Diving angle of great cormorants

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Abstract: Seabirds can maximize the relative time spent at depths where prey occur by minimizing the commuting time taken to reach these depths. One way to achieve this goal is to modify dive angle, but there are few measures of dive-angle in free-foraging seabirds. In 2003, we monitored simultaneously the swimming speeds and diving depths of great cormorants (*Phalacrocorax carbo*) foraging off the Greenland coast, and used these data to reconstruct their descent angle. Both males and females dived on average $<$ 5 m, but some dives were up to 26 m. Dive angles did not differ between dive types (benthic, pelagic). Angles did not change much for dives $<$ 12 m but increased with increasing maximum depth in both males and females for dives $>$ 12 m. We suggest that birds are able to reduce their descent time for dives beyond this depth by performing pre-dive leaps that allow them to use the momentum of the fall to descend almost vertically and at great speeds. Such pre-dive leaps in shallower dives would be unsuitable because of the proximity of the seabed and the risk of startling prey. Finally, in contrast with deeper divers, descent angles were not steeper when undulations were observed in the depth profile of the previous dive, probably because birds feed on dispersed prey.

key words: great cormorants, dive angle, shallow divers, prey-predators, pre-dive leap

Introduction

Seabirds can maximize the relative time spent at depths where prey occur by minimizing the commuting time taken to reach these depths. However, body size (Wardle, 1975), mode of propulsion and buoyancy (Wilson and Wilson, 1995) limit the speed that an animal can use to reach a given depth. Consequently, many diving seabirds have strategies to minimize commuting times, such as increasing swim speeds (Otani *et al*., 1998) or modifying their buoyancy by swallowing stones (Murphy, 1936) or reducing air in the plumage (Wilson and Wilson, 1995). However, seabirds cannot change their speed without moving away from their minimum cost of transport (Boyd *et al*., 1995) and thus, the easiest way to reduce commuting times, *i.e.* to optimize foraging times, is to modify their angle of diving (*cf.* Wilson *et al*., 1996; Ropert-Coudert *et al*., 2001). Knowledge of the angle at which seabirds choose to commute between surface and foraging depth is difficult to assess using direct observation (but see Wilson and Wilson, 1988). Progress in this domain has come from the use data-log-

gers attached to free-ranging animals to monitor their activities at sea (Boyd *et al.*, 2004). Recent technological advances have allowed swim speed and depth to be monitored concomitantly on diving seabirds, enabling reconstruction of dive angles (Wilson *et al.*, 1996; Ropert-Coudert *et al.*, 2001). To date, studies on dive angles in seabirds have concentrated on deep-diving species, such as Adélie penguins (*Pygoscelis adeliae*). For instance, empirical observations of several cormorant species indicated that steeper dive angles are used when birds dive in deeper water (Wilson *et al.*, 1992a). However, little information is available for shallow divers, where the consequences of high positive buoyancy near the water surface are likely to be most marked (Wilson *et al.*, 1992b).

In boreal summer 2003 we monitored simultaneously and for the first time the swim speed and diving depth of great cormorants (*Phalacrocorax carbo*) foraging off the Greenland coast. These birds feed mainly on benthic and demersal prey (Grémillet *et al.*, 2004), showing a combination of benthic and, to a lesser extent, pelagic dives. We report here on the dive angle of free-ranging cormorants inferred from data loggers and discuss the change of the angle with dive profiles and dive depth.

Material and methods

Loggers were deployed on 10 great cormorants raising chicks on Qeqertaq (69°30´N, 54°05´W) in the Diskofjord area, Disko, West-Greenland during June/July 2003.

Swim speed and depth were measured with a 12-bit resolution, three-channel UWE200-PDT logger (102 mm long, 20 mm in diameter and weighing 50 g, Little Leonardo, Japan) with 16 Mb memory. The loggers had a relative accuracy of 0.05 m and 0.05 ms^{-1} for depth and speed, respectively, with a maxmim depth range of 0–200 m. Data were recorded every second. Speed was measured by counting the number of revolutions of an anteriorly-mounted propeller. This was converted into flow speed (ms^{-1}) using data obtained from calibration experiments in a 60 m tow tank (Ocean Engineering, Vancouver, Canada). Here, speed loggers were placed in water currents running at 0.5, 1, 2, 3 and 4 ms^{-1}. Regression equations between flow speed and number of propeller rotation were calculated for each logger. For all the equations, the coefficient of determinations were >0.99.

Adult cormorants feeding small chicks were caught at their nest using a noose mounted onto a telescopic pole. We covered the head of each individual with a black hood to reduce stress. Handling lasted less than 10 min in all cases. Each device was attached with four strips of waterproof TESA tape to feathers of the middle upper back, parallel to the bird's main axis. Birds were released in the vicinity of the colony, and all returned to their nests within five minutes.

Care was taken to ensure that bird fitness and activity would not be impaired by the loggers. The use of TESA tape allowed us to attach the device quickly, minimizing handling stress (Le Maho *et al.*, 1992). It also allowed us to recover the loggers without causing damage to the feathers (Wilson *et al.*, 1997). The loggers accounted for $<2\%$ of the bird's body mass, well below the 5% threshold beyond which behavioural disruptions are likely to occur in flying seabirds (Croll *et al.*, 1992). All equipped birds went at sea and brought back food to their chicks, and continued to raise their chicks normally following recovery of devices. Data loggers were retrieved 1–2 days after deployment. Over the deployment period, the birds performed several foraging bouts, *i.e.* sequences of continuous diving activity where

dives were not separated by more than 10 min.

Three categories of dives were identified based on their depth profiles. Square-shaped dives had acute descent and ascent rates and a constant depth at the bottom phase of the dive (maximum amplitude of the depth changes <0.65 m) (*cf.* Ropert-Coudert *et al.*, 2001). Other dives were divided into V-type and W-type, based on the absence or presence, respectively, of undulation (maximum amplitude of depth change >0.65 m) in the depth profiles (*cf.* Wilson, 1995). The value 0.65 m was chosen arbitrarily as it is the value that gave the best results when compared with visual estimation of dive shapes. Only dives >1 m were considered for analysis. The change of diving depth and swim speed over the foraging trip has been analysed elsewhere (Ropert-Coudert *et al.*, 2004b) and the present study focuses only on dive angles. Because descent phases of dives were very short, lasting on average 5.8 ± 1.7 s, angles of descent (β) in radians (although subsequent results are presented in degrees) were calculated as follows :

$$\mathrm{Sin}(\beta) = \Delta D / Sp,$$

where ΔD represented the depth change between surface and the start of the bottom phase of the dive and Sp represented the swim speed averaged over the descent period. Only dives with descent duration >2 s were used to calculate dive angles. The ascent angle was not analysed because birds may use buoyancy to glide up to the surface (*e.g.* Ropert-Coudert *et al.*, 2004a) and swim speed in these cases may be overestimated. In some instances, seaweed obstructed the propeller, which prohibited free rotation, leading to aberrant results, *i.e.* a speed suddenly dropping to 0 in the middle of a dive and remaining at 0 throughout the rest of the dive, or no swim speed data. For these dives descent angles were not calculated.

Comparisons of number of bouts, bout duration and number of dives per bouts, as well as comparisons of dive parameters between males and females, were conducted using Student t-tests. Relationships between descent angle and maximum depth of dives were tested using simple regressions. For this, descent angles of each bird were averaged over categories of maximum dive depth at 2 m intervals so that, for instance, for each individual there was one angle value for the 0–2 m dive category. All statistical tests were performed using Statview (version 4.57, Abacus Concepts Inc. 1996) following Sokal and Rohlf (1969). The statistical threshold was 0.05. Values are presented as means $\pm$ standard deviation.

Results

All birds were recaptured and all data loggers retrieved. Reliable diving and speed data were obtained for 10 birds, 5 males and 5 females. Aberrant dives accounted for, on average, $27.9 \pm 21.1\%$ of dives in all birds. Males (3455.0 ± 115.1 g, $n=5$) were significantly heavier ($t_{8df} = -8.03$, $P<0.0001$) than females (2750 ± 159.1 g, $n=5$) but the maximum dive depth of males (4.80 ± 2.47 m) was not significantly different ($t_{8df} = 0.21$, $P=0.84$) from that of females (4.54 ± 1.15 m). Although birds dived principally in the top 5 m of the water column, depths in excess of 20 m were occasionally reached.

Because there was no statistical difference between sexes, their data were pooled. Dive angles between square-shaped ($42.5 \pm 14.4°$), V-shaped ($35.1 \pm 10.5°$) and W-shaped dives ($41.3 \pm 10.9°$) were not significantly different ($F_{2,27} = 1.093$, $P=0.35$). The relationships between the descent angle and the maximum depth of dives being similar for males and
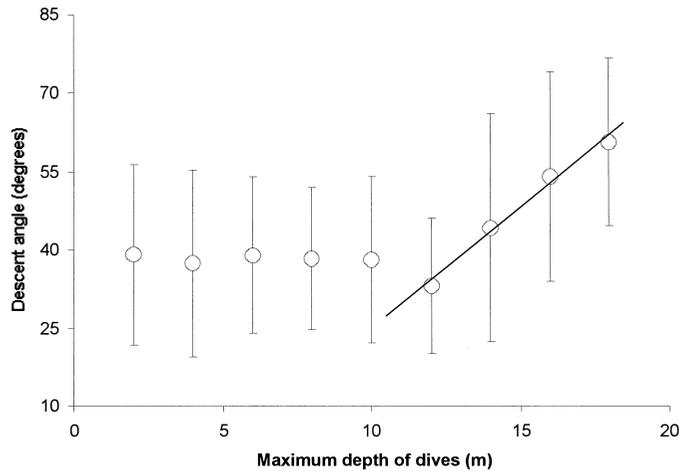
Fig. 1. Relationship between dive angles during the descent phase and maximum dive depth (open circles). For dives deeper than 12 m the relationship was best-fitted with a linear function (equation in the text). Vertical bars indicate standard deviation.

females, data were pooled. Dive angles were constant until 12 m depth ($F_{1,4} = 3.38$, $P = 0.14$) but there was a clear, positive, linear relationship between dive angle and maximum depth beyond 12 m (Fig. 1; $Y = -21.19 + 4.61 * X$; $R^2 = 0.99$, $F_{1,2} = 152.8$, $P = 0.007$). Finally, there was no significant relationship between the descent angle and the number of undulations (generally taken as an index of prey encounters in birds foraging in the mid-water zones, *cf.* Simeone and Wilson, 2003) in the previous dive ($F_{1,1525} = 22.24$, $P < 0.0001$).

Discussion

Our data revealed that shallow-diving great cormorants do not change their diving angle according to the depth profiles of their dives or the presence of undulations in the previous dives. This is probably because cormorants in Greenland feed mainly on demersal or bottom-dwelling fish (Grémillet *et al.*, 2004). For the cormorants prey, camouflage under rocks or being hidden in the sand are the most appropriate anti-predatory mechanisms. In order to locate the fish, cormorants may have to slow down and search around rocks or near the bottom. Most dives of cormorants are, therefore, benthic and birds would have no advantage in scanning the water column during the descent phase. They should rather head directly towards the seabed, adopting acute angles to reduce the descent time.

In our data, the dive angle of cormorants did not vary much with increasing maximum depth until dives with a 12 m maximum depth, beyond which the dive angle started to increase substantially. Indeed, since body size, among other things, limits the swim speed attainable (Wardle, 1975), birds would adopt a steeper angle to reach deeper depths in a minimum time so as to optimize the time spent at the bottom of the dive where prey are more likely to be found. Foot-propelled divers have been shown to engage often in pre-dive leaps when diving in deep waters, supposedly using the momentum of the jump to increase descent

speed and thus reduce transit time (Wilson *et al*., 1992a). This technique is, however, unsuitable for shallow dives because high descent speeds are dangerous close to the seabed and the leap may startle potential prey. We suggest, therefore, that great cormorants perform full pre-dive leaps for dives deeper than 12 m to increase their descent speed, adopting a virtually vertical descent angle to reduce transit times. Based on the risks that pre-leaping incurred for shallow divers, 12 m may be the safety margin below which great cormorants may not use pre-dive leaps. Cape cormorants, *Phalacrocorax capensis*, are predicted to perform full pre-dive leaps for dives to 6 m depth, while larger whitebreasted cormorants, *P. carbo*, start to perform quasi-dive leaps at 7 m (Wilson *et al*., 1992a). Since Great cormorants are much larger than both Cape and whitebreasted cormorants, a deeper safety margin (12 m) is to be expected. Another possibility is that buoyancy decreases with depth and birds can descend easily in water deeper than 12 m (Wilson *et al*., 1992b). Further data are required to test such hypothesis.

Acknowledgments

References

Boyd, I.L., Reid, K. and Bevan, R.M. (1995): Swimming speed and allocation of time during the dive cycle in Antarctic fur seals. Anim. Behav., **50**, 769–784.

Boyd, I.L., Kato, A. and Ropert-Coudert, Y. (2004): Bio-logging Science: sensing beyond the boundaries. Mem. Natl Inst. Polar Res., Spec. Issue, **58**, 1–14.

Croll, D.A., Gaston, A.J., Burger, A.E. and Konnoff, D. (1992): Foraging behavior and physiological adaptation for diving in thick-billed murres. Ecology, **73**, 344–356.

Grémillet, D., Kuntz, G., Delbart, F., Mellet, M., Kato, A., Robin, J.-P., Chaillon, P.-E., Gendner, J.-P. and Le Maho, Y. (2004): Linking the foraging performance of a marine predator with local prey abundance. Funct. Ecol., **18**, 793–801.

Le Maho, Y., Karmann, H., Briot, D., Handrich, Y., Robin, J.-P., Mioskowski, E., Cherel, Y. and Farni, J. (1992): Stress in birds due to routine handling and a technique to avoid it. Am. J. Physiol., **263**, 775–781.

Murphy, R.C. (1936): Oceanic Birds of South America. Vol. 1. New York, Am. Mus. Nat. Hist.

Otani, S., Naito, Y., Kawamura, A., Kawasaki, M., Nishiwaki, S. and Kato, A. (1998): Diving behavior and performance of Harbor porpoises, *Phocoena phocoena*, in Funka bay, Hokkaido, Japan. Mar. Mammal Sci., **14**, 209–220.

Ropert-Coudert, Y., Kato, A., Baudat, J., Bost, C.-A., Le Maho, Y. and Naito, Y. (2001): Time/depth usage of Adélie penguins; an approach based on dive angles. Polar Biol., **24**, 467–470.

Ropert-Coudert, Y., Grémillet, D., Ryan, P.G., Kato, A., Naito, Y. and Le Maho, Y. (2004a): Between air and water: the plunge-dive of the cape gannet *Morus capensis*. Ibis, **146**, 281–290.

Ropert-Coudert, Y., Grémillet, D. and Kato, A. (2004b): Swim speed of male and female great cormorants in rela-

tion to prey escape speeds. submitted to Mar. Ecol. Prog. Ser.

Simeone, A. and Wilson, R.P. (2003): In-depth studies of Magellanic penguin (*Spheniscus magellanicus*) foraging: can we estimate prey consumption by perturbations in the dive profile? Mar. Biol., **143**, 825–831.

Sokal, R.R. and Rohlf, F.J. (1969): Biometry. San Francisco, W.H. Freeman, 776 p.

Wardle, C. (1975): Limit of fish swimming speed. Nature, **255**, 725–727.

Wilson, R.P. (1995): Foraging ecology. Bird Families of the World: The Penguins Spheniscidae, ed. by C. Perrins *et al.* Oxford, Oxford University Press, 81–106.

Wilson, R.P. and Wilson, M.-P.T. (1988): Foraging behaviour in four sympatric cormorants. J. Anim. Ecol., **57**, 943–955.

Wilson, R.P. and Wilson, M.-P. (1995): Buoyancy and depth utilisation in foraging cormorants: wet feathers and that sinking feeling. Le Gerfaut, **85**, 41–47.

Wilson, R.P., Wilson, M.-P.T. and Nöldeke, E.C. (1992a): Pre-dive leaps in diving birds: why do kickers sometimes jump? Mar. Ornithol., **20**, 7–16.

Wilson, R.P., Hustler, K., Ryan, P.G., Burger, A.E. and Nöldeke, E.C. (1992b): Diving birds in cold water: do Archimeds and Boyle determine energetic costs? Am. Nat., **140**, 179–200.

Wilson, R.P., Culik, B.M., Peters, G. and Bannasch, R. (1996): Diving behaviour of Gentoo penguins, *Pygoscelis papua*; factors keeping dive profiles in shape. Mar. Biol., **126**, 153–162.

Wilson, R.P., Pütz, K., Peters, G., Culik, B., Scolaro, J.A., Charrassin, J.-B. and Ropert-Coudert, Y. (1997): Long-term attachment of transmitting and recording devices to penguins and other seabirds. Wildl. Soc. Bull., **25**, 101–106.