

WING-SPREADING BEHAVIOUR OF THE CORMORANT

Phalacrocorax carbo

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ABSTRACT This paper describes an investigation into the factors influencing the occurrence and duration of the wing-spreading behaviour of the Cormorant. It was found to occur only after a period in the water (that is, when the plumage was wet), and its duration to be inversely related to wind speed and the length of time spent in the water. In addition birds tended to face into the wind during wing-spreading and, at low wind speeds, away from the sun. The extent to which the wings were spread was also inversely related to wind speed. The results are discussed with respect to five proposed functions of wing-spreading (wing-drying, thermoregulation, balancing, intraspecific signalling and as an aid to swallow fish) and it is concluded that they support overwhelmingly the wing-drying (or more generally plumage-drying) explanation, with the ultimate goal of conserving metabolic energy.

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INTRODUCTION

Wing-spreading is one of the most characteristic features of the behavioural repertoire of cormorants *Phalacrocoracidae*. Its function has long been a matter of conjecture, explanations ranging from wing-drying (Berry 1976, Clark 1969, McAtee & Stoddard 1945, Rijke 1967, 1968, 1970, Siegfried *et al.* 1975) to signalling foraging success (Jones 1978), balancing (Stabler 1957, Austin 1961), thermoregulation (Curry-Lindahl 1970), and as an aid to swallow fish (Smout & Smout 1991). Until the recent work of Hennemann (1983, 1984) and Winkler (1983) little detailed study of the habit had been undertaken and evidence in support of these interpretations was meagre. Hennemann investigated the Double-crested Cormorant *Phalacrocorax auritus* in Florida, U.S.A. and the Flightless Cormorant *Nannopterum harrisi* in the Galapagos Islands and found that wing-spreading was only observed when the plumage was wet, that too little time was spent wing-spreading to allow any significant supplementation of metabolism, that Double-crested Cormorants stood erect regardless of sun position, and orientated more strongly to

the wind than to the sun, and concluded that the behaviour was associated with wing-drying. Winkler's study, carried out in Sri Lanka, concerned the Little Cormorant *P. niger*. He too found that wing-spreading occurred only after a period in the water and that its duration was correlated with the time spent in the water and inversely with the temperature and the humidity deficit, and likewise concluded that wing-drying was the main reason for wing-spreading. This paper reports a study of wing-spreading, and the factors influencing its occurrence and duration, in the Cormorant *P. carbo*.

METHODS

Observations were made mainly from the east bank of the River Severn near Berkeley Power Station, Gloucestershire, England (51°41'N, 2°29'W) between September 1983 and April 1989. Cormorants are predominantly winter visitors to the Severn Estuary, and use the Berkeley part of the river for feeding, as a daytime resting area and, at certain times of year, as a night-time roost. The preferred daytime haul-out points were the

baffle wall separating the Power Station's cooling water intake and outfall (uncovered only at low water), and the navigation posts at either end of the baffle wall, where most wing-spreading behaviour was observed. A third navigation post to the north of the baffle wall, the river bank adjacent to the Power Station and a sandbank (Lydney Sand) on the opposite side of the river were also occasionally used. A fuller description of the area is given by Moyser & Sellers (1985). A number of observations of birds wing-spreading on the harbour wall at Thurso, Caithness, Scotland (58°36'N, 3°30'W) are also included. At both sites birds usually fed within a few hundred metres of the haul-out points where wing-spreading took place.

The time spent wing-spreading and its relationship to other activities was determined by recording the sequence and duration (as measured by stop-watch) of each type of behaviour in the first 20 minutes following a period in the water (the choice of 20 minutes is somewhat arbitrary, but virtually all birds had completed wing-spreading in this time). Birds which resumed foraging or left the study area within this time were excluded from the main part of the analysis. Behaviour was classified as either wing-spreading, high-intensity preening (continuous preening), low-intensity preening (preening interspersed with brief periods of resting), resting or other (mainly flying between perches, sleeping or agonistic behaviour towards other Cormorants). Where possible the duration and success of the period of foraging prior to wing-spreading was also recorded; however, full details were obtained for only 33 of the 126 birds studied. For all instances of wing-spreading observed, whether the bird's previous activity was known or not, orientation (assigned to one of the sixteen main compass points, N, NNE, NE *etc*), wind direction and speed (Beaufort scale assessed according to criteria given by the Meteorological Office 1982) cloud cover, rainfall, the direction of the sun and the bird's age were recorded.

RESULTS

Wing-spreading in relation to feeding and other behaviour

Wing-spreading occurred almost exclusively after a period of feeding, that is after having been in the water, and was only once observed in a bird which had definitely not been in the water in the previous 30 minutes. At the end of a period of foraging Cormorants underwent a very characteristic sequence of behaviour regardless of whether prey had been caught or not. This began with the bird splashing water over its back by vigorous opening and closing of its wings just under the surface of the water, coupled with dipping of the head and neck, somewhat after the fashion of a gull bathing. This "bathing" behaviour lasted typically 30 s and was usually repeated a number of times. After a further short pause of up to a minute or so, the wings were spread clear of the water, and held there momentarily as if allowing water to drain, before flying off to a convenient perch. Birds did not appear to experience any great difficulty in flying direct from the water. Occasionally in flight a bird would give a brief judder producing a shower of water droplets, rather like a dog drying itself. Wing-spreading as such was never observed on the water, though this has been reported in both the Cormorant and the Shag *P. aristotelis* (Fry 1957).

On landing Cormorants rested for a minute or so before holding their wings outstretched. This behaviour was almost always accompanied by spreading of the tail and often by fanning or flapping of the wings, and was interspersed with periods of preening or resting. Preening tended to become less intense as time passed and it was very unusual for wing-spreading or high-intensity preening to extend beyond the initial 20 minutes period. Some typical behavioural sequences in the first 30 minutes after landing are shown in Fig. 1. A period of immersion in the water was not invariably followed by wing-spreading, however. On 126 occasions when an individual Cormorant was followed after leaving the water, wing-spreading was observed in only 117 (93%)

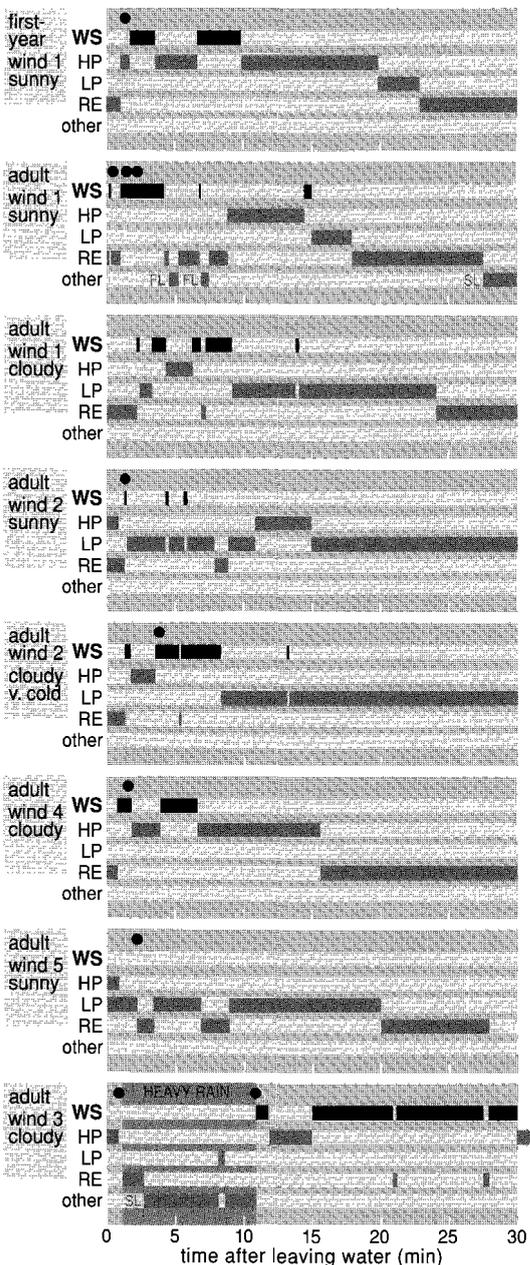


Fig. 1. Typical behavioural sequences in the first 30 minutes after leaving the water. WS wing-spreading, HP high intensity preening, LP low intensity preening, RE resting, SL sleeping, FL flying. The black dots indicate wing-flapping or fanning.

instances in the first 20 minutes after landing. Of the nine cases when it was not observed, four were associated with high winds (see below), two with rain, one with high temperatures, one apparently because it was dark and one apparently because the bird was hardly wet (the bird concerned had been in the water for less than a minute trying to snatch an Eel *Anguilla anguilla* from another Cormorant).

Wing-spreading was performed both by birds which had caught fish and those which had not, and no connection could be found between the incidence of wing-spreading and foraging success (Table 1).

Table 1. Incidence of wing-spreading in relation to foraging success. No significant difference in occurrence of wing-spreading was found between cases of successful birds (prey caught and swallowed) and unsuccessful birds (prey caught/released and no prey caught) (Fisher exact test, $p = 0.525$).

	wing-spreading	no wing-spreading
prey caught, swallowed	16	2
prey caught, released	5	0
no prey caught	8	0

Duration of wing-spreading

Up to nine individual periods of wing-spreading were recorded in the first 20 minutes after leaving the water. The median number of such periods was 4 at wind speeds of 0/1 (range 0-9, $n = 46$) falling to 2 at wind speeds ≥ 4 (range 0-6, $n = 14$). The total time spent with wings spread showed considerable variation. Just over half the birds studied (55 of 101) spent less than 4 minutes in this attitude (in the first 20 minutes after leaving the water) and only 8% devoted more than 10 minutes to it. The greatest total time spent wing-spreading was 18.5 minutes. The following sections consider possible causes of this variation.

Table 2. Behaviour of Cormorants in the first 20 minute. after feeding. Mean figures are shown for time spent wing-spreading (WS), high intensity preening (HP), low intensity preening (LP), resting (RE) and Others (sleeping, flying and antagonistic behaviour). Wind speed according to Beaufort-scale.

wind speed	<i>n</i>	WS	HP	LP	RE	Others
0/1	46	4.75	7.16	1.93	5.31	0.85
2	27	4.41	5.05	3.11	6.40	1.03
3	14	3.08	6.62	2.67	6.37	1.26
≥ 4	14	2.55	5.84	5.08	6.26	0.27

Wind speed Wing-spreading showed a marked dependence on wind speed and this appeared to explain a major source of variation in the time spent wing-spreading (Fig. 2, Table 2). A regression of duration of wing-spreading (t_{WS}) on wind speed (V , Beaufort scale) gave (coefficients $\pm SE$):

$$t_{WS} = 5.974 (\pm 0.740) - 1.052 (\pm 0.324)V$$

the downward trend in t_{WS} with increasing wind speed being statistically significant ($p < 0.002$). The variation with wind speed of the mean periods spent wing-spreading, preening, resting, etc. are shown in Table 2. As with wing-spreading, less time was devoted to high-intensity preening as the wind speed increased (though the trend was less pronounced), whilst the time spent in low-intensity preening increased. Evidently there is a tendency to switch from high to low-intensity preening with increasing wind speed, though other factors may also be involved.

Time spent foraging A Cormorant's plumage is not fully wetted immediately it enters the water. Close observation of birds which had just left the water showed that only after at least 5 minutes in the water was the whole plumage properly wetted and birds which spent less than 5 minutes in the water spent appreciably less time wing-spreading than those which had been in the water longer than this (Table 3).

Air temperature Initial analysis showed the time spent wing-spreading to be significantly longer at temperatures below 5°C than above this figure

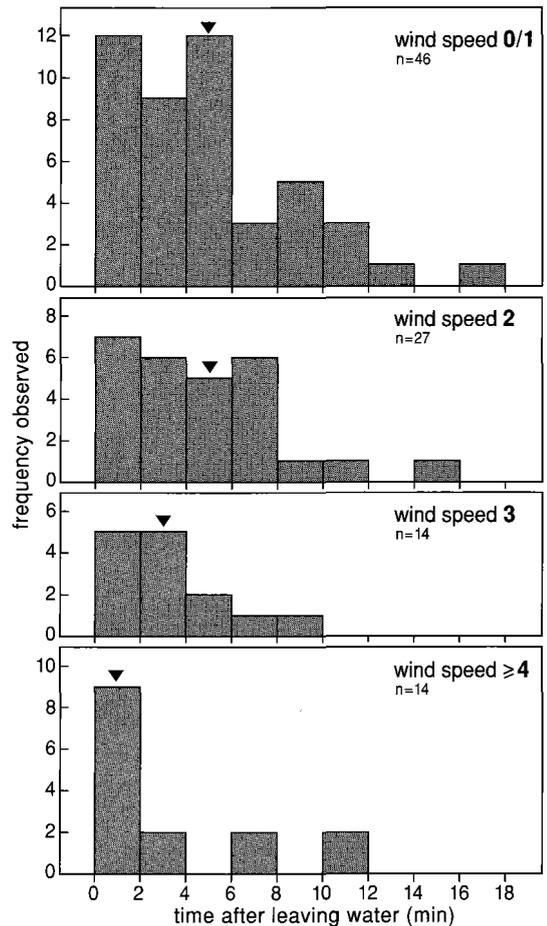


Fig. 2. Duration of wing-spreading in relation to wind speed (Beaufort scale), recorded during the first 20 minutes after leaving the water. Arrows indicate medians.

Table 3. Duration of wing-spreading in relation to sun, temperature (maximum daytime value), immersion time and age of the bird. All records refer to conditions with wind speeds of 0-2 Beaufort. *t* values according to Student's *t*-test (2-tailed), * $p < 0.05$.

	<i>n</i>	mean \pm <i>SD</i>	
Sun:			
sunny	25	4.80 \pm 4.54	<i>t</i> = 0.157
cloudy but dry	17	5.00 \pm 3.04	
Temperature:			
-5 to 5°C	15	6.02 \pm 3.46	<i>t</i> = 22.510*
5 to 15°C	14	3.04 \pm 2.87	
Immersion time:			
0-5 min.	7	1.47 \pm 1.55	<i>t</i> = 2.073*
\geq 5 min.	19	4.75 \pm 4.04	
Age:			
first-year	14	5.54 \pm 3.94	<i>t</i> = 0.859
adult	31	4.47 \pm 3.86	

(Table 3). A downward trend in time spent wing-spreading with increasing temperature was also apparent when t_{WS} was regressed on temperature, but this trend was not significant even when additional constraints were applied (e.g. restricting the analysis to data obtained at wind speeds of 0/1).

Rainfall The first 20 minutes after a period in the water coincided with falling rain on nine occasions. On four, during moderate to heavy continuous rain, the times spent wing-spreading were 0, 0, 0.3 and 0.4 minutes respectively. In a further four instances brief showers of rain temporarily inhibited wing-spreading, but in all of them it resumed as soon as the rain had stopped (cf. bird H in Fig. 1). The ninth bird spent a total of 2.2 minutes wing-spreading during continuous light rain (wind force 3). On the basis of these

rather fragmentary observations it seems that all but the lightest rain tends to inhibit wing-spreading, and that moderate to heavy rain almost completely curtails it. Precipitation, or its cessation, at times other than shortly after a bout of feeding was never observed to induce wing-spreading, though Jones (1978) states that "the posture is sometimes adopted by roosting [Long-tailed] Cormorants following a sudden rain-storm".

Insolation No evidence was found for any marked difference between sunny and overcast (but dry) conditions in the time spent wing-spreading (Table 3). It seems unlikely, therefore, that insolation has any appreciable effect on wing-spreading time.

Age On average first-year birds spent slightly longer than adults with their wings spread, but the difference was not statistically significant (Table 3).

Fanning and flapping of the wings during wing-spreading

Wing-spreading was accompanied by fanning or flapping of the wings in just under half of the birds studied (Table 4). The incidence of wing-fanning was not more prevalent at low wind

Table 4. Incidence of wing-fanning and flapping during wing-spreading. Figures shown are number of cases in %. Wind force according to Beaufort scale. FA fanning only, FF fanning and flapping, FL flapping. Difference in occurrence of fanning/flapping behaviour was not significant between the different wind force categories (Student's *t*-test).

wind force	<i>n</i>	FA	FF	FL	neither
0/1	46	7	17	26	50
2	27	11	26	33	30
3	14	0	21	50	29
\geq 4	14	7	7	3	43
all categories	101	7	19	34	41

speeds, as might have been expected if its function was to increase air flow over the wings in still air. Neither was the period spent in the water significantly longer for birds which wing-flapped than those which did not (11.73 ± 2.48 (SE) minutes compared with 9.50 ± 2.74 (SE) minutes, $t_{15} = 0.567$, $p = 0.29$, n.s.). Furthermore, birds which flapped or fanned their wings did not wing-spread for shorter periods on average than those which did not (Table 3).

Orientation during wing-spreading

Cormorants showed a strong tendency to face into the wind during wing-spreading (Fig. 3). Overall, 62.5% of birds orientated within one compass point of the wind direction, but this percentage varied with wind speed, from 54% at wind speeds of 0/1 to 81% at wind speeds of 4 or more (Fig. 3B). The failure of some birds to orientate into the wind appeared to be due to the proximity of other birds (especially on the navigation posts at Berkeley) and the orientation of the perch.

At higher wind speeds (≥ 2) the sun did not have any obvious effect on orientation, but at wind speeds of 0/1 it was an important determi-

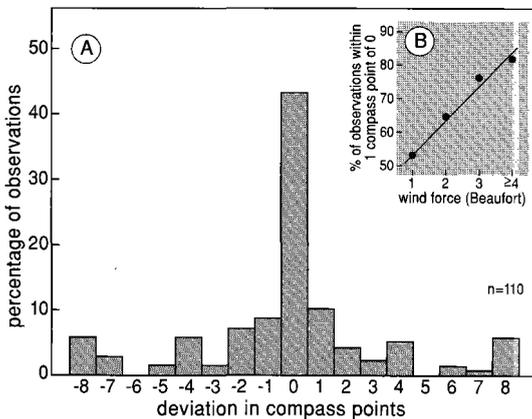


Fig. 3. Orientation during wing-spreading in relation to wind direction. Indicated is the deviation in compass points towards the wind direction (0). Negative figures for anti-clockwise deviation, positive figures for clockwise deviation. Number of observations within 1 compass point of 0 in relation to wind force.

Table 5. Extension of wings during wing-spreading in relation to wind force (Beaufort). Figures shown are number of cases (%) for each wing-spread category. (1) 2 x 2 table (0.25 / 0.50 / 0.75 versus 100); (2) 2 x 3 table (0.25 / 0.50 versus 0.75 versus 100); (3) 2 x 2 table (0.25 / 0.50 versus 0.75 / 100).

wind force	n	part of wing extended (%)				sign. ¹
		0.25	0.50	0.75	1.00	
0	41	0	2	61	37	NS (1)
1	69	0	0	55	45	** (1)
2	43	0	9	77	14	* (2)
3	22	0	50	41	9	** (3)
≥ 4	17	24	76	0	0	

¹ Level of significance according to contingency table; * $p < 0.01$; ** $p < 0.001$:

nant of the direction in which the bird was facing, as shown in Fig. 4. In 51% of cases under these

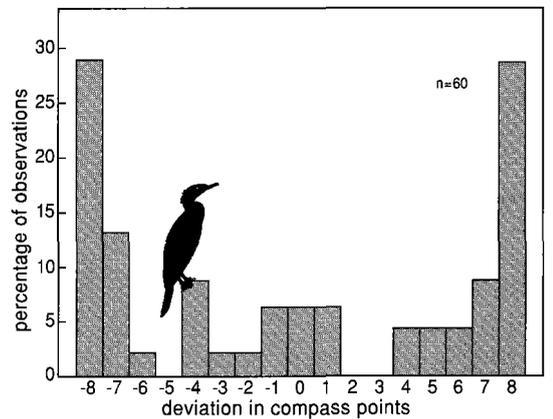


Fig. 4. Orientation during wing-spreading in relation to the direction of the sun. Data refer to situations with wind force of 0 or 1 Beaufort. Indicated is the deviation in compass points towards the direction of the sun (0). Negative figures for anti-clockwise deviation, positive figures for clockwise deviation.

circumstances orientation was directly away from the sun or within one compass point of this. The remaining 49% of cases were more or less evenly distributed between other orientations.

Extension of the wings during wing-spreading

Cormorants did not always extend their wings fully during wing-spreading. Indeed, birds with wings three-quarters spread were observed more frequently (55%) than were those holding them fully spread (28%). Increasing wind speed brought about a progressive decrease in the extent to which the wings were extended (Table 5) and at wind speeds of 4 or more birds were never seen to extend their wings more than about 50%.

DISCUSSION

Function of wing-spreading

Of the five functions which have been proposed for wing-spreading in the Phalacrocoracidae (wing-drying, thermoregulation, balance, intra-specific signalling and as an aid to swallowing fish) the evidence from this study supports overwhelmingly the wing-drying hypothesis. Thus it was found that (1) wing-spreading occurred almost exclusively when the plumage was wet (that is after having been in the water), (2) the longer the period of immersion (and so the wetter the plumage) the longer was the time spent wing-spreading, (3) the duration of wing-spreading was shorter the higher the wind speed, (4) birds tended to face into the wind during wing-spreading, and (5) birds tended to face away from the sun at low wind speeds. Possible effects of air temperature and heavy rain are also consistent with this interpretation.

The extent to which the plumage of cormorants and other water birds is wetted during foraging has been much commented upon. There is no doubt that the plumage of cormorants does become wet after a reasonable period in the water (*P. carbo* this study; *P. aristotelis* R.M. Sellers unpubl.). The uropygial gland of cormorants is of normal size (i.e. of comparable dimensions to

those of other aquatic birds) (Jacob & Ziswiler 1982, Johnston 1988) and birds can be seen transferring preen oils to their plumage. There is no reason, therefore, to believe that the wettability of cormorant's plumage is due to any deficiency in their uropygial glands.

An attempt to quantify the water repellency of the plumage of water birds has been made by Rijke (1967, 1968, 1970, 1987). Drawing on the theoretical work of Cassie & Baxter (1944) on the wettability of textiles, he noted an apparent correlation between a wettability index defined as $(r + d)/r$, where r is the radius of the "fibres" of the material, d is half the distance between the fibres, and the fibres are assumed to be circular in cross section, and the occurrence of wing-drying in cormorants and darters Anhingidae (index low) and absence in ducks Anatidae (index high). Although the validity of such an approach for feathers has been questioned (e.g. Hailman 1969, Elowson 1984, but see reply by Rijke 1987), it does seem that the rather open structure of Cormorants' feathers is at least partly responsible for the wettability of their plumage.

A direct investigation of plumage wettability was carried out by Mahoney (1984) who determined how much mass was gained when various aquatic birds were held briefly under water. How realistically these experiments mimic what happens in the wild is open to question, but in the Double-crested Cormorant mass gains of typically 1-3%, depending on the condition of the plumage, were found. Assuming these figures are applicable to cormorants in general, then it would seem that some 30-90 g (1-3% of 3 kg, the typical mass of Cormorants in Britain, cf. Cramp & Simmons 1977) of water would need to be expelled from the plumage of a Cormorant by wing-spreading. If metabolic heat were used to evaporate this water, the cost to the bird would be about 74-222 kJ per feeding bout, taking the heat of vaporisation of water as 2.47 kJ g^{-1} at 10°C (Hodgman *et al.* 1957). Presumably Cormorants are able to save most of this by wing-spreading.

The question as to whether it is the wings or the body plumage which are being dried is more

difficult to answer, but it appears likely that both are important. That wing-spreading is interspersed with periods of preening directed at the body feathers points to a role in drying the latter. On the other hand wing-fanning and flapping during wing-spreading suggest that wing-drying is also involved. Although Cormorants have no obvious difficulty in flying from the water, wet plumage no doubt hinders flight to a certain extent. It may be, therefore, that rapid drying of the plumage, especially the wings, is important to ensure a quick and efficient departure in the event of danger or disturbance. However, as Hennemann (1984) has pointed out, this explanation cannot apply to the Flightless Cormorant.

The suggestion that wing-spreading functions in balance (Stabler 1957, Austin 1961) finds no support in either this or the earlier work of Hennemann (1983, 1984) or Winkler (1983). Balance may however be the explanation of the effect of wind speed on the degree to which the wings are extended during wing-spreading (Table 4), for it seems likely that Cormorants would have difficulty in balancing at higher wind speeds with their wings fully spread.

The hypothesis that wing-spreading might be a form of display to indicate foraging success derives from some observations of Jones (1978) on the Long-tailed Cormorant *P. africanus* in Lesotho. He compared the frequency of wing-spreading with fishing success and showed that wing-spreading was much more common among birds which had caught prey than those which had not. Whether other explanations of the findings are tenable is difficult to say but it may be relevant to note the following: (1) the comparatively small sample size ($n = 27$), (2) the short immersion times (which in *P. carbo* and *P. niger* give rise to comparatively short periods of wing-spreading and may inhibit it altogether), (3) the failure to consider the role of wind or other weather variables in modifying wing-spreading behaviour, (4) a possible bias arising in some of the observations (in at least three instances, when two or more birds were diving simultaneously for fish, Jones deliberately forced the birds to leave the

water when one had made a catch; the unsuccessful birds did not spread their wings, but this might have been because they intended to return to the water as soon as the observer retreated), and (5) the possibility that wing-spreading in *P. africanus* functions in thermo-regulation (see also comments below).

The possibility that wing-spreading is an aid to fish digestion (Smout & Smout 1991) is not consistent with the observation that birds which have been unsuccessful in foraging nevertheless spread their wings and this suggestion can be rejected.

The Cormorant spends far too little time in wing-spreading for it to play any significant part in thermoregulation. Heat dumping is in any case intrinsically unlikely at the comparatively low temperatures experienced in south-west England or northern Scotland in the winter months. By contrast in the Anhinga *Anhinga anhinga*, in which wing-spreading unquestionably serves in both plumage drying and thermoregulation, 31% of the birds' time overall and up to 88% in cool sunny weather is spent with wings spread (Hennemann 1982).

Wing-spreading in the Phalacrocoracidae

In the four cormorant species in which wing-spreading has been investigated in detail (*P. auritus*, *P. niger*, *P. carbo*, and *P. harrisi*) there is little doubt that plumage drying is the prime function, and less complete evidence suggests that this is true of at least two other species, *P. aristotelis* (R.M. Sellers unpublished) and *P. neglectus* (Siegfried *et al.* 1975). For two further species, *P. africanus* (Siegfried *et al.* 1975) and *P. capensis* (Berry 1976), both of which have a tropical/sub-tropical distribution (Tuck 1978) wing-spreading may also be used in thermoregulation in a manner similar to that of the Anhinga. Finally it should be mentioned that wing-spreading is unknown in Antarctic populations of the Blue-eyed Shag *P. atriceps* (Bernstein & Maxson 1982) but occurs in birds of this species breeding in Chile (Rasmussen & Humphrey 1988). Why this should be is not known, but, in view of the marked inhibitory

effect of wind demonstrated in this study, it seems possible that the persistent strong winds at high latitudes have played a part in the elimination of wing-spreading behaviour amongst the Antarctic populations.

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SAMENVATTING

Dit is een studie naar het vleugelspreidgedrag bij 126 afzonderlijk waargenomen Aalscholvers op verzamelplaatsen in ZW-Engeland en N-Schotland. Hieruit blijkt nadrukkelijk dat de voornaamste functie van dit gedrag bestaat uit het drogen van vleugels of zelfs het gehele verenkleed. Dit voor de gehele familie karakteristieke gedrag trad alleen op onmiddellijk na een verblijf in het water en de duur ervan was omgekeerd evenredig met de duur van de voorafgaande periode in het water en met de windsnelheid. Bovendien neigden

de vogels ertoe om zich tijdens het vleugelspreiden tegen de wind in te oriënteren en bij geringe windsnelheden van de zon af. Ook de mate waarin de vleugels werden gespreid nam af bij toenemende windsnelheden. Door het bevorderen van de luchtstromingen door vleugels en lichaamsveren tijdens het vleugelspreiden kan naar schatting een energiebesparing van 74-222 kJ (de energie nodig voor het doen verdampen van de in het verenkleed opgenomen hoeveelheid water) per fourageerperiode worden bereikt.

Voor in het verleden voorgestelde mogelijke alternatieve functies (thermoregulatie, handhaven van even-

wicht, intraspecifieke signaalfunctie en ondersteuning voor de vertering van vis) zijn in deze studie geen aanwijzingen gevonden. Daarentegen zijn de twee laatstgenoemde functies onaannemelijk, omdat het gedrag niet beïnvloed werd door het al of niet succesvol zijn van de voorafgaande fourageerperiode. Thermoregulatie is als functie onaannemelijk vanwege een te gering voorkomen van het gedrag en met name het door vleugelspreiden tegengaan van warmte stress (zoals aangetoond bij Amerikaanse Slanghalsvogels) lijkt bij de overheersende luchttemperaturen in de gematigde luchtstreken onwaarschijnlijk.

