopus* is reviewed and the taxonomy of the group is discussed. The distinctions between species and subspecies are stressed and applied to the classification of Oystercatchers; alternative taxonomic rank is suggested for some forms, but the ideas require testing in the field.

INTRODUCTION

Oystercatchers are a cosmopolitan group of wading birds, found on the temperate or tropical shores of every continent except Antarctica. They are conspicuous by their large size, shrill cries and, not least, by their striking plumage. Most forms are pied but a few are completely black. Throughout most of their range they are coastal, with inland range extensions in certain regions.

The classification of Oystercatchers within the family Haematopodidae has been the subject of controversy, the main point of confusion being the differentiation between species and subspecies. It may therefore be of use at this time to survey the general taxonomy of the family, taking as a starting point Peters' classification (1934) in which Oystercatchers are arranged in four species, each with a number of subspecies, thus:

Family Haematopodidae:

1. *Haematopus ostralegus bachmani**
   frazari
   palliatus
   prattii
   galapagensis
   pitanay
   durnfordi
   ostralegus
   H. o. occidentalis
   malacophaga
   longipes
   osculans
   meade-waldoi
   *moquini**
   longirostris
   *unicolor**
   chathamensis
2. *Haematopus fuliginosus fuliginosus**
   *ophthalmicus**
3. *Haematopus leucopodus*
4. *Haematopus ater**

(Black forms marked with an asterisk)

This scheme is basically acceptable, although the subspecies of *ostralegus* have been arranged in a number of ways. The position is complicated by the existence of black and melanistic populations, regarded by some as mutants — and hence as subspecies (e.g. Stresemann 1927), and by others as distinct species (e.g. Bent 1929; Gill 1936).

An acceptable definition of a species has been given by Mayr (1940, 1963). If a group of populations is capable of interbreeding with a second group, then they both belong to the same species; they may in fact be prevented from interbreeding by geographic isolation, but as Mayr states (1940) it is " necessary to leave to the judgement and systematic tact of the individual taxonomist whether or not he considers two particular forms as ' potentially capable ' of interbreeding; . . . whether he considers them as species or subspecies." Mayr expanded this idea further (1963) and stressed that subspecies are to be distinguished only if they differ by diagnostic morphological characters; they must also inhabit definite geographical sub-divisions of the species' range. Thus at the present time, species are separated on the basis of interbreeding potentialities and subspecies are distinguished by morphological features and geographical distribution.

In the absence of contrary evidence, the ideas in this paper are based on the following points:

(a) forms with sympatric (overlapping) ranges are distinct at the species level and are able to co-exist by the subdivision of the habitat in time and/or space;

(b) forms with allopatric (exclusive) ranges (see Cain 1954) can be either distinct at the subspecific or specific level. It is more likely that two forms with adjacent ranges will be separate subspecies, being prevented from occupying the same range by the threat of competition; in the case of two forms whose ranges are not contiguous, rank has to be decided arbitrarily as a taxonomic expedient.

DISTRIBUTION (see Figure 1)

South America:

The distribution of Oystercatchers in this region is summarised by Goodall *et al.* (1951). Three forms are known: *H. ostralegus pitanay, H. ater* (black) and *H. leucopodus.* Along the western seaboard of S. America *pitanay* overlaps with *ater,* but although *ater* continues around the southern tip of the continent and up the eastern side, *pitanay* is here replaced by *leucopodus.* Thus *pitanay* and *leucopodus* may be considered allopatric.

Australia:

There are two species (Condon & McGill 1960; Rutgers 1967): *H. o. longirostris* (pied) occurs right around the continent; *H. fuliginosus fuliginosus* also is found on all Australian shores except those in the Gulf of Carpentaria where it is replaced by *H. fuliginosus ophthalmicus.*

New Zealand:

The Oystercatchers of New Zealand have recently been described by Falla *et al.* (1970) who noted three separate species: *H. reischeki, H. finschi* and *H. unicolor.* Peters (1934) incorporated all these into one single species *H. ostralegus unicolor. H. finschi* is very similar in

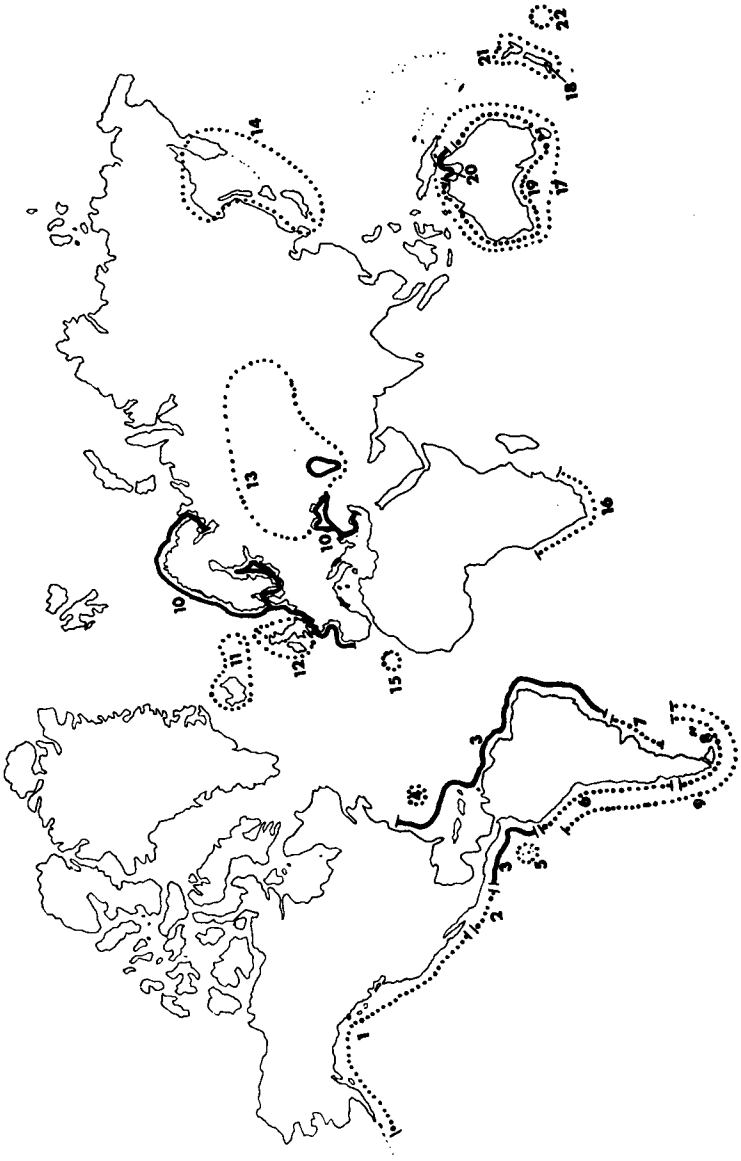

FIGURE 1 — World distribution of Oystercatchers (after Larson 1957)

Key

1 *Haematopus ostralegus bachmani*
2 *H. o. frazari*
3 *H. o. palliatus*
4 *H. o. prattii*
5 *H. o. galapagensis*
6 *H. o. pitanay*
7 *H. o. durnfordi*
8 *H. leucopodus**
9 *H. ater*
10 *H. o. ostralegus*
11 *H. o. malacophaga**
12 *H. o. occidentalis*
13 *H. o. longipes*
14 *H. o. osculans*
15 *H. o. meadewaldoi**
16 *H. o. moquini**
17 *H. o. longirostris*
18 *H. o. finschi*
19 *H. fuliginosus fuliginosus*
20 *H. fuliginosus ophthalmicus*
21 *H. unicolor*
22 *H. unicolor chathamensis**

* see text

appearance to *H. ostralegus* of Europe and indeed some authors (e.g. Sibson 1966) refer to it as *H. o. finschi. H. reischeki* is a melanistic type with individuals ranging in plumage colour from pied (similar to *finschi*) to entirely black forms not unlike the third N.Z. type, *unicolor,* a black Oystercatcher with which it is sometimes confused. Thus *reischeki* forms an almost complete connecting link between the pied and black populations of the islands.

The Chatham Islands (400 miles from the mainland) have a form of their own, *chathamensis,* which shows small but consistent morphological differences from *finschi* (Fleming 1939; Falla *et al.* 1970). Its breeding has not yet been documented.

Europe:

There are three subspecies according to Peters (1934). The British form *H. o. occidentalis* is very similar in appearance to the continental form *H. o. ostralegus* which breeds from Archangel (USSR) to Spain. *H. o. malacophaga* is found in Iceland and the Faeroe Is, in which latter place the Oystercatcher has become a national emblem (Williamson 1948).

North and Central America:

Five subspecies of *H. ostralegus* exist, one of which, *bachmani,* is black. All have allopatric ranges and there are no grounds to question the systematic status given to them by Peters (1934); consequently they will not be considered in the discussion following.

A number of other, isolated, forms of Oystercatcher are known to exist: *H. o. longipes* breeds near inland waters of south-east Russia and Siberia (Grote 1931), a distribution thought to be a relict from the Pliocene era when this region formed part of a vast inland sea (Voous 1960); *H. o. osculans* is found in the Far East, where it breeds along the shores of Korea, China and Japan. Fisher (1967) considers that this form, too, is a relict distribution from past ages; *H. o. galapagensis* — the Galapagos Is; *H. o. prattii* — the Bahamas; *H. o. meadewaldoi* is a subspecies of dubious existence, having been sighted in the Canary Is. only four times, between 1889 and 1913. It is probable that these records represent vagrants of the South African Oystercatcher (Etchecopar & Hue 1967), but Bannerman (1963) argues that on account of the smaller size of *meadewaldoi* it should be classed as a subspecies of the South African Oystercatcher, considered by Gill (1936) and Hall (1959) to be a separate species, *H. moquini,* though Peters treats it as a subspecies of *H. ostralegus.*

DISCUSSION

A striking impression of the general allopatric nature of Oystercatcher distribution is given in Fig. 1. In no area are three forms found together and there are only four instances of overlap:

(a) *H. fuliginosus* and *H. o. longirostris* — there are no details of comparative breeding but the fact that one is black *(fuliginosus)* and the other pied suggests that interbreeding would be rare and that they are probably separate species.

(b) *H. o. pitanay* and *H. ater.*

(c) *H. leucopodus* and *H. ater* — of these last three forms only *ater* is black and the argument put forward under (a) applies.

(d) *H. o. finschi* and *H. o. unicolor* — these species breed in entirely different habitats.

In all these cases one member of the pair of sympatric species is black or nearly so. This may be a gamosematic character sufficiently distinct to effect reproductive isolation in the areas of range overlap (Lack 1940). The sexually-oriented displays of one species would fail to elicit the appropriate response from the second species on account of plumage colour. Besides this plumage factor, two species may be reproductively isolated as a result of certain evolutionary factors, in particular the timing of the ' arrival ' of the pairs of species in any given area, a matter which Larson (1957) has discussed in some detail.

He suggested that the ancestral Oystercatchers originated in Eurasia with a black plumage and from this stock emigrants moved south during the Pliocene era (12 million years ago) becoming established as isolated new species. Many of the original, northern, stock then mutated to light (pied) forms, which possibly have selective advantages over the dark forms (Larson 1957) and the new species *H. ostralegus* was formed. During the Pleistocene era some of these new forms moved south and settled, as secondary immigrants, either where no earlier (black) immigrant had become established, or in areas where the earlier form had evolved to such an extent that the two forms were able to co-exist. If Larson's ideas hold good, then all species other than *ostralegus* should have black plumage, having originated from the black ancestor of the Pliocene. This is indeed so — with one exception, *H. leucopodus* of S. America and the Falkland Islands.

South Atlantic Oystercatchers:

That *H. leucopodus* is a different species from its compatriot *H. ater,* can be accepted on the grounds that interbreeding is unknown and that they co-exist peacefully (Mr I. Strange, pers. comm.). However, the evidence upon which it is given completely separate specific status is lacking. Follow Larson's interpretation of Oystercatcher evolution; if *leucopodus* were an early immigrant it would have a black plumage, but if it was one of the later, secondary, immigrants, it would probably have stemmed from the pied stock of *H. ostralegus.* There is thus some justification for reconsidering the taxonomic position of *leucopodus,* which should be classed as a separate subspecies of *H. ostralegus; leucopodus* is a pied Oystercatcher closely resembling *H. ostralegus* in appearance and its two adjacent neighbours are both subspecies of *ostralegus* viz *pitanay* and *durnfordi.* Their contiguous ranges suggest that they are all closely related and that competition would occur if they met.

Isolated Oystercatcher groups:

With limited opportunities for gene-exchange with neighbouring populations, such groups are probably correctly given subspecific status viz *H. ostralegus galapagensis, H. o. longipes, H. o. osculans, H. o. prattii, H. o. meadewaldoi* (see above) and *H. o. chathamensis* (see below). The South African Oystercatcher, in view of Larson's work (1957), should be classed as a separate species, *H. moquini.* The status of *H. o. malacophaga* is open to question. This form vacates its breeding grounds in Iceland and Faeroe to winter with British birds in the Irish Sea (Dare 1970) but as yet there is no evidence of any consistent morphological differences between the two groups; the existence of a separate subspecies here must be considered as doubtful.

New Zealand Oystercatchers:

The status of Oystercatchers on the mainland of New Zealand is complicated by the existence of three types, pied *(finschi),* black *(unicolor)* and one of intermediate plumage *(reischeki).* The breeding grounds of *reischeki* and *unicolor* overlap, both are coastal breeders and mixed breeding pairs are not uncommon. *H. finschi,* however, tends to breed in an entirely different habitat along the river valleys of the South Island, a habit very similar to that of *H. ostralegus occidentalis* in inland areas of Scotland (Heppleston 1972). The taxonomic problem is whether they all be designated as separate species (e.g. Falla *et al.* 1970) or as subspecies under other species. Oliver (1930) in one of the first reviews of New Zealand Oystercatchers, recognized two species, *ostralegus* (pied) and *unicolor* (black), stating that *reischeki* and *finschi* represented hybrids of these two species. Later (Oliver 1955) he added another species, *longirostris* (pied) and upgraded *finschi* to a subspecies of *ostralegus,* leaving as before *reischeki* as a hybrid. In a classic work Falla (1939) considered them all as separate species, *H. finschi, H. reischeki* and *H. unicolor,* a classification followed by Falla *et al.* (1970). Since taxonomic positions depend on morphological characteristics and whether or not interbreeding occurs or is likely to occur, it is necessary to consider the problem from these standpoints.

Interbreeding has been known to occur between black *(unicolor)* and mottled *(reischeki)* Oystercatchers (Brathwaite 1950; Falla 1939) which suggests that the parents were both of the same species. Interbreeding has *not* been reported as occurring between other NZ Oystercatchers e.g. pied *(finschi)* and black *(unicolor).* Furthermore, these latter two forms breed in different habitats and have greatly differing plumage; *finschi* is morphologically and behaviourally very similar to the European *H. ostralegus.*

I take the view that, in the absence of sound breeding data, it is undesirable to assign birds to new species when there may be good grounds for placing them in new subspecies under existing species.

In other words, taxonomists should consider them for specific status (with confirmed breeding data) only when the possibilities for subspecific status have been exhausted. Following this approach the New Zealand Oystercatchers are grouped thus:

Haematopus ostralegus finschi — South Island Oystercatcher

Haematopus unicolor with two subspecies:

H. u. unicolor — Black Oystercatcher

H. u. reischeki — Variable Oystercatcher.

This arrangement is an extension of that put forward by Larson (1957) and is followed in the latest ornithological checklist of New Zealand birds (OSNZ 1970). Further research on the taxonomic status of *reischeki* is, however, desirable and it is possible that *reischeki/unicolor* plumage patterns are under a complex genetic control system similar to that described for Arctic Skuas *(Stercorarius parasiticus)* on Fair Isle, Scotland, where there are dark, pale and intermediate morphs of one species (Williamson 1965).

The Chatham Is Oystercatcher has been variously described as a separate species (Falla 1939; Fleming 1939) and as an outlying group of the North Island Pied Oystercatcher (Oliver 1955). However, owing to its morphological similarities to *H. ostralegus,* it is probably more correct to ascribe it to this species, as *H. ostralegus chathamensis* as do Peters (1934) and Hartert (1927 *in* Falla 1939); this satisfies the conditions stated by Mayr (1963) with regard to the description of subspecies (see Introduction).

Future Research:

Three situations, forming an evolutionary series, deserve particular attention:

1. Scotland — one species breeding in two different habitats, coastal and inland (Heppleston 1972).
2. New Zealand — two species breeding in separate habitats, coastal and inland.
3. Falkland Is — two species breeding in one habitat, coastal.

Scotland — the division of breeders into coastal and inland populations represents an ecological isolating mechanism which, if maintained, could lead to complete speciation. The initial divergence may have already brought about a certain degree of genetic isolation which could be tested by analysis of egg albumen proteins, as has been done with the Eider *(Somateria mollissima)* (Milne & Robertson 1965). *New Zealand* — it is suggested that the later arrival (pied) was sufficiently dissimilar to the earlier immigrant (black *unicolor*) that interbreeding was precluded, but at the same time was similar in enough respects that co-existence was prevented by competitive factors. Thus the pied forms *(finschi)* was forced inland where it now breeds. This represents an intermediate situation.

Table 1 - Suggested taxonomic revision of some members of the genus *Haematopus*.

	Peters (1934)	Larson (1957)	Recent works	Present work
moquini	*H. ostralegus moquini*	*H. ostralegus moquini*	Hall 1959, *H. moquini* (also Gill 1936)	*H. moquini* (based on Larson's hypothesis)
meadewaldoi	*H. o. meade-waldoi*	*H. o. meade-waldoi*	Bannerman 1963, *H. moquini meade-waldoi*	*H. moquini (? H. moquini meadewaldoi)*
malacophaga	*H. o. malacophaga*	*H. o. malacophaga*		existence doubtful
leucopodus	*H. leucopodus*	*H. leucopodus*		*H. o. leucopodus*
finschi	incorporated into *H. o. unicolor*	*H. o. finschi*	Sibson 1966; Soper 1963 *H.o. finschi*	*H. o. finschi*
unicolor	*H. o. unicolor*	*H. unicolor*	Falla *et al.* 1970 *H. unicolor; H. reischeki* OSNZ 1970 *H. unicolor unicolor, H. unicolor reischeki*	*H. unicolor unicolor* and *H. unicolor reischeki*
chathamensis	*H. o. chathamensis*	*H. u. chathamensis*		*H. o. chathamensis*

Falkland Islands — the later arrival (pied *leucopodus*) was already so dissimilar from the original immigrant *(ater)* that interbreeding was ruled out, but co-existence was possible as a result of differences in habitat selection, food supply, etc. Thus the two do not compete with each other for essential commodities.

These hypotheses could be tested in the field by making observations on the differences and similarities of the pairs of species in each locality. Detailed information is required on the factors that prevent interbreeding, such as courtship behaviour, and those that have prevented co-existence, e.g. habitat selection and food habits.

CONCLUSIONS

The biological relationships between species and subspecies have been clarified by Mayr (1963) and others; it is now appropriate to re-examine the taxonomic status of members of the Oystercatcher family in the light of the accepted definitions. Such an examination reveals certain irregularities which result from the past use of taxonomic rules of varying validity. I have tried to draw attention to these points and have made suggestions in respect of the status of some forms of Oystercatcher (Table 1).

In reviewing the genus *Haematopus* I have based my arguments to a large extent on those of Gause (1934) who was the first worker to point out that no two species with the same ecological requirements could exist together at the same place and at the same time. It follows that within one genus, those forms with adjacent ranges, that replace each other geographically, are likely to be closely related; likewise those forms with overlapping (sympatric) ranges would exhibit isolating mechanisms enabling them to co-exist peacefully. These hypotheses require testing and in order that the above ideas can carry any weight, they must be substantiated by further evidence from detailed field observations. Until then, all suggestions must be considered only as hypothetical possibilities even though some of them may be highly probable. Knowledge on many aspects of Oystercatcher biology is sadly lacking; in particular much work remains to be done on the inter-relationships of closely allied forms and species; such work is most easily carried out where populations of two different forms are readily accessible e.g. South America and Australia and New Zealand. Oystercatchers are birds which lend themselves admirably to field investigation. Not only are they large and distinctive but they live in open habitats affording favourable conditions for observation. In addition, a large amount of information has been gathered in the past and is available as a sound foundation upon which further comparative studies can be based.

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