



Why is wing-spreading behaviour absent in blue-eyed shags?

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Wing spreading is a general behaviour in cormorants, and has been described worldwide in most species (Orta 1992). Yet, this behaviour is missing (with some exceptions, see below) in the species belonging to the so-called 'blue-eyed shag complex' (Bernstein & Maxson 1981), hereafter referred to as 'the complex', a group of cormorants living on the coasts and islands of the waters of the Southern Ocean between roughly 40°S and 70°S latitude (Patagonia, Antarctic Peninsula, subAntarctic Islands, New Zealand) and comprising 13 species that have close morphological similarities (Siegel-Causey 1988).

The following observation is an example of what is very rarely seen in blue-eyed shags. A wing-spreading behaviour was observed in an adult Kerguelen shag, *Phalacrocorax verrucosus*, on 29 December 2005. This behaviour was noticed on the coast of Stoll Island (49°26'S, 69°55'E), Morbihan Gulf, Kerguelen Island. Around 1130 hours, two shags were resting on a large rocky surface down near the sea, one of which began adopting a wing-spread posture. The posture lasted 2–3 min (estimated retrospectively), the bird unmistakably spreading its wings in a typical 'full wing-spreading posture', that is, bird standing on legs, body upright and wings outstretched in extension on either flank perpendicularly to body axis and protracted (wing extended at wrist and elbow joints and protracted at the shoulder). Throughout the posture, the bird remained immobile, facing the sea with the sun overhead, with no associated behaviour such as wing flapping, wing fanning, or preening. After wing spreading, the shag regained a normal roosting posture, standing with wings folded, and was not seen displaying this behaviour again. The observation was then abandoned after another 5 min for logistical reasons. The bird was observed with binoculars (8 × 42) at a distance of about 150 m. We have no data on whether the bird had recently come back from the sea after a foraging trip, or on its reproductive status. Temperature at that time was mild (around 10°C), the sky was clear and there was no wind.

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This is the first time wing-spreading behaviour has been recorded for the Kerguelen shag. Moreover, in 2005–2006 we followed many hundreds of shags over several days and did not observe the wing-spreading posture. The present observation is therefore rare and intriguing. This posture has not been reported for species inside the complex from other localities where most studies have been done, in particular at Macquarie, Heard, South Georgia, in New Zealand, on the Antarctic Peninsula and at Crozet (see Kato et al. 1996; Bevan et al. 1997; Green & Williams 1997; Brown 2001; Casaux 2004; Tremblay et al. 2005). In Patagonia, Rasmussen & Humphrey (1988) noted a wing-spread posture in several individuals, associated with preening and wing flapping. Otherwise, apart from their study and the present observation, blue-eyed shags are notorious for not displaying the wing-spreading behaviour so common to other species of cormorants.

The situation in the complex thus appears to diverge from what is found in cormorant species elsewhere. Though the function of wing spreading has been subject to debate for many years, there have been few articles actually dealing with it when compared to other issues on behaviour and the subject has been of interest to only a minority of specialists. The purpose of this commentary is to raise the question of why wing spreading is generally absent in the blue-eyed shag species, using all available data in the literature, and focusing, in particular, on comparing the most common paradigms on the question with the situation in the complex.

Historically, wing spreading has been documented for several orders of birds, mainly the Pelecaniformes, Ciconiiformes and Falconiformes (see Clark 1969; Curry-Lindhal 1970; Kahl 1971; Houston 1980; Francis 1981; Hennemann 1982). An evolutionary affinity between some of these orders encouraged the notion that this behaviour could have phylogenetic origins (Clark 1969). This posture has also been suggested to have different functions from one order or family to another (Hennemann 1988), or to serve nonexclusive multipurpose functions in same species (Clark & Ohmart 1985). Defined as a 'rather simple behavioural trait' (Clark 1969), it could thus have emerged conjointly in different taxa. The different functions hypothesized for this behaviour include feather maintenance, social display, shading of nest

content, wing drying and thermoregulation (for a review, see Hennemann 1988 or Schmidt 1994).

In cormorants, the function of wing spreading has been subject to several interpretations. According to Rijke (1968), it serves to dry feathers because cormorants are 'wetable' compared to other seabirds, although other studies on feather structure have used the probably more suitable term of 'partially wettable' (Elowson 1984; Mahoney 1984; Grémillet et al. 2005a). Partially wettable plumage is thought to be a way of eliminating a part of the air from the plumage to reduce costs related to swimming downwards against buoyancy. Conjointly, cormorants maintain the ability to fly by having partially pneumatic bones (an evolutionary pathway in diving birds not adopted by penguins, e.g. which have a nonwettable plumage but very dense bones, and have therefore lost the ability to fly). Studies relying on behavioural observations (e.g. relating frequency of behaviour to ambient temperatures and solar intensity) have also supported the 'wing drying' hypothesis (e.g. Hennemann 1984). Others have suggested a thermoregulatory function: heat could be gained either passively (e.g. Schmidt 1994), or actively through wing flapping, for example when birds use the excess heat generated to facilitate digestion of ingested cold prey (Grémillet 1995). In the latter case, wing spreading could consequently become a social messenger as well (Jones 1978), as the behaviour would indicate foraging success. Therefore, while wing spreading may ease the process of feather drying, this imputed function does not preclude the possibility of a thermoregulatory function.

In the case of blue-eyed shags, if their plumage appears to be rather close to that of cormorants that display wing spreading (Bernstein & Maxson 1982), why is this behaviour almost never observed in the complex? At Kerguelen, blue-eyed shags do not seem to have problems drying, even though they do not spread their wings. Indeed, upon returning from the sea, they shake energetically, and are afterwards only superficially wet, as handling shows, and are completely dry after 5–10 min (rainy or snowy weather excluded; personal observation). They also gular-flutter very readily in summer (the whole colony can be seen gular-fluttering as soon as the sun appears), indicating that they can get overheated. Contrary to our observation at Kerguelen, the blue-eyed shags from Northern Patagonia (Chile) observed by Rasmussen and Humphrey (1988) always combined wing spreading with preening of breast, abdomen or flanks, and sometimes wing flapping, a group of behaviours that could simply have a feather-maintenance function. These authors suggested that Chilean blue-eyed shags might display wing spreading to enable heat gain since temperatures are mild at those latitudes, compared to further South where colder temperatures would discourage this behaviour (a theory advanced by Bernstein & Maxson, 1982). If this is true, it means that wing spreading could be observed in blue-eyed shags from lower and milder latitudes, such as those in New Zealand, for example, although such records are lacking at present.

The counterpart to the environmental conditions of the Southern Ocean exists in the Northern Hemisphere, with

some differences. In Greenland, where the great cormorant *Phalacrocorax carbo* is found, winter sea water temperatures are around -1.5°C and atmospheric temperatures may drop to -30°C (Grémillet et al. 2001). Comparatively, at Kerguelen, for example, water temperatures in winter are around 1.5°C and air temperature can drop to -10°C (Duchêne 1989). Temperatures can be even colder for *Phalacrocorax bransfieldensis*, the Antarctic blue-eyed shag. In this regard, shags from the complex will spend nearly 6 h per day at sea during chick rearing (Wanless et al. 1995, Tremblay et al. 2005) versus 1 h for the great cormorant in Greenland (Grémillet et al. 2001). Blue-eyed South-Georgian shags appear to experience important metabolic depression via body cooling when diving (Bevan et al. 1997), associated with bradycardia, as could be the case with most cormorant species (Enstipp et al. 2001; Grémillet et al. 2005b), and perhaps anaerobic metabolism as well. Mean minimum abdominal temperature while diving is around 31°C . In comparison, the abdominal temperature of great cormorants from Greenland does not appear to reach such low values (Grémillet et al. 2005b). When coming back from the sea, Greenland great cormorants often display wing-spreading behaviour (Kuntz 2004). Why do great cormorants in Greenland spread wings and blue-eyed shags do not? Temperatures in the Southern Ocean are cold, yet relatively constant all year round (Antarctica excluded), while in Greenland, even if cormorants spend shorter daily periods in the water, the sea is near freezing, and heat loss to the air in the winter is also potentially important. If the absence of wing spreading in blue-eyed shags functions to reduce heat loss by reducing body surface, the absence of this behaviour should be equally or more apparent in great cormorants of Greenland.

In the Cormorant family, wing spreading (or sometimes improperly 'wing drying') reasonably appears to have strong phylogenetic grounds, as it is common to several families of the Pelecaniformes order. It is particularly present in the closely related Phalacrocoracidae (cormorants) and Anhididae (darters). It could be that the loss of this trait was related to the history of the blue-eyed shag complex. The sporadic emergence of wing spreading in individuals, such as in Chile (Rasmussen & Humphrey 1988), or in the present case at Kerguelen, only strengthens Clark's hypothesis of a 'rather simple behavioural trait', perhaps resurfacing from time to time or when certain environmental conditions are favourable, particularly in a family with a phylogenetic predisposition. Yet, if this behaviour has disappeared, it is most likely because it has a cost (for muscles involved in the wing-spread posture, see Meyers 1997). One can assume that a better strategy was found in species from the complex to cope with the phylogenetic pressures (partially wettable, little blubber) of being a flying diving seabird originating in the tropics (Van Tets 1976) and living in cold regions. If birds do not assume the wing-spread posture upon returning from the water, it is probably of no benefit to them, costs outweighing other factors. Blue-eyed shags may have adjusted quite well to a cold climate, excluding wing spreading because it promotes heat loss to the air (particularly in the winter), as suggested by

Bernstein & Maxson (1982). Whereas great cormorants from Greenland or Northern Norway (Johansen et al. 2001), may only recently have arrived in the Arctic (Ruxton & Humphries 2001), and continue living with a behavioural trait inherited from an adaptation to conditions in lower latitudes. To conclude, it appears that if wing spreading and flapping do indeed ease digestion through heat gain (Grémillet 1995), the cormorants in the Arctic profit from this, while blue-eyed shags do not. This raises the question of how these birds manage to cope with body temperature fluctuations and digestion processes. Recording stomach and abdominal temperatures of free-ranging individuals over a short period of time would probably help answer this. In this context, it might also be essential to reiterate the experiment conducted by Grémillet (1995), an approach which seems most promising. Also, controlling air and water temperature on a group of experimental birds might help to detect how temperature can trigger the onset of the wing-spreading behaviour or not. If an experimental design can be easily set up for great cormorants because they are abundant or readily found captive (e.g. in zoos), the same is less easy for blue-eyed shags because of their isolated locations that render them difficult to study and their frequent high protection conservation statuses.

At the present time, it appears essential to use an ecophysiological approach to tackle the question of wing spreading and evolution in the blue-eyed shag complex. Yet, there are few such studies (only one has been done on blue-eyed shags: Bevan et al. 1997) and long term monitoring of physiological variables (e.g. heart rate or abdominal temperature) is still lacking within the complex. Eventually, although the wing drying hypothesis seems less attractive today than formerly, rigorous comparative studies on behaviour, as well as on feather and plumage structure, must be carried out among cormorant species from different habitats before final conclusions can be drawn. For example, the hypothesis that the plumage of blue-eyed shags may contain more air than species from other habitats as an adaptation to longer daily periods spent in cold water (Quintana et al. 2007) must be tested, particularly as it would contradict the results found by Bernstein & Maxson (1982) suggesting that their plumage is equally or more wettable than great cormorants. Future studies should thus focus on behaviour, but also on more proximal parameters such as plumage, body composition, physiology and energetics. Finally, observations such as the one presented in this study, although they may appear anecdotal, are important and necessary to reopen the debate.

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