

PLUMAGE AND ECOLOGY OF CORMORANTS

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ABSTRACT

The paper draws on data attending the etho-ecology of four species of cormorants (Phalacrocoracidae) in support of an hypothesis for the adaptive significance of the predominantly dark plumage of these birds. It is suggested that a dark plumage, primarily by being most receptive to solar radiation, assists cormorants in supplementing metabolic heat for maintenance of normal body temperature. In those cormorants which have white extending over ventral and frontal aspects of the body, it is suggested that this is an adaptation to the feeding situation and that it promotes 'hunting camouflage' through countershading.

INTRODUCTION

In a recent review of the adaptive significance of seabird plumage patterns, Simmons (1972) classified species according to the relative amount of dark and light coloration. Simmons argued that all the plumage types in seabirds have been evolved in relation to the feeding situation; and, while other selection pressures must also operate, he suggested that these are of only secondary importance and that adaptations for feeding are primary. Briefly stated, the adaptations take three main forms which need not be mutually exclusive.

1. *Selection for social inconspicuousness*

Evolution of dark or mainly dark plumage which functions to reduce competition between solitary foraging conspecifics.

2. *Selection for social conspicuousness*

Evolution of light or mainly light plumage which functions in promoting social gatherings at food resources.

3. *Selection for hunting camouflage*

Evolution of intermediate plumage with dark and light areas promoting 'hunting camouflage' through countershading.

Simmons (*op. cit.*) assigned all cormorants (Phalacrocoracidae) to either Category 1 or Category 3 in the above classification. Further than that, however, cormorants received no special attention from Simmons, and nowhere did he consider their dark plumage in relation to a situation other than feeding.

The purpose of this paper is to present a restricted, and preliminary, model of the functional

role of plumage in the ecology of cormorants, and to state and to examine some predictions derived from the model. Finally, concepts and hypotheses developed by Simmons (*op. cit.*) are evaluated in relation to the ecology of cormorants.

The paper draws on published data and unpublished information attending a study of the comparative etho-ecology of cormorants in southern Africa. At least four species are involved: Cape cormorant *Phalacrocorax capensis*, bank cormorant *P. neglectus*, white-breasted cormorant *P. lucidus* and crowned cormorant *P. africanus*. All four are marine, coastal species, but *lucidus* and *africanus* have inland, freshwater populations as well. The study is being undertaken by personnel of the Percy FitzPatrick Institute.

THE MODEL

The plumage of cormorants is generally dark and usually black with a greenish or bluish metallic sheen. Sexes are alike, and immature birds are duller and browner than adults. Some species have white underparts to the body region. These white areas occur in the immature and non-breeding plumages of some species which are wholly dark when in adult breeding plumage. Bright colours are restricted to the gular pouch, beak-lining, iris and feet. During the breeding season, some species have feather crests and others have patches of white on the rump, thighs and head (Thomson 1964).

Cormorants are of ancient descent, fossils attributable to the Phalacrocoracidae have been found in Palaeocene deposits (Fisher & Peterson 1964). Cormorants, and their close allies the anhingas (Anhingidae), differ from other diving birds in having plumage with a relatively low level of water repellency (Rijke 1968, 1971). This feature and the close agreement in the general coloration of plumage suggest that a predominantly dark plumage is an adaptation with a function common to all members of the Phalacrocoracidae.

All cormorants hunt by swimming on the surface from which they dive in pursuit of prey under water. Natural selection has shaped cormorants' anatomical, physiological and behavioural characters which contribute to efficient diving ability and under-water foraging (Casler 1973). Pertinent to the model is the fact that in cormorants a reduction of buoyancy is promoted by water absorption by the plumage (Owre 1967; Rijke 1968).

While poor water repellency enhances the cormorant's ability to achieve negative buoyancy, the phenomenon probably imposes a penalty in that water-logging of feathers impairs the bird's thermoregulatory properties, draining body heat and consequently extra energy for maintenance of normal body temperature. This 'trade-off' arrangement forms the basis of the model, and it is suggested that a predominantly dark plumage and black skin primarily by being most receptive to solar radiation assist the cormorant in supplementing metabolic heat for maintenance of normal body temperature.

The full significance of black coloration in relation to sunbathing as a means of supplementing metabolic heat, and consequently conservation of energy, has been appreciated only recently (Ohmart & Lasiewski 1971; Hamilton 1973). In certain cormorants which have white extending over ventral and frontal aspects of the body, it is suggested that this is an adaptation to a feeding situation and that it functions as hunting camouflage (*sensu* Simmons 1972).

PREDICTIONS

The model allows *inter alia* the following predictions.

1. Cormorants should spend relatively brief periods in water.
2. Cormorants should occur relatively close to land.
3. Cormorants with white undersurfaces should feed on relatively active prey.
4. Cormorants with wholly dark plumage should feed on relatively sessile prey.
5. Cormorants should demonstrate relatively low tolerance to intense insolation.

The predictions are examined below, employing information on the ecology of southern African cormorants. In *Phalacrocorax neglectus*, *P. africanus* and *P. capensis* adult breeding birds wear wholly black plumage. In *P. lucidus* the birds have white undersurfaces. (See McLachlan & Liversidge (1970) for further detail on the plumage characters of the four species considered here.)

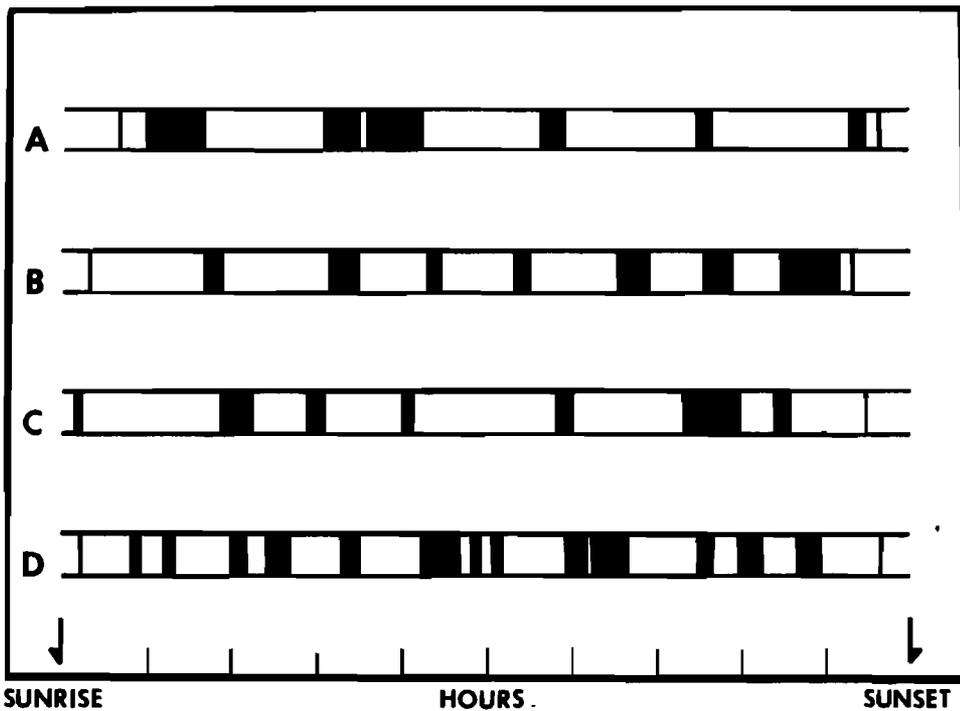


FIGURE 1

In-water (shaded blocks) and out-water (clear blocks) daily time schedule of four individual non-breeding, adult cormorants on an inland body of water. A, B & C, *P. lucidus*; D, *P. africanus*.

Prediction 1

Individual, non-breeding cormorants spend an 'average' day indulging in alternating bouts of intensive foraging in water and longer-lasting comfort behaviour on land (Figure 1). The only time that this sequence is interrupted is when a bird enters the water to bathe or flies to a new feeding and/or resting site. Bathing bouts are typically brief (62 ± 40 seconds, $n = 50$, for *capensis*). In short, time spent in water by cormorants is almost exclusively devoted to feeding activities, normally involving relatively short bouts of intensive diving behaviour (Table 1).

Prediction 2

During 1954–1960 the South African Government Research Vessel *Africana II* made monthly cruises in the neighbourhood of St. Helena Bay (see Marchand (1952) for positions of cruise stations). Cormorants are abundant in this region (Davies 1955, 1958; Rand 1960, 1963). On several stages of the cruises the distribution and numbers of cormorants were regularly recorded by Commander A. Thomas. Additional data for 1958–1968 were made available by Mr. P. Zoutendyk who recorded seabirds whilst cruising with the University of Cape Town's Research Vessel *T. B. Davie* (Zoutendyk 1965). We have recorded cormorants observed during boat trips

TABLE 1

Average duration of complete resting (out of water) and foraging (in water) bouts of non-breeding adult cormorants.

Species	Time (minutes) resting bout				Time (minutes) foraging bout			
	\bar{x}	S.D.	range	n	\bar{x}	S.D.	range	n
<i>capensis</i>	19	8	10–33	26	27	4	20–32	8
<i>neglectus</i>	34	34	9–127	16	41	11	26–58	12
<i>lucidus</i>								
marine	101	70	34–265	23	49	19	29–82	9
freshwater	48	27	11–100	14	16	12	5–43	9
<i>africanus</i>								
marine	39	26	7–96	47	26	3	21–32	9
freshwater	28	20	5–137	71	20	22	5–140	65

between Cape Town and the nearby offshore islands, and have made observations from vantage points on land. Table 2 summarizes these data on the incidence of cormorants in relation to nearest land along the west and south coasts of South Africa. It is evident that the birds generally occur close inshore.

Prediction 3

Phalacrocorax lucidus takes mainly dispersed, active, swimming prey (Rand 1960; our unpublished data).

Individuals of this species tend to forage solitarily and close inshore (Tables 2 and 3).

TABLE 2

Percent frequency of occurrence and percent numerical abundance (figures in italics) of cormorants at sea in relation to distance from nearest land.

Species	Distance (km) from nearest land										Number bird sightings	Number birds
	0-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90	91-190		
<i>capensis</i>	21 <i>66</i>	15 <i>25</i>	4 <i>1</i>	2 <i>6</i>	1 <i>1</i>		1 <i>1</i>				85	3890
<i>neglectus</i>	96 <i>91</i>	4 <i>9</i>									44	60
<i>lucidus</i>	100 <i>100</i>										32	55
<i>africanus</i>	100 <i>100</i>										38	49
Unknown	37 <i>87</i>	24 <i>6</i>	5 <i>1</i>	3 <i>1</i>	2 <i>1</i>	1 <i>1</i>	3 <i>1</i>	3 <i>1</i>	1 <i>1</i>		72	3280
Number observation stations	223	110	99	97	151	44	65	56	72	79		

Prediction 4

Phalacrocorax neglectus and *P. africanus* (in the marine environment) take mainly dispersed, relatively sessile prey (Rand 1960). Individuals of both species tend to forage solitarily and close inshore (Tables 2 and 3). Freshwater populations of *africanus* take mainly slow-moving prey, and individuals normally forage solitarily (Bowmaker 1963).

Prediction 5

Table 1 summarizes data on time spent resting on land in the sun. After bouts of swimming, cormorants move to exposed sites where they perch in the sun. Typically, the individual bird first perches facing away from the sun and indulges in one or more relatively short bouts of wing-spreading. (Wing-spreading is not considered further here, but we regard its function essentially as promoting drying of wet feathers.) Following wing-spreading, the bird continues to perch with its back to the sun for a varying period of time which is influenced by a number of interacting factors, most importantly wind direction and speed, ambient temperature and insolation. Next, the bird turns to face the sun and indulges in gular flutter. Temporal details attending these behavioural changes and differences between species are not treated in this paper. It suffices to say that onset of gular flutter occurs at relatively low ambient temperature (*ca.* 23 °C) on clear

TABLE 3

Typical group size* of cormorants at sea in relation to nearest land. Figures in italics refer to birds observed to be feeding. Sample sizes as in Table 2.

<i>Species</i>	<i>Distance (km) from nearest land</i>							
	<i>0-10</i>	<i>11-20</i>	<i>21-30</i>	<i>31-40</i>	<i>41-50</i>	<i>51-60</i>	<i>61-70</i>	<i>71-190</i>
<i>capensis</i>	376 <i>71</i>	147 <i>193</i>	16 <i>18</i>	40 <i>57</i>	20		23	
<i>neglectus</i>	1 <i>1</i>	1						
<i>lucidus</i>	2 <i>1</i>							
<i>africanus</i>	1 <i>1</i>							

* For computation of 'typical group size' see Jarman (1974).

sunny days, indicating that the birds rapidly build up heat loads under conditions of only moderate solar radiation.

With the exception of *capensis* (see below), the species considered here build substantial nests, raised above the ground, on scattered rocky stacks, pinnacles, ledges of cliffs, in trees and generally in sites exposed to relatively cool air movement. *Phalacrocorax neglectus* tends to nest on the tops of isolated small pinnacles of rock often standing well out to sea and exposed to cool winds and fine spray. The species builds a large and well 'cemented' raised nest. Parents are able to invest considerable time and energy in this construction, presumably because the species feeds close inshore and on food which is not patchily distributed. Indeed, relatively dependable, sustained and evenly dispersed food supplies probably underlie the temporal and spatial patterns of breeding in *lucidus*, *africanus* and *neglectus*. All these species breed in all months, but tend to do so at a low level during the warm time of the year (Rand 1960, 1963).

THE CAPE CORMORANT: AN APPARENT ANOMALY

Phalacrocorax capensis has a wholly dark plumage, yet is extremely gregarious when breeding, roosting and foraging. It feeds on highly active, pelagic, shoaling fish (Davies 1955, 1958; Rand 1960). It nests in dense concentrations of many thousands, building flimsy nests on the ground often located in areas of reduced air movement and high insolation. Breeding is highly synchronized, with peaks during the warmest months of the year (Rand 1960, 1963). Breeding is timed presumably to take advantage of the seasonal availability of abundant shoals of pelagic fish (Cushing 1971).

Because of the somewhat ephemeral and patchily dispersed nature of the food resource, it is thought that selection has favoured highly synchronized, concentrated, mass breeding in *capensis*. Time and effort invested in construction of a nest is reduced, presumably to facilitate rapid exploitation of a favourable food situation which may occur some distance from the nesting site. Failure of the food supply early in the season results in the birds *en masse* not breeding that year or moving elsewhere to breed. Sudden interruption of mass breeding, with desertion of whole colonies of thousands of eggs and chicks, is not an uncommon event (Davies 1958; Rand 1960, 1963).

At other times of the year Cape cormorants extend their range and disperse more widely along the coast but, nevertheless, do so in relatively large flocks (Rand 1960). These phenomena strongly underline the Cape cormorant's specialized, highly social behaviour which is assumed to function in promoting co-operative food-finding and feeding. This imposes a constraint on the availability of suitable nesting areas, and the birds may have little or no choice between attempting breeding with attendant formidable problems of heat-loading and no breeding at all. It is suggested that the iridescent plumage of breeding *capensis* be investigated for its potential effectiveness in reflecting solar radiation and heat re-radiated from guano-bleached rocks and soil.

The Cape cormorant feeds on highly active, free-swimming prey. Thus, one might expect evolution of a plumage incorporating hunting camouflage (*sensu* Simmons 1972). However, the phenomenon of social co-operative feeding, involving many birds diving from swimming posi-

tions and pursuing pelagic fish tightly packed into vast shoals, apparently has not favoured selection for white underparts to the bird's plumage. Since *capensis* has a social system involving communal gatherings and co-operative feeding at patchily distributed, concentrated food sources, one might expect evolution of a light or partly light plumage as a consequence of selection for social conspicuousness (*sensu* Simmons *op. cit.*). For *capensis*, there can be little doubt about selection pressure for adaptations facilitating the principle of feeding by 'local enhancement' (Thorpe 1956). For instance, communal roosting is a year-round phenomenon and large flocks depart with 'purposeful' flying in fixed directions from the roost in the morning (Davies 1955), consistent with the functional behaviour described for some other gregarious species which feed by enhancement (Ward & Zahavi 1973). During foggy mornings Cape cormorants will delay their departure from the roost, but not so members of the other cormorant species which tend to forage solitarily.

How, then, is the dark plumage of *capensis* to be explained? In summary, we think it likely that selection has favoured wholly dark coloration in relation to the poor water repellency of the bird's plumage and consequently its need for conserving body energy by means of enhanced absorption of solar energy; and, that the advantage gained by a wholly dark plumage must outweigh any disadvantages attending other aspects of the species' general fitness. Thus, selection for plumage adaptation in relation to social conspicuousness could be secondary, but we are not convinced that under certain conditions of light, position of sun, cloud and the flight behaviour of the birds themselves (Cape cormorants typically fly in long skeins very low over the water), dark coloration is necessarily less conspicuous than white.

DISCUSSION

We believe that our thesis for the adaptive significance of dark coloration applies to all southern African cormorants, and possibly to many other members of the family. We cannot agree with Simmons (1972) that in cormorants dark plumage has been selected primarily for social inconspicuousness, which functions to reduce competition and interference with skilled solitary hunting by conspecifics, since amongst the four taxa considered here there is an extremely skilled solitary feeder (*neglectus*) and by complete contrast a highly social, co-operative, 'gross' feeder (*capensis*). Yet both are wholly dark. Dark plumage as an adaptation promoting inconspicuousness in response to predators and food pirates (skuas, frigate birds and any other examples) is not a consideration affecting southern African cormorants. Neither can we accept the hypothesis that dark plumage might function to promote hunting camouflage in water-to-water feeding situations (see Simmons *op. cit.*), as it attends *neglectus* and *capensis*. We agree with Simmons (*op. cit.*) that the adaptive significance of white ventral coloration resorts to the concept of countershading bestowing hunting camouflage during foraging in *lucidus*, and probably also in *africanus* when in immature plumage and in non-breeding adult plumage as well (see Bowmaker 1963) under certain critical feeding conditions. Notable exceptions, however, occur elsewhere. For instance, the guanay cormorant *P. bougainvillii*, the South American counterpart of *capensis*, is white below. Like *capensis*, the guanay is a gregarious feeder exploiting pelagic fish shoals.

Finally, we wish to make it clear that we fully appreciate that our model encompasses speculation and some inconclusive and overly simple contentions. We recognize the complexity of natural selection processes and their often conflicting natures and resulting compromises, and multi-functional adaptations. Like Simmons (*op. cit.*), however, we conclude that plumage types in cormorants are adaptive, and that while the exact details thereof remain to be demonstrated there exists circumstantial evidence for believing that the main significance is related directly and indirectly to the food-getting situation. As an advance on this we suggest that consideration be given to developing thermal and energy budgets for cormorants to assess the functional significance of our model.

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