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(*Phalacrocorax carbo*) and Shag (*P. aristotelis*)**

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THE ECOLOGY OF CLOSELY RELATED SPECIES WITH SPECIAL REFERENCE TO CORMORANT (*PHALACROCORAX CARBO*) AND SHAG (*P. ARISTOTELIS*)

By DAVID LACK

1. INTRODUCTION

This paper is a sequel to one on the ecological aspects of species formation in passerine birds (Lack, 1944). Gause (1934) contends that two species with similar ecology cannot live in the same area, and in the earlier paper this principle was shown to hold among closely related species of passerine birds, both in Britain and on oceanic islands. Such species either frequent different regions, or different habitats, or, when they live in the same place, they eat mainly different foods, the latter commonly being associated with a difference in body size.

I originally intended to follow this paper with a second one analysing the extent to which the same might apply in British non-passerine birds. Among these birds, examples of closely related species which breed in a similar habitat but in mainly different regions are provided by the mute and whooper swans (*Cygnus olor* and *C. cygnus*), the curlew and whimbrel (*Numenius arquata* and *N. phaeopus*), and the common and arctic terns (*Sterna hirundo* and *S. macrura*). In each of these pairs, the first-mentioned species breeds mainly south of the second. Examples of related species which breed in the same regions but in mainly different habitats include: the long-eared owl *Asio otus* in woods and the short-eared owl *A. flammeus* in open country; the marsh harrier *Circus aeruginosus* in very damp marshland and the Montagu harrier *C. pygargus* in dryer marshland and on heaths; the goosander *Mergus merganser* primarily by swift-flowing streams and the red-breasted merganser *M. serrator* primarily by lochs.

Two species which overlap widely in both region and habitat but differ in food are the hobby *Falco subbuteo* and kestrel *F. tinnunculus*. Both frequent open country with trees in southern England, but the hobby feeds primarily on insects and on small birds caught on the wing, and the kestrel primarily on rodents and to a much smaller extent on small birds and insects caught on the ground. A case of a difference in both habitat and food is provided by the four species of gallinaceous birds in northern Scotland, of which the ptarmigan (*Lagopus mutus*) lives in the alpine zone feeding primarily on *Empetrum* and *Vaccinium*, the red grouse (*Lagopus scoticus*) on moorland feeding primarily on *Calluna*, the black-cock (*Lyrurus tetrix*) on the wood edge feeding primarily on *Betula*, and the capercaillie (*Tetrao*

urogallus) in forest feeding primarily on *Pinus* needles. (Though the two latter species are placed in separate genera from the two former, they are probably closely related. In making generic distinctions, undue weight would seem to have been given to male characters. The females of the four species are rather similar in appearance, while interbreeding has been recorded not infrequently.)

In the earlier paper, instances were also given in which two related passerine species frequent the same habitat, but differ markedly in body-size and in food. British non-passerine birds probably provide several further examples, but in most cases insufficient is known of the food of the birds concerned to say whether or not the size difference is correlated with a difference in diet. Examples are the great and lesser spotted woodpeckers (*Dryobates major* and *D. minor*), mallard and teal (*Anas platyrhynchos* and *A. crecca*), great-crested and little grebe (*Podiceps cristatus* and *P. ruficollis*), little, common and sandwich terns (*Sterna albifrons*, *S. hirundo* and *S. sandvicensis*), and several species of gulls (*Larus* spp.).

The idea of a complete survey of British non-passerine birds was eventually abandoned owing to the many cases in which two closely related species appear to overlap widely in ecology, but insufficient is known to state definitely whether or not this is the case. From the information available in general works on British birds, notably Witherby (1938-41), the following species appear to come in this category: tawny and long-eared owls (*Strix aluco* and *Asio otus*), both living in woods and eating similar prey; teal and garganey (*Anas crecca* and *A. querquedula*) on southern marshes and inland waters; gadwall, wigeon and pintail (*Anas strepera*, *A. penelope* and *A. acuta*) on northern waters; and among sea birds, cormorant and shag (*Phalacrocorax carbo* and *P. aristotelis*), storm and fork-tailed petrels (*Hydrobates pelagicus* and *Oceanodroma leucorhoa*), roseate and common terns (*Sterna dougallii* and *S. hirundo*) and herring and lesser black-backed gulls (*Larus argentatus* and *L. fuscus*).

2. CORMORANT AND SHAG

From the above list, one pair of species has been singled out for detailed analysis. The cormorant and shag are two closely related species, and are suffi-

ciently similar in appearance and habits for inexperienced ornithologists to confuse them in the field. Both are common in Britain and occur round most of the south-west, west and north coasts, but they are absent from most of the east and south-east. Nearly everywhere the shag is much the commoner of the two, but in a few places, such as the Isle of Wight, the cormorant breeds but not the shag. Both species nest on cliffs overlooking the sea, and both feed by swimming under the water for fish. At first sight they appear to overlap widely in ecology, an impression supported by the information in general works on British ornithology. Therefore, since they commonly occur in the same regions, they might be thought to provide an exception to Gause's thesis. Fortunately, sufficient facts are available for a detailed analysis, and this shows that the two species differ widely in both nesting and feeding requirements.

Nesting habitat. Though both species nest on rocky places overlooking the sea, the shag mainly selects caves, holes, hollows among boulders, and narrow cliff ledges. The cormorant, on the other hand, nests chiefly on flat broad cliff ledges and on the flat tops of stacks and islets. Occasionally, as on the Calf of Eday in the Orkneys, the two species nest on the same cliff face; but here the shag nests on the narrow lower ledges and the cormorant on the wide upper ledges and on the flat ground just above the cliff, and there is only an extremely small overlap (Lack, 1943). A similar difference holds for other parts of Europe. For instance, in the Faeroes, Salomonsen (1935) found the shag nesting among boulders at the foot of mountains, and the cormorant on the cliff ledges. On the mainland of Europe, the cormorant also nests inland by fresh waters, sometimes in trees, which the shag does not do.

Food. The information given in general works on British birds and by Collinge (1924-7) suggests that the cormorant and shag eat largely the same types of food. However, Steven (1933) has made a detailed analysis in Cornwall which shows that, here at least, the two species have almost completely different diets, and, moreover, feed mainly in different places. The cormorant feeds chiefly in the shallow waters of estuaries and harbours, also inland on large rivers and on reservoirs. Only occasionally does it forage farther out at sea. On the other hand, the shag feeds mainly out at sea, and seeks food in estuaries and sheltered waters only during stormy weather. Hence the two species rarely feed together.

In Cornwall the staple food of the shag throughout the year is the sand eel *Ammodytes*. Out of 188 birds examined by Steven, just over half contained *Ammodytes*, and 37% contained nothing else. About one-quarter of the birds contained clupeoid fish, chiefly the sprat *Clupea sprattus*, these fish being taken mainly in winter. On the other hand, only 3% of the birds had eaten flat-fish, though a special effort

was made to obtain shags from estuaries, where they might be likely to feed on them. The number of shags which had eaten shrimps or prawns was also small.

On the other hand, of 27 cormorants examined by Steven, just over half contained flat-fish, 37% contained prawns and shrimps, while only one had eaten a sprat and none had taken sand eels. The diet was almost totally different from that of the shag, but dragonet (*Callionymus*), wrasse (labrids) and gobies

Table 1. *Differences in diet of shag and cormorant*

Based on 188 shags and 27 cormorants examined by Steven (1933).

Food	Percentage of stomachs in which found	
	Shag	Cormorant
<i>Ammodytes</i> spp. (sand eel)	51	—
<i>Clupea sprattus</i> (sprat)	11	4
Pleuronectids (flat-fish)	3	52
Crangonidae (shrimps)	3	33
Palaemonidae (prawns)	5	15
<i>Ctenolabrus rupestris</i> (gold-sinny wrasse)	13	17
<i>Labrus bergylta</i> (ballan wrasse)	6	15
<i>Callionymus</i> spp. (dragonet)	10	11

Food	No. of individuals of each food species, expressed as percentage of all individuals present	
	Shag	Cormorant
<i>Ammodytes</i> spp. (sand eel)	33	—
Small Clupeoids (sprat, sardine, brit)	49	1
Pleuronectids (flat-fish)	1	26
Palaemonidae (prawns) and Crangonidae (shrimps)	2	33
Labrids (wrasse species)	7	5
<i>Gobius</i> spp. (goby)	4	17
Other kinds	4	17

Note. In Part B, the high total of small clupeoids in the shag stomachs is due to the fact that two individuals between them contained 350 brit. If these had been omitted, the figures for the shag would have been *Ammodytes* 45%, small clupeoids 31%.

(*Gobius*) were taken in small numbers by both birds. The diet of the cormorant in fresh water was not examined by Steven; the eel *Anguilla anguilla* is known to be a favourite food. The shag does not normally feed in fresh water.

Steven's data show a further difference in the feeding habits of the two species, since the cormorant feeds primarily on fish which live on or close to the bottom, while the shag feeds mainly on free-swimming forms. This suggests that the conclusions given

above apply more widely than to Cornwall alone, though a general survey has not yet been undertaken. It would be of particular interest to make a detailed survey throughout the year in a region where the cormorant comes in contact with different species of *Phalacrocorax* as it does in Australia (Serventy, 1938).

3. OTHER SEA BIRDS

A parallel with the cormorant and shag is provided by two other related species of British sea birds, the common guillemot *Uria aalge* and black guillemot *U. grylle*. The former breeds on cliff ledges and the tops of stacks, the latter in crevices and among boulders. The common guillemot feeds out at sea on free-swimming fish, particularly *Ammodytes*, and in America also on lant and capelin. The black guillemot feeds inshore, primarily on the butterflyfish (or rock-eel) *Pholis gunnellus*, which lives on the sea bottom, also on molluscs and Crustacea (Bent, 1919; Salomonsen, 1935; Witherby, 1938-41). Hence these two species, like the cormorant and shag, do not seriously overlap in either nesting sites or food. It is interesting that the common guillemot parallels the cormorant in its nesting but the shag in its feeding, while the black guillemot parallels the shag in nesting and the cormorant in feeding.

In the earlier paper it was concluded that the habitat differences between related species are a result of natural selection, each species being better adapted than the other in the habitat where it normally occurs. Consequent on this, each species has evolved behaviour responses enabling it to select its specific habitat. Hence the individuals of two related species rarely come into competition. However, their ecological differences are a result of former mutual competition, and this competitive element is still potentially present. For occasionally an individual breeds outside its specific habitat, and the reason that such cases do not become commoner is presumably that they are quickly eliminated by natural selection.

A parallel argument doubtless applies to the differences in nesting habitat between related species of sea birds, as it is difficult to see how otherwise such differences could persist. But concrete evidence is lacking. Thus it is difficult to see any character which gives the shag an advantage over the cormorant when nesting in caves, boulders, etc., or any which gives the cormorant an advantage on flat ledges. But if an adaptive difference does not exist, the difference in nesting site between the two species is even harder to explain. In the case of the two guillemots discussed above, a probable adaptive difference is known, since it is usually considered that the pointed egg of the common guillemot is less easily rolled over a cliff edge than is the blunter egg of the black guillemot.

This does not, of course, account for the avoidance of holes and crevices for nesting by the common guillemot.

Sea birds show all the main types of ecological isolation found in passerine birds—by region, by nesting habitat and by food. In one case there is also isolation by breeding season, since Murphy (1938) states that on Kerguelen Island the tern *Sterna virgata* breeds in October and November, while in January and February the same nesting grounds are used by another species, *S. vittata*. *S. virgata* feeds inland on insects and spiders, *S. vittata* at sea, so the two species also differ in food.

4. ECOLOGICAL ISOLATION IN OTHER ANIMALS

The main types of ecological isolation found in birds are also found in mammals. Thus in Scotland the common hare *Lepus europaeus* occurs on low ground and the mountain hare *L. timidus* on high ground. Barrett-Hamilton & Hinton (1913-14) have provided strong evidence that this habitat difference is due to competition, since Hinton's hare *L. anglicus*, which is a form of the mountain hare, was widespread on low ground in Britain during Pleistocene times, but became extinct after the colonization of the common hare. Further, Ireland appears to have been cut off from England before the arrival of the common hare, and, in the absence of the latter species, the Irish form of the mountain hare is common on low ground. Barrett-Hamilton & Hinton have demonstrated a similar situation in the two European bank voles *Clethrionomys (Eutamias) glareolus* and *C. nageri*. In western Europe, at the latitude of Britain, the later arrival *C. glareolus* has eliminated the formerly widespread *C. nageri* from the low ground habitats except on a few outlying western islands, such as Jersey, Skomer, Mull and Raasay. Forms of *C. nageri* persist on high ground in western Europe.

In British mammals there are also parallels with those birds in which two related species occur in the same habitat but differ markedly in size, and by inference in food. Huxley (1942) has cited the common and pygmy shrews (*Sorex araneus* and *S. minutus*), and the stoat and weasel (*Mustela erminea* and *M. nivalis*). An example of four mammal species which live in the same habitat but differ in food was cited in the earlier paper for the four Antarctic seals (Lack, 1944). As discussed more fully in the earlier paper, ecological differences are found between species because, in their absence, one species eliminates the other. An example of such elimination is evidently occurring in Britain at the present time, since the native red squirrel *Sciurus vulgaris* is decreasing rapidly before the introduced grey squirrel *S. carolinensis*.

Ecological isolation is also a widespread phenomenon among closely related species of insects. Thus Elton (1927) cites from Shelford (1907) that of the five species of tiger-beetles (*Cicindela*) found round Lake Michigan, each frequents a different habitat. Likewise in many of the phytophagous insects, related species frequent different food plants. However, there are many other insects in which closely related species appear to feed together on the same food plants. In this connexion, G. C. Varley has suggested to me that if the numbers of two related species are controlled primarily by parasites or predators, then they may be greatly below the limit set by food, so that the two species could live in the same area and eat the same types of food without effectively competing. This type of situation is probably commoner in insects than in birds.

Fresh-water biologists have tended to attribute the habitat differences between species to simple behaviour responses towards temperature, salinity, pH and other physical factors. But though such responses may account for how each species finds and stays in its habitat, it is also necessary to explain the evolution of the behaviour responses concerned. The latter have presumably been brought about through natural selection, those individuals surviving whose behaviour responses have brought them to a favourable environment, and those being eliminated which found unfavourable environments. I formerly made the same omission in interpreting habitat selection in birds (Lack, 1933, 1944). That the presence or absence of related species is one of the most important factors in limiting the habitats of fresh-water organisms has been clearly demonstrated by Beauchamp & Ulllyott (1932) for fresh-water planaria, while another suggestive case is that of the copepod *Eurytemora lacimulata* (Elton, 1927).

It is not the object of this paper to elaborate on ecological isolation in other types of animals or in plants, but merely to draw the attention of specialists in other groups to this problem. Gause's thesis that two species with similar ecology cannot persist together in the same area is logically unassailable when the two species compete for food. Further, it is fully substantiated in wild birds, though superficial appearances often suggest that there is marked ecological overlap—as in cormorant and shag. It would be possible to cite many further cases of ecological isolation in other groups of organisms, but the significant study is to take every species in a whole

group, and to analyse how many of them differ from each other in ecology, and in what ways. Particular attention should be given to cases of ecological overlap, as it is extremely difficult to see how these could occur except (a) temporarily, where one species is in process of eliminating another, (b) in an area where two species meet along an environmental gradient, one end of which favours one species and the other end the other, and (c) where the species do not compete for food, but are kept in check by predators or parasites.

There is the further important problem of how ecological differences arise. Huxley (1942, pp. 265-84), who cites numerous further cases of ecological isolation in both animals and plants, suggests that ecological differences have led to the origin of new species. In birds, on the other hand, I consider that new species have arisen primarily through geographical isolation, and that ecological isolation is enforced through competition when two species later meet in the same area. The arguments for this are set out in the earlier paper, and in more detail in a book (Lack, 1944, and *in press*). The extent to which these views may hold in other animals and in plants is a subject for future research.

5. SUMMARY

1. Many closely related species of British non-passerine birds differ in their ecology, but in other cases there is apparently an overlap.
2. In one case of apparent overlap, that of the cormorant *Phalacrocorax carbo* and shag *P. aristotelis*, close analysis shows that in fact the two species differ markedly in both nesting sites and food.
3. Ecological separation may be through a difference in region, habitat or food, while in one case in terns there is isolation by breeding season.
4. The main types of ecological isolation found in birds are also found in mammals, and the subject should be further investigated both in other groups of animals and in plants.

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