PHYLOGENETIC PATTERNS OF SIZE AND SHAPE OF THE NASAL GLAND DEPRESSION IN PHALACROCORACIDAE

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ABSTRACT.—Nasal glands in Pelecaniformes are situated within the orbit in closely fitting depressions. Generally, the depressions are bilobed and small, but in Phalacrocoracidae they are more diverse in shape and size. Cormorants (Phalacrocoracinae) have small depressions typical of the order; shags (Leucocarboninae) have large, single-lobed depressions that extend almost the entire length of the frontal. In all Phalacrocoracidae I examined, shape of the nasal gland depression did not vary between freshwater and marine populations. A general linear model detected strongly significant effects of species identity and gender on size of the gland depression. The effect of habitat on size was complex and was detected only as a higher-order effect. Age had no effect on size or shape of the nasal gland depression. I believe that habitat and diet are proximate effects. The ultimate factor that determines size and shape of the nasal gland within Phalacrocoracidae is phylogenetic history. *Received 28 February 1989, accepted 1 August 1989.*

THE FIRST investigations of the nasal glands of water birds indicated that these glands were more developed in species living in marine habitats than in species living in freshwater habitats (Heinroth and Heinroth 1927, Marples 1932). Schildmacher (1932), Technau (1936), and others showed that the degree of development among species was associated with habitat. Later experimental studies (reviewed by Holmes and Phillips 1985) established the role of the nasal gland as an extrarenal excretory organ that maintains electrolyte homeostasis and water balance during conditions of salt-loading.

The size of the nasal gland and its degree of function varies also within species. Marine populations have larger glands and greater functional activity than do freshwater populations of a given species (Schmidt-Nielsen 1959, 1960, 1965; Peaker and Linzell 1975). Experimental studies with captive wild and domestic birds indicate that gland size (i.e. mass) and function increased quickly in individuals of some species when subjected to high electrolyte stress or low water intake (Holmes et al. 1961, Ellis et al. 1963, Peaker and Linzell 1975).

In other species, accommodation to salt-loading is less effective (Skadhauge 1981). Development and growth rate in captive Mallards (*Anas platyrhynchos*) that were fed 1% solutions of sodium chloride were reduced compared with development and growth of birds fed fresh water (Schmidt-Nielsen and Kim 1964). Data from field populations of wild birds are uncommon (e.g. Technau 1936, Zaks and Sokolova 1961, Thomson and Morley 1966), and only a few studies have focused on the cranial structure associated with the nasal gland (Marples 1932; Bock 1958, 1963; Staaland 1967; Watson and Divoky 1971; Lavery 1972).

Unlike most other birds, Pelecaniformes have nasal glands situated in depressions found in the anteromedial roof of the orbit (Siegel-Causey 1988). In species with extra- or supraorbital nasal glands, glandular tissue can enlarge by growth outward from the skull (Owen and Kear 1972) and by increase in width (Bock 1958), but rarely by increase in length (Staaland 1967, Peaker and Linzell 1975). Because cranial bone is membranous, mesenchymal, and nonintussusceptive, and because it grows very slowly if at all after ossification and maturation (de Beer 1937, Bellairs and Jenkin 1960), change in bony outline of the gland depression must occur slowly. Thus, functionally induced growth of the nasal gland in the orbit is constrained in Pelecaniformes because substantial thickening of the gland without osteological accommodation could distort the eye.

I have shown qualitatively (Siegel-Causey 1988) that the size and shape of the nasal gland depression is variable within shags and cormorants (Phalacrocoracidae). In this study, I surveyed the variation in size and shape of the nasal gland depression in the orbit of selected members of this family. I examined its presumptive association with gland size relative to

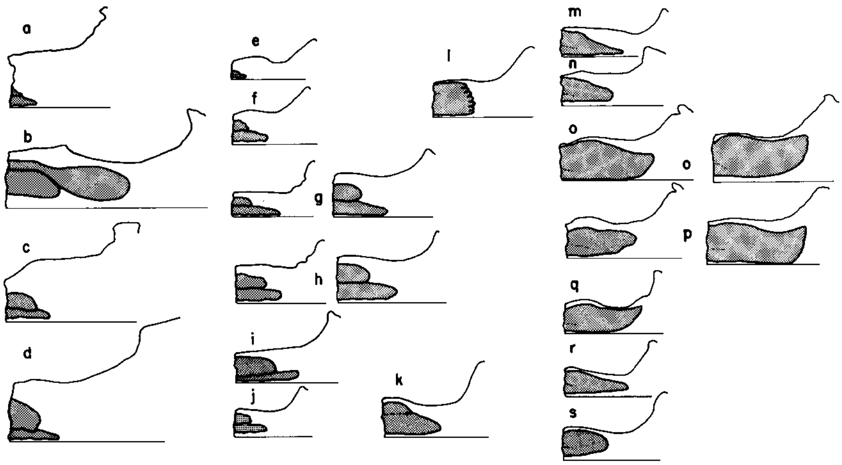

Fig. 1. Outlines of the ventral view of the frontal bone and nasal gland depression in selected Pelecaniformes. All views represent the area indicated in Figure 2: lower; shaded areas represent the nasal gland depression: (a) Great Frigatebird; (b) White Pelican; (c) Red-footed Booby; (d) Northern Gannet; (e) Anhinga; (f) Little Pied Cormorant; (g) Olivaceous Cormorant (left, freshwater; right, marine); (h) Double-crested Cormorant (left, freshwater; right, marine); (i) Pied Cormorant; (j) Little Black Cormorant; (k) Brandt's Cormorant; (l) Black-faced Cormorant; (m) Socotra Shag; (n) Cape Shag; (o) Imperial Shag, marine (left, ♀; right, ♂); (p) Imperial Shag, freshwater (left, ♀; right, ♂); (q) Rock Shag; (r) Pelagic Shag; (s) Red-legged Shag.

collection habitat, age (measured by size of bursa of Fabricius), size, and species identity.

METHODS

All skeletal measurements were done on museum specimens. Scientific names and sample sizes of species used in this study are in parentheses: Reed Cormorant (*Microcarbo africanus;* 15), Little Pied Cormorant (*M. melanoleucos;* 21), Brandt's Cormorant (*Compsohalieus penicillatus;* 4), Black-faced Cormorant (*C. fuscescens;* 2), Olivaceous Cormorant (*Hypoleucus olivaceus;* 50), Double-crested Cormorant (*H. auritus;* 57), Little Black Cormorant (*H. sulcirostris;* 3), Pied Cormorant (*H. varius;* 4), Great Cormorant (*Phalacrocorax carbo;* 11), Socotra Shag (*Leucocarbo nigrogularis;* 3), Cape Shag (*L. capensis;* 4), Imperial Shag (*Notocarbo atriceps;* 12), Antarctic Shag (*N. bransfieldensis;* 19), Kerguelen Shag (*N. verrucosus;* 2), South Georgian Shag (*N. georgianus;* 2), Rock Shag (*Stictocarbo magellanicus;* 73), Pelagic Shag (*S. pelagicus;* 10), and Red-legged Shag (*S. gaimardi;* 30). See Siegel-Causey (1988) for details on systematics and nomenclature.

For comparative purposes, depression outlines for Great Frigatebird (*Fregata minor;* 2), American White Pelican (*Pelecanus erythrorhyncos;* 4), Red-footed Booby (*Sula sula;* 2), Northern Gannet (*Morus bassanus;* 2), and Anhinga (*Anhinga anhinga;* 5) are illustrated (Fig. 1). The nasal glands of tropicbirds (*Phaethon* spp.) do not occur within the orbit and are not illustrated. A list of specimens and data are available from the author.

I measured cranium length and frontal width by dial calipers to a 95% replicated accuracy (RA) of 0.1 mm. The least frontal width was the minimum width measured on the frontal (Fig. 2: upper). Length and width of the bursa of Fabricius were measured in the field to nearest mm with dial calipers, but determinations of RA were not made.

I classified collection localities as freshwater and marine (saltwater) habitats; ambiguous cases were classified as missing. Species identity, gender, and age were determined at the time of collection or, in the case of museum specimens, from the label. Unknown gender was coded as missing. I coded those specimens without age determinations as adults unless there was evidence (e.g. partly ossified bone) to indicate juvenile status.

I approximated the area of the nasal glands in species with fused lobes by the product of the greatest length and width of the nasal gland depression in the cranium. For species with bilobed nasal glands, I used the product of the greatest length of the medial lobe and the greatest combined width of both lobes. Measurements (see Fig. 2: lower) were made by dial calipers (±0.2 mm RA). These approximations may overestimate the actual area of the nasal gland depression, especially in cormorants, which have less rectangular depressions than do shags. All analyses were done using log-transformed data.

I performed multivariate analyses using the BMDP statistical programs (Dixon [Ed.] 1988). Because of the sensitivity of the analysis of covariance (ANCOVA) program to small samples, I excluded cells with sam-

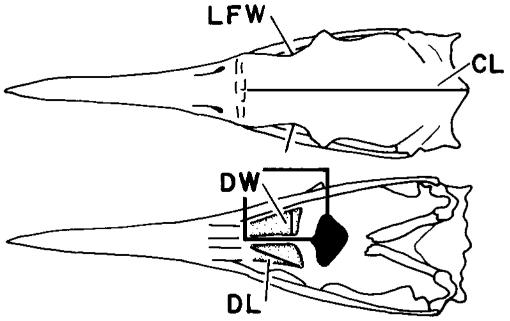

Fig. 2. Generalized phalacrocoracid cranium and gland depression-related measurements. Upper: dorsal view (LFW = least frontal width, CL = cranium length). Lower: ventral view with palatines removed (rectangle represents view in Figure 1, DW = depression "width," DL = depression "length").

ple sizes of <3. I excluded all cases with missing data for the variables under analysis. Equality of slopes (parallelism) of the regressions of the dependent variables on the covariate cranium length was tested by ANOVA, and no significant differences ($P < 0.05$) were detected. All slopes were significantly ($P < 0.05$) different from zero.

Results

Types of nasal gland depression of the cranium.—Three types of depressions were recognizable within the Pelecaniformes (Fig. 1). Most of these were of two main categories, either bilobed or single-lobed (fused). Macroscopic examination of the nasal glands in spirit specimens of Double-crested Cormorants, Rock Shags, and Pelagic Shags revealed that they lie completely within the depression, they are flush with the interior surface of the orbit, and they extend somewhat anteriorly into the nasal cavity. The external morphology of the gland within the orbit is reflected precisely by the shape and size of the nasal gland depression, and therefore gland shape and size can be studied in skeletal specimens. Only Leucocarboninae (shags) have single-lobed (fused) nasal glands (Fig. 1: m–s); Phalacrocoracinae (cormorants) and the remaining Pelecaniformes have small bilobed glands (Fig. 1: a–k). The Galápagos, Bank, and Black-faced cormorants have very broad depressions of unusual shape. The nasal gland depressions of these species are anteriorly bilobed as in other cormorants (Fig. 1: l), but the posterior edges of the depressions are scalloped and all margins are shallow and sloping. The depression surfaces of all specimens I examined were composed of smooth, dense bone. There was no osteological evidence of vascularization or incomplete ossification as is seen in species that have extra- or supraorbital glands (e.g. Procellariiformes and Charadriiformes).

Phalacrocoracidae are unique within Pelecaniformes and show intrafamiliar variation in depression shape. Four qualitative characters varied within the cormorants and shags (characters 12–15 in Siegel-Causey 1988), but only the shape of the lateral edge of the depression showed intraspecific variation. This feature is influenced by the width of the frontal and the length of the cranium (e.g. the lateral curvature increases as the least frontal width decreases relative to cranium length). This variation in lateral curvature was evident in Double-crested and Olivaceous cormorants collected from different habitats (Fig. 1: g, h), but it was most pronounced in comparisons between freshwater and marine Imperial Shags (Fig. 1: o, p). The relation between area of the gland depression and frontal curvature differed in subfamilies. For Phalacrocoracinae, depression area did *not* correlate with least frontal width, although other cranial measures were significant (Double-crested Cormorant: cranium length, anterior frontal width, $F = 14.87$, df = 2, $r = 0.596$, $P < 0.01$; Olivaceous Cormorant: cranium length and width, anterior frontal width, $F = 10.93$, df = 3, $r = 0.615$, $P < 0.01$; Reed Cormorant: cranium length, anterior frontal width, $F = 7.23$, df = 2, $r = 0.802$, $P < 0.001$; Little Pied Cormorant: cranium length, $F = 5.56$, df = 1, $r = 0.426$, $P < 0.05$). For Leucocarboninae, depression area correlated most significantly with frontal curvature (Imperial Shag: cranium length, least frontal width, $F = 78.17$, df = 2, $r = 0.771$, $P < 0.001$; Rock Shag: least frontal width, $F = 6.17$, df = 1, $r = 0.283$, $P < 0.01$).

General model.—The size of the nasal gland is correlated with body size (fig. 11.1 *in* Peaker and Linzell 1975). For the analyses that follow, I used cranium length as the size covariate because it was highly correlated with limb length and other estimates of size ($P < 0.01$ for humerus, ulna, femur, tibiotarsus length for all species) and highly correlated with area of the nasal gland depression and the least frontal width ($P < 0.01$ for area and width for all species).

Analysis of covariance (ANCOVA) revealed that the significant simultaneous effects on area of the nasal gland depression among five species (Imperial Shags and Double-crested, Olivaceous, Reed, and Little Pied cormorants) were species identity ($F = 452.14$, df = 4 and 248, $P < 0.001$), gender ($F = 9.73$, df = 1 and 248, $P = 0.002$), and habitat. The significant effects of habitat were complex and in interaction with species identity alone ($F = 13.91$, df = 4 and 248, $P < 0.001$) and with species identity and gender in a second-order interaction ($F = 3.23$, df = 4 and 248, $P = 0.013$). No other interaction or variables (i.e. age class) had any significant effects. The results were similar for least frontal width except that no second-order interaction was significant (species: $F = 4.55$, df = 4 and 248, $P = 0.014$; gender: $F = 7.47$, df = 1 and 248, $P = 0.007$; species-habitat: $F = 21.74$, df = 4 and 248, $P < 0.001$).

The underlying pattern of these effects can be visualized by plotting the regression means of the area of the nasal gland depression and least frontal width on cranium length for each category of birds (Fig. 3). The greatest difference among groups for depression area and frontal width was species identity. The next consistent pattern was sexually dimorphic (i.e. females always had smaller depression areas and frontal widths than their male counterparts). Both of these results are predicted by the first-order ANCOVA effects.

The relation between freshwater and marine forms within a species is more complicated. For nasal gland depression area, there appear to be two habitat-related patterns (Fig. 3: upper). The first is that, depending upon the species, the mean regression values of marine birds vary relative to their freshwater counterparts. For Reed, Little Pied, and Olivaceous cormorants, for example, the marine forms generally have smaller nasal gland depressions and longer heads, whereas the opposite is true for Imperial Shags. Double-crested Cormorants have no apparent differences between populations. The second pattern is related to the first but involves a gender component in addition. For example, the change in mean score between freshwater and marine Reed and Little Pied cormorant females was greater than the change in males, and it was greater than the change in male and female Double-crested Cormorants. These habitat patterns are predicted by the first- and second-order ANCOVA effects.

The patterns related to habitat for least frontal width were simpler (Fig. 3: lower). Here, the change in mean score between freshwater and marine groups varied with the species, but it appeared similar for each sex within a species. In other words, there is only a first-order effect between habitat and species identity. These results are also predicted by the ANCOVA and, in addition to the patterns observed for depression area, prompted a closer examination of the effects of habitat on depression area and frontal width.

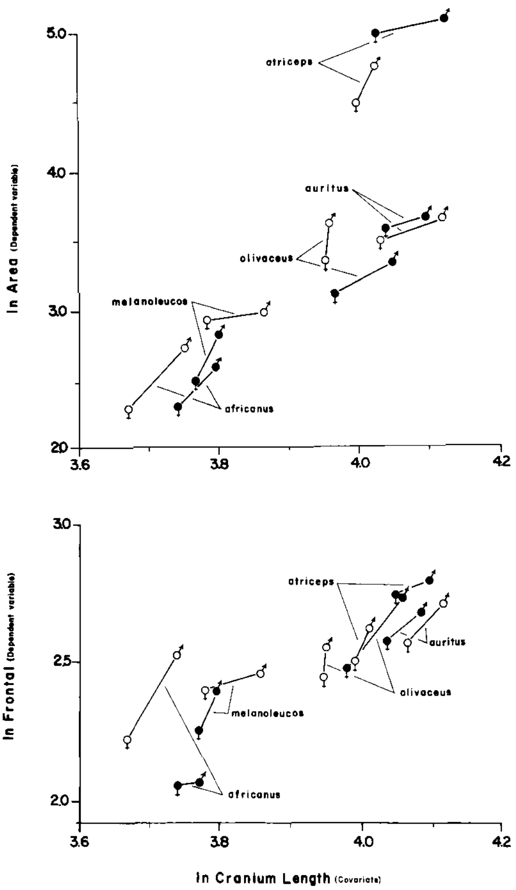

Fig. 3. Habitat and gender patterns in depression area and frontal width in five species of phalacrocoracids. Upper: relation of gland depression area to the covariate cranium length. Lower: relation of least frontal width to the covariate cranium length. Open symbols indicate mean values from freshwater habitats, closed symbols are mean values from marine habitats. Species are indicated by name; genders are marked.

Habitat-related effects.—Intraspecific comparisons by habitat of cranial length, of the nasal gland depression area, and of least frontal width

TABLE 1. Comparison of cranial measurements ($\bar{x} \pm$ SD) between freshwater and marine populations[a] for six species of Phalacrocoracidae.

Species	Habitat	n	Cranium length (mm)	Area of gland depression (mm^2)	Least frontal width (mm)
Reed Cormorant	Freshwater	7	41.03 ± 1.55	12.64 ± 4.33	11.06 ± 1.61
	Marine	8	42.84 ± 1.37	12.75 ± 0.98	8.20 ± 0.42***
Little Pied Cormorant	Freshwater	10	44.57 ± 1.79	18.74 ± 2.86	11.34 ± 1.28
	Marine	11	43.87 ± 1.85	11.97 ± 3.13***	10.98 ± 2.89
Olivaceous Cormorant	Freshwater	24	52.25 ± 1.31	34.78 ± 6.66	13.00 ± 1.24
	Marine	26	56.34 ± 3.43***	27.36 ± 5.28***	13.68 ± 2.09
Double-crested Cormorant	Freshwater	32	61.21 ± 2.06	38.69 ± 7.57	14.59 ± 1.61
	Marine	38	58.32 ± 3.75***	38.94 ± 10.76	13.78 ± 1.50
European Cormorant	Freshwater	4	59.65 ± 3.37	40.64 ± 4.56	14.70 ± 1.78
	Marine	5	63.75 ± 2.47	42.88 ± 2.55	14.96 ± 1.77
Imperial Shag	Freshwater	16	55.54 ± 2.05	106.23 ± 11.21	13.05 ± 1.08
	Marine	96	58.69 ± 2.64***	160.51 ± 15.76***	15.82 ± 1.61***

[a] Significance levels were assessed using the sequential Bonferroni inequality (Holm 1967); *** = $P < 0.001$, two-tailed.

revealed that 5 of 6 species (not European Cormorant) demonstrated significant habitat-related variation in at least one of these variables (Table 1). There were no differences in cranium length between freshwater and marine populations of European, Reed, and Little Pied cormorants. Imperial Shags and Olivaceous and Double-crested cormorants all showed strongly significant differences in cranium length between habitats.

The area of the nasal gland depression varied significantly between habitats within Imperial Shags and Olivaceous and Little Pied cormorants. Freshwater populations of the Olivaceous and Little Pied cormorants had larger depression areas than did the marine populations. The source of this difference in Olivaceous Cormorants was the greater depression width of freshwater birds ($t = 6.68$, df $= 48$, $P < 0.001$). The depression length, however, was greater in marine birds ($t = 2.43$, df $= 48$, $P < 0.05$). As expected from the general model analysis, the least width of the frontal varied significantly between habitats for Imperial Shags and Reed Cormorants (Table 1), but the patterns were different between subfamilies. Marine populations of Reed Cormorants had narrow frontals, whereas marine populations of Imperial Shags had wider frontals. For the other species examined, I found no differences in least frontal width between habitats.

Age-related effects.—For most specimens used in the ANCOVA, age determinations were made from the specimen or its label; I found no significant effects. For selected Olivaceous Cormorants and Imperial, Rock, and Red-legged shags, I made indirect age determinations by field measurements of the bursa of Fabricius. Size of the bursa of Fabricius has been used as an index of age because its growth occurs early in life, and its involution is complete by sexual maturity (cf. Davis 1947, Johnson 1956, McNeil and Burton 1972, Siegel-Causey 1989). In all cases in which I examined bursae, bursa area was uncorrelated with body mass, cranium length, or any other length measurement. Bursa area was similarly uncorrelated with area of the nasal gland depression or least frontal width when the log-linear effects of cranium length were removed.

DISCUSSION

Species identity and gender were highly significant effects that determined size of the gland depression and least frontal width. Habitat (marine vs. freshwater) was significant only as a higher-order effect. Most other interaction effects were nonsignificant. Of these variables, habitat showed the most complex pattern among species. In general, marine cormorants had narrower frontals and smaller nasal gland depressions than did freshwater species, but for Imperial Shags, marine forms had wider frontals and larger depressions. The gender-related effects on the area of nasal gland depressions and least frontal width were predictable. For all species, females had relatively smaller depressions and frontals.

These differences did not have an age component independent of size, although young birds had smaller depressions and narrower frontals than adults. Young are smaller than adults, and gland and frontal dimensions were

TABLE 2. Nasal gland mass ($\bar{x}$ ± SD) for marine and freshwater populations of New Zealand cormorants. Data used with permission of Thomson and Morley (1966). Sample size is in parentheses.

Species	Nasal gland mass (mg/100 g body mass)		
	Freshwater		Marine
European Cormorant	5.5 ± 2.30 (16)	$P < 0.001$	14.4 ± 1.70 (13)
Little Pied Cormorant	13.3 ± 4.34 (26)	$P < 0.001$	26.6 ± 6.32 (21)
Little Black Cormorant	10.9 ± 2.80 (20)		29.4 (1)
Pied Cormorant	—		26.7 ± 1.82 (3)
Black-faced Cormorant	—		30.2 ± 4.73 (30)

simply related to body size. Moreover, age as measured by bursa size had no effect on the dimensions of the nasal gland depression. If age influences depression size, it must occur quite early in life. In a comparable study on the cranial development in Short-tailed Shearwaters (*Puffinus tenuirostris*), the relative size and shape of nasal gland depressions were the same among birds aged 1 month to 5 years (Sugimori et al. 1985).

The strongest effect on the area of the nasal gland depression and least frontal width detected by the ANCOVA was species identity. The greatest contrast was found between subfamilies (e.g. Double-crested Cormorant vs. Imperial Shag), but I detected significant effects between more closely related species (e.g. Imperial vs. Rock shags). Overall, cormorants have small, bilobed glands, whereas shags have large, fused glands. I observed a similar, corroborating pattern of cranial pneumatization within the family (Siegel-Causey 1989). Shags, which have large glands, lacked the posterofrontal pneumatization center present in all cormorants.

The relationship between lateral curvature of the frontal and depression area also differed between subfamilies. For cormorants, there was no correlation between least frontal width and area of the nasal gland depression. In shags, the relation between frontal width and gland area was strongly significant. Least frontal width varied between habitats in Reed Cormorants and Imperial Shags, but for reasons yet unclear the patterns were different. In Reed Cormorants, marine populations had narrower frontals than freshwater populations, but in Imperial Shags, the marine birds had wider frontals.

Depression shape reflected exactly the shape of the nasal gland within the orbit. Given the difference in tissue lability to salt-loading (i.e. bone vs. glandular tissue), it seems clear that shape of the depression in adult birds determines the shape of the nasal gland in the orbit, and not the reverse. Although in most other birds gland size seems related to body size (Peaker and Linzell 1975), the pattern within the Phalacrocoracidae is different. For example, European Cormorants, four times the body mass of Little Pied Cormorants, had nasal glands that weighed only 50% as much (see also Table 2).

Phylogenetic patterns of size and shape diversity of the gland depression within Phalacrocoracidae do not appear to be caused by environmental effects. This is in contrast to Thomson and Morley's (1966) hypothesis that diet determined the ultimate size and shape of the nasal gland in Australian cormorants. Schmidt-Nielsen et al. (1958) showed experimentally that Double-crested Cormorants, like other marine birds, obtained sufficient water from an exclusive diet of marine fish, which are hypotonic to the environment. In field conditions, ingestion of seawater is inevitable, and the diet could include invertebrates, which are isotonic. Thomson and Morley (1966) proposed that, because feeding in a marine environment induces salt loading, nasal gland size should be determined by dietary proportions of fish, invertebrates, and fresh water. They reasoned that the nasal glands of European Cormorants were (relatively) the smallest (Table 2) because they had free access to fresh water or freshwater invertebrates. The nasal glands of Black-faced Cormorants were (relatively) the largest because of their exclusive diet of marine fish. Watson and Divoky (1971) invoked this notion independently to account for differing widths of gland furrows in the genus *Diomedea*.

My results do not support this hypothesis. First, small bilobed gland depressions are a feature of most of the extant species of Pelecaniformes (including the fossil pseudodontorns [Harrison and Walker 1976, Olson 1985]). Only shags (Leucocarboninae) have large, fused gland depressions, yet this feature is unlikely to be related to diet because most (85%) cormorants (Phalacrocoracinae) and all shags are marine, and they eat marine food. Second, functional responses of the nasal gland to salt-loading apparently do not affect depression size or shape as much as the phylogenetic patterns. All previous physiological studies (e.g. Schmidt-Nielsen 1960, Thomson and Morley 1966) measured the size and mass of the nasal gland only in the orbit (i.e. that in the nasal gland depression), and thus those results may be compared directly with this osteological study.

The contrast between phylogenetic and functional patterns is even more striking in comparisons made within subfamily or genus, e.g. Brandt's (Fig. 2: k) vs. Black-faced cormorants (Fig. 2: l), Imperial (Fig. 2: o, p) vs. Rock (Fig. 2: q) or Red-legged shags (Fig. 2: r). Furthermore, the Imperial, Rock and Red-legged shags coexist throughout the marine littoral of Fuego-Patagonia (Humphrey et al. 1970; Siegel-Causey 1986, 1987), but they have diets (Siegel-Causey unpubl. data) contrary to what Thomson and Morley's (1966) diet hypothesis predicts. Overall, Rock Shags eat a greater proportion of crustaceans than either Imperial or Red-legged shags eat, and Rock Shags are not known to drink fresh water (Siegel-Causey 1986), yet their gland depressions are intermediate in size in relation to the other two species, both of which eat a greater proportion of fish.

Thomson and Morley's (1966) diet hypothesis requires that species that eat isotonic food from the sea (e.g. crustaceans, cephalopods) must ingest a compensatory amount of fresh water or hypotonic food. Otherwise, the relatively small glands of European and Little Pied cormorants (which eat marine invertebrates in amounts up to 37% of the diet) and the relatively large glands of Black-faced Cormorants (which eat only fish) cannot be explained (see Thomson and Morley 1966: tables 3-5). There is no evidence that European or Little Pied cormorants actively seek out "freshwater" sources of food while feeding in marine habitats (cf. Serventy 1938, Falla and Stokell 1945, van Dobben 1952, Madsen and Sparck 1950, McNalley 1957, Coulson 1961, and others).

Nyström and Pehrsson (1988) came to similar conclusions using an energetic model. They predicted that diving ducks could minimize salt intake by habitat selection (i.e. low salinity), diet (i.e. eating smaller mussels or switching to hypotonic food), drinking fresh water, increasing body size in order to minimize the physiological effects of salt-loading, and minimizing foraging energy. Their analysis indicated that different species of ducks may use various means to minimize salt-loading, and that possible evolutionary strategies might include increased body size and eating larger food items. Curiously, they did not consider the effect of nasal gland size or what interspecific differences might exist in gland size or function. These and other weaknesses notwithstanding, it is significant to my study that they concluded that salt-loading may act as a constraint on habitat selection and food choice, and not the reverse.

None of the results presented here support a phenomenon of rapid, temporary cranial accommodation of changing nasal gland dimensions, as proposed in other groups (Bock 1958, 1963). In all cases I examined within Phalacrocoracidae, bony margins of the nasal gland depression had the appearance of mature bone, even in partially ossified or pneumatized crania. This implies that depression size in Phalacrocoracidae is set early in life, but it is not clear whether temporary functional accommodation to salt-loading might involve higher gland activity, denser glandular tissue, or increased gland mass outside of the orbit (i.e. within the nasals). Bock (1958, 1963) concluded that the width of the supraorbital gland furrows in plovers (Charadriinae) was due solely to habitat, but his evidence was interspecific comparisons. In contrast, Staaland (1967) hypothesized that [supraorbital] gland size in Charadriiformes was the ultimate factor in their ecology, because the greatest range of habitats and diets were experienced by species with the largest glands.

The perplexing pattern of smaller nasal glands in marine cormorants might be an artifact of taxonomy (e.g. the marine forms may be sibling species), or it may indicate a decoupling of gland size from gland function. It is clear that although depression size indicates size of the gland in the orbit, it may reflect little of its potential physiological activity. The ultimate factor affecting the size of the nasal gland depression in Pelecaniformes is not related to functional demand but instead to phylogenetic history.

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