Introduction

Who does not know what a pelican looks like? Pelicans, and the other members of the traditional family Pelecaniformes, are common inhabitants of the marine littoral and are found almost everywhere along the margins of the world ocean. They are medium-sized to very large aquatic birds found commonly near coastal marine and inland waters, feeding mainly on fish and less commonly on small arthropods and mollusks. Pelicans typify two of the traditionally shared features of this order of birds, including a large distensible pouch under the bill and a totipalmate foot (four toes connected by three webs). Other features traditionally ascribed to Pelecaniformes are less exclusive but altogether have been diagnostic of the group since early times. The feet are set far back on the body for efficient swimming, but on land, most belonging to this group are clumsy and almost immobile. The eggs and chicks are incubated on the feet, the adults lacking brood patches. In most, chicks are born blind and naked, and down feathers appear after a few days. Chicks feed on regurgitated food taken by inserting their head into the parent’s throat. Most species breed in large, dense colonies, and in places, the birds are a valuable source of guano – a source of nitrates and a valuable fertilizer. Colonies are susceptible to disturbance by humans and small mammals when eggs and chicks are lost through temperature imbalances after the adults leave the nest or by predation. Because of their proximity to humans, and dense aggregations in feeding and breeding activities, most pelecaniform birds – cormorants and pelicans in particular – are persecuted by fishermen under the mistaken belief that they deplete fishing stocks.

Systematics

General

The traditional order Pelecaniformes are an order of birds easily identified by a few key characters, the most noticeable being a totipalmate foot, that is, one with all four toes joined by a web. No other assemblages of birds possess this trait: gulls and waterfowl have only three toes joined by a web, and some birds have only a single web between two toes. Other features have been associated with this group, including a gular pouch, or the unfeathered, loose folds of skin underneath the bill, and a lack of brood patches on the abdomen. Six families have traditionally considered to be placed in the order: tropicbirds (Phaethontidae), frigatebirds (Fregatidae), pelicans (Pelecanidae), gannets (Sulidae), cormorants (Phalacrocoracidae), and darters (Anhingidae). Recent studies on the morphology and molecular variation in the traditional species of pelecaniform birds suggest, however, that these groups may not be as closely related as formerly thought (Kennedy and Spencer, 2004; Siegel-Causey, 1996; Smith, 2010). The primary characters used since Aristotle (e.g., totipalmate foot and gular pouch) are most likely primitive characters that arose very early in the evolutionary history of birds and therefore are unreliable to serve as features that unite them (Siegel-Causey, 1996). For example, there is increasing evidence that tropicbirds are not pelecaniform birds and instead ought to be placed within other

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Figure 1 is added by DC; Figures 2–4 are renumbered but otherwise unchanged.
Table 1 is unchanged.
groups, such as the tubenoses (Procellariiformes), herons and storks (Ciconiiformes), or their own order (Phaethontidae). It also appears that, except for the lack of toe webbing, the shoebill (Balaeniceps rex) and hammerhead (Scopus umbretta) herons are most closely related to pelicans and may represent aberrant members of the Pelecaniformes (Siegel-Causey, 1996; Smith, 2010). For these and other reasons, this traditional order of birds is now considered as problematic, and recent molecular research indicates that tropicbirds, shoebill, and hammerhead may be unrelated to the others (Figure 1). The most recent consensus among North American ornithologists is that tropicbirds are in their own order (Phaethontiformes); frigatebirds, gannets and boobies, cormorants, and anhingas are a natural group (order Suliformes); and pelicans, herons, and storks (including whalebills and

Figure 1  Comparison of waterbird phylogeny based on morphological (a) and molecular (b) evidence. Double hash marks in (b) indicate that the clade containing tropicbirds (Phaethon) is not related to pelecaniform birds and other waterbirds. Branch colors represent traditional avian orders: Gaviiformes (purple); Podicipediformes (yellow); Sphenisciformes (brown); Procellariiformes (blue); Ciconiiformes (orange); Pelecaniformes (green). Nodes that conflict between topologies are indicated with red circles. Redrawn from Smith, N. D. (2010). Phylogenetic analysis of Pelecaniformes (Aves) based on osteological data: implications for waterbird phylogeny and fossil calibration studies. PLOS One 5(10), e13354, with permission.
hammerheads) have a distinct evolutionary history and thus now are members of the newly constituted order Pelecaniformes (Chesser et al., 2010). This taxonomy may change yet again with more studies and new information. We here will use the term pelecaniform birds to refer to the traditional grouping of birds and use Pelecaniformes, Suliformes, and Phaethontiformes as taxonomic designations of the putative new groups.

The pelecaniform birds and other large waterbird orders (i.e., Sphenisciformes, Gaviiformes, Podicipediformes, Procellariiformes, and Ciconiformes) are considered by most systematists to comprise the early branching lineages of birds with flight. The earliest known fossil pelecaniform is thought to be *Eloperyx* from the Cretaceous (70 Ma), but as with all early bird fossils, there is considerable debate about its identity – even whether or not it is avian! Cormorants are among the earliest known pelecaniforms, with fossil elements recovered from as early as the Eocene–Oligocene boundary (~55 Ma). There are approximately an equal number of extinct and extant species described, but the fossils are often from single bones and of dubious affinities.

The species-level taxonomy has been very neglected, with some families having many species and subspecific forms described (e.g., cormorants with 39 species and 57 taxa), while others have had little attention. For example, the anhingas (or darters) are variously described as comprising one, two, or four species, but with few data to back up any of the competing schemes (Siegel-Causey, 1996). As a whole, the group is drab or monochrome or both, and sexes are dimorphic only in the darters and the frigatebirds.

**The Pelecaniform Birds (Pelecaniformes, Phaethontiformes, and Suliformes)**

The groups traditionally considered to be extant (nonfossil) members of the order Pelecaniformes comprise 6 families and include 6 genera, 67 species, and about 120 described subspecies, races, or types (Figure 2). See previous text (‘Systematics’) for recent taxonomic groupings. Cormorants are the most diverse group, with half of the extant species; tropicbirds and anhingas are the least diverse, with 3–4 species known at present. Pelecaniform birds are found on every continent, along most marine coasts and major freshwater drainages, and are absent only from extreme deserts and the ice-covered regions. The nest is built by the female with material usually brought by the male and is situated on the ground or in trees, selected to be well protected from predators. Reproductive behavior is complex and involves primarily visual displays near the nest site; vocalizations are rare and often described as being grunts, croaks, or strident.

**Phaethontidae (Phaethontiformes)**

A single genus, *Phaethon*, and three species are found throughout the tropical waters of the world ocean. Tropicbirds differ from the typical pelecaniform birds and really only share a single feature – the totipalmate foot – with the other species. (Recent studies suggest that tropicbirds may not be a member of this family and that the totipalmate foot is an ancestral, primitive feature.) The chicks hatch fully covered with down feathers; they are fed by the adults from the bill rather than the throat as in other species; courtship displays are aerial, noisy, and synchronized; the bill lacks a terminal hook; the gular pouch is feathered and obsolete; and there are many other distinctions.

All are medium-sized – about the size of a small gull – and white with black eyes and wing barring, with long tapering wings and gull-shaped bills, and with very elongated tail feathers forming streamers often longer than the rest of the body. The white parts of the plumage are often tinted pink or gold; the sexes are alike in appearance. Species range widely over the warm tropical and subtropical waters and represent the most oceanic of all pelecaniform birds. They only come to land for breeding, on remote oceanic islands, and select nest sites that are inaccessible to terrestrial predators and have some shade, such as might be provided by overhanging rocks on cliffs or within caves.

Little is known about the ecology and behavior of the family; the birds are rarely seen in groups or flocks, often only singly, and usually in flight. Feeding seems to be in low light (i.e., early morning or late evening) and by plunge-diving into local concentrations of cephalopods and flying fish. Hovering over schools and ship-following have been noted and gathering with multispecies feeding flocks. More commonly, though, tropicbirds tend to forage solitarily, dive abruptly, capture food close to surface, and then take to the air soon after swallowing their prey.

**Pelecanidae (Pelecaniformes)**

Pelicans are the largest members of the order and are distinguished by their large body, long, heavy bill, and huge distensible gular pouch. Seven species are recognized, and all are found not far from water and rarely out of sight of land. Plumages are generally light-colored – only the brown pelican is dark – and in the breeding season, the bare facial and gular skin and often bills become brightly colored in both sexes. Because of the size and large broods, pelicans are voracious feeders. They predominately eat fish and feed by plunge-diving into surface shoals of fish with the bill opened. Most pelicans are found near lakes and large water bodies, and only the brown pelican is primarily marine.

Pelicans are gregarious and are rarely encountered alone. They breed almost exclusively in large colonies; the precplied young form large créches within the breeding colony; and roosting and flight are done in large groups. Pelicans have the best-documented communal feeding, in which large groups will coordinate fishing in fresh or brackish waters as a group. From 10 to 50 birds will alight on the water in a row and drive surface-schooling fish toward shallow water by paddling, flapping wings, and plunging their bills in the water, sometimes feeding and sometimes not. Other birds plunge-dive into the water after fish or swim from beneath; when captured, the fish are retained in the gular pouch as the water drains away. They are then eaten, often after being flipped up into the air to be swallowed headfirst.
Pelicans, along with cormorants, are among the birds most affected by human disturbance and environmental pollution, particularly by chlorinated pesticides such as DDT and dieldrin. Pelicans and humans have long been associated, and freshwater species are vulnerable to habitat loss and pollution. Fishermen have persecuted pelicans and other fish-eating birds in times of low fish catch, but most studies indicate that the take by pelicans is primarily of noncommercial fish. In every case, low fishing yields are due to poor management or poor environmental stewardship and not due to pelican–human competition. Pesticide
constriction of breeding range, and low productivity in raising chicks to breeding adults.

Annual nesting is the norm among many species of Sulids, though it is not uncommon for birds to skip a year between breeding attempts. This is usually because of low food supplies, which may also explain why gannets, boobies, and other Suliformes delay their first breeding attempt until they are 5–6 years old and live 20–40 weeks. This slow development is attributed as an evolutionary response to the unpredictable and distant feeding grounds of the adults, but the evidence is not clear. Abbott’s booby is also the most threatened as a result of habitat loss.

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The breeding season seems to be determined by local conditions, such as seasonal onset of oceanographic or weather patterns, abundance of food, and appearance (or nonappearance) of neighboring breeding species. The reproductive cycle is longer than for most of the other Pelecaniformes, with incubation lasting as long as 60 days, fledging as long as 7 months, postfledging dependence on adults lasting on average between 9 and 12 months, and age of first breeding from 6 to 11 years. This seems to be related to the unpredictable nature of the food supply, low chick productivity, and low breeding success. While the birds are not threatened at present except in a few localities, these aspects of natural history make them particularly vulnerable to human disturbance and habitat destruction.

**Fregatidae (Suliformes)**

Frigatebirds are found throughout tropical and subtropical oceans of the world, commonly associated with the regions of trade winds. They are large – roughly the size of large gulls – and predominantly black, with some species having white breasts or bellies. Five species are described, but there is substantial confusion on the status of certain island forms, plumage variants, and size differences. The wings are large, elongated, and pointed, with a distinctive open W-shaped flight silhouette, and all species are quite deft in the air. During breeding, males inflate their scarlet gular pouch to nearly half the size of the body and do so in groups and alone, on ground and in the air, and at times will vibrate it with the bill, as though drumming.

Frigatebirds will leave the roosts at dawn and spend the rest of the day foraging alone or in small groups. They are known for feeding by theft (‘kleptoparasitism’; hence, their common names of frigatebirds or man-o’-war birds) but commonly feed on shoals of flying fish, cephalopods, and rarely krill. They rarely dive in the water, preferring instead to feed by surface-dipping or even aerial captures of emergent flying fish. Every tropical seabird colony seems to be attended by several frigatebirds, and unattended eggs and chicks are taken by swooping after an aerial dive. Fish are snatched from the bills of other seabirds, whether at sea or on the nest.

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**Sulidae (Suliformes)**

The sulids and gannets and boobies (genera Morus and Sula) include nine species found throughout the tropical and temperate regions of the marine environment. Generally, they are duck-sized, with a long conical bill finely serrated along the edges. Gannets are found in high-latitude waters, while boobies tend to be more tropical; both are exclusively marine and piscivorous. Sulids feed by plunge-diving and then often shallow pursuit (usually to no greater than 15 m depth) after fish in the upper water levels. The plumage is thought to reflect this behavior, as the light chest and abdomen will provide little contrast when seen from below and prove indistinct when seen from above. Whether related to camouflage or swimming ability, sulids are very efficient in capturing small schooling fish such as anchovy (Engraulis) and sardines (Sardinops).

The timing of breeding seems mostly associated with local conditions of food and nest site availability and occurs annually in most species. In very good conditions, the tropical boobies will breed at intervals less than 12 months, and the red-footed booby in the Galápagos often breeds once in 15–18 months. These nonannual periods have been thought to be a response to bad (or good) oceanographic conditions related to the El Niño Southern Oscillation, or conversely La Niña, or as a means to desynchronize breeding with potential nest predators such as frigatebirds or both. In both gannets and boobies, the reproductive cycle is similar to other seabirds, in that chicks fledge, leave the nest, and are independent before the end of the 1st year. Sulids usually do not breed for the first time until they are 3–6 years old and live 10–20 years.

The largest clutches are found in the species breeding in upwelling regions with high fish production (e.g., Peruvian and blue-footed boobies) and average two to three eggs. Other tropical boobies such as brown and masked boobies will lay two eggs, laid 4–6 days apart; the larger and stronger chick – not always the first one hatched – will often push the weaker chick from the nest to its demise. All other sulids lay a single egg. The most aberrant and presumed the most primitive sulid is Abbott’s booby, which is now restricted to Christmas Island, Indian Ocean. Chicks take 20–24 weeks to fledge and are fed by adults for an additional 20–40 weeks. This slow development is attributed as an evolutionary response to the unpredictable and distant feeding grounds of the adults, but the evidence is not clear. Abbott’s booby is also the most threatened as a result of habitat loss, constriction of breeding range, and low productivity in raising chicks to breeding adults.

**Phalacrocoracidae (Suliformes)**

There are nearly as many species of cormorants and shags as all of the remaining members of the Pelecaniformes. This family has about 60 described taxa; these are sometimes lumped into as few as 26 species or as many as 40 or more. The discrepancy lies in the many related island forms found throughout the Southern Ocean, including Antarctic, Subantarctic, and southern subtemperate waters. There are two distinct subfamilies, the cormorants (Phalacrocoracinae) and the shags (Leucocarboninae), although the common names often do not correspond so neatly; the pied shag of the antipodes is in fact a cormorant, and the pelagic cormorant of the North Pacific is a shag. The two groups are distinguished by clear morphological and genetic differences and represent an early divergence as far back as the Miocene, perhaps 15–20 Ma. Cormorants are generally heavy-bodied birds with labored flight, commonly found on freshwater systems, often far into the interior. Shags are smaller and slimmer, are more powerful fliers, and are common inhabitants of the marine littoral, neritic, and pelagic waters.

In many species, particularly those of the Northern Hemisphere, the plumage is basically black or very dark, often with metallic or iridescent sheens to the feathers. Most shags and cormorants of the Southern Hemisphere have in addition a white abdomen; in
a few species such as the red-legged shag and spotted shag (*Stictocarbo gaimardi* and *S. punctatus*), the plumage is predominantly gray. In breeding, adults will often undergo dramatic changes in color and appearance that affect both bare parts and the plumage. The naked skin of the face, gular pouch, bill lining, and rarely feet become more intensely colored, change color, or even assume color, and these changes are often accompanied by enlarged or increased carunculations near the eyes and face. Many species produce long white filoplumes and breeding plumes on the head and neck (*great cormorant*, *Phalacrocorax carbo sinensis*), and in a few species (red-faced, pelagic cormorants *Stictocarbo urile* and *S. pelagicus*), a conspicuous white patch appears on the thigh.

Unlike many other Pelecaniformes, cormorants and shags have very flexible requirements for nesting and nest construction. They are known to breed in diverse habitats including on level ground, on cliffs and embankments, in trees, on bridge supports, and on wharfs: generally, on objects large and sturdy enough to support the weight of the nest and occupants while affording protection from ground predators. Proximity to water is an absolute requirement because cormorants are nearly exclusively piscivorous, and the size of breeding colonies in continental interiors correlates with how close they are to feeding areas (*Figure 3*). By virtue of wing morphology and aerodynamics, cormorants are indifferent fliers and do not range far from roosting or breeding areas. Colony and perch sites as a consequence are located near foraging areas, tend to be patchily distributed throughout the landscape, and concentrate large numbers of birds. Recent studies indicate that colonial breeding may be the result of limited nesting habitats rather than an evolutionary behavioral adaptation, but there seem to be as many strategies as there are types of colonies. There is an ongoing debate whether cormorants in colonies share information in some way about feeding areas, but the phenomenon of social feeding in cormorants – as in pelicans – is well observed. Two patterns are known: line

![Figure 3](image-url)

*Figure 3* Colony size (breeding pairs) of great cormorants *Phalacrocorax carbo* in relation to available feeding habitat (0–20 m water depth) without overlap with their colonies with a range of 20 km from the colony. Maximum colony size (open circles) and, if different, most recent colony size (dark circles) indicate the effects of oversaturation of feeding resources. The recent colonies in Denmark (shaded circles) are undersaturated with respect to available feeding resources and are fast expanding in size. Both effects suggest the existence of ‘sustainable’ and a ‘maximum’ density. The oversaturated effect is particularly noticeable in the Brandegård colony (1) in Denmark. Numbers refer to monitored colonies in Denmark (1–3) and the Netherlands (4–6). Redrawn with permission from van Eerden and Gregersen (1995).
hunting, in which cormorants move through the water in a straight line in a rolling flock, and zigzag hunting, in which individuals search and change directions. Line hunting is usually associated with smaller fish like smelt (Osmerus) and ruffe (Gymnocephalus), whereas zigzag fishing is seen when cormorants pursue larger fish like roach (Rutilus) and perch (Perca).

Anhingidae (Suliformes)

Darters are fairly large birds (‘goose-sized’) with a very long, slender neck with a pronounced ‘S-shaped’ kink, a long spear-like bill, and a large fanlike tail resembling that of a turkey. The taxonomy is contentious: variously one, two, four, or more species have been described for the family. Darters are primarily aquatic and spend their life in water or on branches overhanging protected, usually freshwater, streams, and ponds, especially swamps and marshy areas. Darters are widely distributed throughout tropical and subtropical zones and are sometimes found in warm temperate habitats. They are the least marine of the Pelecaniformes but can be observed in brackish coastal waters, mangrove and cypress swamps, and coastal lagoons.

They are similar in appearance to cormorants but are easily distinguished in flight, on roosts, and on the water. Darters are good fliers and often alternate powered flight with glides; cormorants use sustained flapping and seem always at risk of not quite keeping airborne. Darters will use thermals for soaring and will soar for extended periods, perhaps while surveying new areas for feeding or roosting. Their long tail and tapered wings allow a much greater agility in air than shown by shags or cormorants, and they are adept at flying through enclosed swamps and thickets. While it is swimming on the surface, the body of a darter is usually submerged, with only the head and snakelike neck visible, making it obvious why the term ‘snake bird’ is often used for them. The wettable plumage of darters results in considerable loss of body heat under water, and they therefore spend large amounts of time sunning and drying feathers.

Darters have several unique anatomical features apparently related to feeding. The distal portions of the upper and lower bill are long, backward-pointing serrations for holding fish. Modifications to the eighth and ninth cervical vertebrae allow a right-angled kink in the neck, and the extensor ligaments of the neck pass through a ‘pulley-like’ loop that allows a fulcrum for the straight-line stabbing motion with which this species spears its prey. Darters have an unusual bony articulation at the base of skull, allowing an even greater forward acceleration of the head and neck, and a hairlike pyloric valve in the stomach. Unlike all other pelecaniform birds, darters will stab fish with the bill, rather than grasping them between the bill, and then flip the fish into the throat headfirst. This type of fishing technique is well suited for the shallow, murky waters they inhabit and deadly to the slow moving, laterally compressed fish the birds pursue. In North America, centrarchid and cyprinodontid fish are most preferred, but freshwater decapods often are eaten when abundant.

Darters are monogamous, as are most Pelecaniformes, with the pair bond lasting many years and breeding pairs returning to the same nest each season. Nesting is usually solitary, but small aggregations are known, and darters will commonly breed in mixed colonies with other waterbirds such as cormorants, herons, egrets, ibises, and storks. Darters are sedentary, rarely dispersing after breeding, but some of the populations breeding in temperate regions will disperse to warmer areas in winter. Owing to their wariness, solitary nature, and preference for impenetrable swampy areas, comparatively little is known about their behavior or natural history.

Ecology

Color has been implicated as an important factor in pelecaniform feeding; it is commonly stated that light-colored plumage affords a minimal contrast against daylight or sky, while dark plumage is especially cryptic in dim light. Pelecaniform birds range in color as adults from mostly white (e.g., gannets and tropicbirds) to mostly black (e.g., cormorants and frigatebirds) and with many intermediate shades, colors, and contrasts (e.g., gray plumage in red-footed cormorants and mottled plumage in boobies and brown pelicans). However, juvenile and immature frigatebirds, sulids, and pelicans are generally darker than adults, while in cormorants and darters and in some frigatebirds and pelicans, the juveniles are lighter. Shags, boobies, and some other pelecaniforms have white and black contrasting patterns on their abdomens and chests, and in species such as brown booby and rock shag, there are morphological variants with the same patterns. Many have speculated that these plumage patterns relate to greater efficiency in capturing fish or avoiding detection, but other factors seem as important. Melanistic plumage is often more durable than light-colored plumage, and thermoregulation is affected strongly by overall coloration. Much more study is required to understand what may be important in plumage color.

Primarily fish-eating birds, the Pelecaniformes, nonetheless utilize a diversity of feeding methods, marine and aquatic habitats, and food items (Table 1). Gregariousness is prominent in the group, with some being groups well known for social feeding (pelicans and cormorants) and with most breeding in large, dense colonies. Nearly every type of freshwater and marine habitat is exploited, but, except for tropicbirds and frigatebirds, the pelecaniform birds are limited to littoral and neritic waters, rarely encountered far from land. Their preference for small schooling fish, and for breeding in large, dense colonies near the feeding grounds, makes their guano production a desirable attribute from the human viewpoint, but interactions with humans are for the most part neutral or negative. Cormorants and pelicans are often – wrongly – implicated in the depredation of fingerling and fry of economically important fish such as trout and salmon and consequently suffer culling and killing campaigns to reduce their numbers.
Behavior

Mostly nonvocal and colonial, pelecaniform birds utilize ground-based visual displays much more prominently than other waterbirds (see Figure 4). When birds live and feed together in close proximity in colonies, the interactions between individuals are much greater than found in solitary nesting or dispersed breeders. Further, because space is limited at most sites suitable for nesting, colonial birds breed in extremely dense conditions, with territories squeezed to a minimal area around the nest or even nonexistent. Most of the pelecaniform birds have a basic courtship sequence that serves to establish the pair bond and maintain it, often for many years. In nearly every case, the male selects the nest site and advertises for a mate; the females choose among males through assessment of no doubt many factors, including the nature of the displays, the excellence of the nest site, and prior history. Copulation occurs on the nest site, usually between bouts of nest building by the male, sometimes by both partners. After the pair bond has been established, both birds take turns guarding the nest, incubating eggs and chicks, and feeding the young. With exceptions noted in the previous text, parental care stops soon after fledging, and young birds will forage independently soon after leaving the nest. Some pelecaniform birds will begin breeding as soon as the 2nd year (e.g., cormorants), although 3 years of age seems to be the norm, while in other species (e.g., Abbott’s booby), many years may pass before individuals breed.

Status and Conservation

Few of the Pelecaniformes are globally threatened, although some island and inland populations of pelecaniform birds have become extinct in the face of habitat loss and contamination. In some species (e.g., double-crested cormorant and white pelican), numbers are increasing with near-exponential growth, while in others (e.g., Dalmatian pelican), population abundance is rapidly decreasing. Island species and populations have been especially hard-hit by the introduction of terrestrial predators such as cats, rats, and pigs; loss of traditional breeding habitat has played a greater role in aquatic and inland-nesting species. Some islands such as Christmas Island (Indian Ocean) and Ascension Island (Atlantic Ocean) are breeding grounds for several pelecaniform species, and their recent protected status has promised a much better future than might have been possible only a few years earlier.
Figure 4  Behavioral displays in the rock shag (*Phalacrocorax magellanicus*). Appeasement displays: (a) landing display approaching a nesting cliff; (b) postlanding or hopping; (c) nest-touching after a threat display. Courtship displays: (d) beginning and (e) ending phase of darting by the male; (f) beginning and (g) ending of throat-clicking by a pair. Pairing displays that terminated in copulation: (h) initial phase of wing-waving by the male (bottom) after approach by the female (top); (i) beginning phase of hop by female, male is wing-waving; (j) conclusion of hop by female followed by nest-indicating, male is wing-waving; (k) full neck extension by male during wing-waving, female is gaping; (l) bill-biting by female and bowing by male. Redrawn from Siegel-Causey, D. (1986). Behaviour and affinities of the Magellanic Cormorant. *Notornis* 33, 249–257, with permission.

**Further Reading**


