



To breathe or not to breathe? Optimal breathing, aerobic dive limit and oxygen stores in deep-diving blue-eyed shags

TIMOTHEE R. COOK*, AMELIE LESCROËL*, YANN TREMBLAY† & CHARLES-ANDRE BOST*

*Centre d'Etudes Biologiques de Chizé, Centre National de la Recherche Scientifique

†Long Marine Laboratory, University of California

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Optimality models exist for diving endotherms, but are rarely tested with behavioural data or used to estimate oxygen reserves. We used a model for avian divers to study the extreme diving performances of blue-eyed shags. Time–depth recorders were deployed on 15 breeding Kerguelen shags, *Phalacrocorax verrucosus*. The shags regularly dived deeper than 100 m and longer than their behavioural aerobic dive limit (4 min). The dive duration to postdive interval ratio peaked for dives lasting 1 min, the dive time theoretically necessary to deplete oxygen reserves from the respiratory tract. Most dive parameters of the Kerguelen shag converged with those known for the Crozet shag, *Phalacrocorax melanogenis*. Yet, whereas the distribution of dive durations matched optimal breathing for the Crozet shag (shallow diving), this was not true for the Kerguelen shag which made mostly deep dives. Thus, regardless of how similar the physiologies of blue-eyed shag species may be, they can adapt their diving behaviour to different environmental conditions, in this case resource distribution. From the model, the volume of body oxygen reserves for blue-eyed shags was calculated as 264 ml/kg, which is significantly higher than values found in the literature for avian divers. The volume of the respiratory tract obtained with the model (830 ml), however, was realistic. We suggest the model overestimated body oxygen stores because blue-eyed shags have numerous means for reducing their deep-diving metabolism, such as bradycardia, hypothermia or anaerobic metabolism.

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Terrestrial lineages of vertebrates have colonized freshwater and saltwater ecosystems over millions of years of evolution. The morphological and physiological adaptations to diving in air-breathing vertebrates have been selected as a response to the constraints of moving in a liquid environment and submerging with a limited store of oxygen. These include hydrodynamic profiles and efficient propulsion systems, increased oxygen stores via augmented haemoglobin or myoglobin concentrations,

reflex bradycardia or increased tolerance to anaerobiosis. In endotherms, heat loss to the surrounding water drastically increases metabolism, particularly in the polar or subpolar regions. Such animals consequently have dense fur or feather coatings, or a thick blubber layer, while peripheral vasoconstriction limits heat transfer from the body core to the aquatic environment (see Kooyman 1989; Butler & Jones 1997; Butler 2001 and associated references).

Correspondence: T. R. Cook, Centre d'Etudes Biologiques de Chizé, CEBC–CNRS UPR 1934, Villiers-en-bois, F-79360, Beauvoir-sur-Niort, France (email: cook@cebc.cnrs.fr). Y. Tremblay is at the Long Marine Laboratory, University of California, 100 Shaffer Road, Santa Cruz, CA 95060, U.S.A.

Yet, for many endotherms, none of these adaptations are fully sufficient to cancel out the high costs of diving. In avian divers, diving metabolic rates are very high and can be 2–10 times the basal metabolic rate (Enstipp et al. 2005). Mass-specific rates are higher for foot-propelled divers (cormorants, diving ducks) than for wing-propelled

divers (aloids, penguins) and increase significantly with decreasing body mass, decreasing water temperature and increasing dive depth (Enstipp et al. 2006). The direct consequence for birds is that the higher the metabolic rate, the faster the oxygen reserves are depleted and the sooner the dive must be aborted.

In this context, avian divers may be expected to deploy behavioural strategies that best use their oxygen reserves to optimize the time spent underwater, time dedicated to foraging, versus time spent at the surface recovering from the dive (oxygen reloading) and thus time lost to foraging. Certain divers are known to extend the duration of their dives past their aerobic dive limit, exploiting anaerobic metabolic pathways (Kooyman et al. 1980). However, this is not true in the majority of cases (Butler & Jones 1997), where the time spent submerged is related to the amount of oxygen stored and the diving metabolic rate. A priori, independently of dive depth, staying underwater until oxygen reserves are entirely depleted appears to be the most efficient strategy, since it allows the animal to stay submerged for longer, thus extending foraging possibilities. However, observations show that for a given species, birds will dive using a wide range of durations and that dive duration is most often positively related to dive depth.

Walton et al. (1998) proposed a model for avian divers that helps us understand why birds choose not to prolong a dive when it is obvious they still have substantial oxygen stores. This model is based on diving models by Kramer (1988) and Houston & Carbone (1992), and is inspired by Charnov's (1976) marginal value theorem. Walton et al. (1998) suggested that dives lasting the time it takes to deplete just the oxygen from the respiratory tract are followed by the proportionately shortest postdive intervals (surface recovery periods), because the time it takes to recover corresponds only to the turnover time of the respiratory gases. Consequently, one of the theoretically most efficient strategies for an avian diver is to target dives lasting as long as it takes to reach the maximum dive duration to postdive interval ratio because it yields the greatest proportion of time submerged, and thus foraging, for the smallest proportion of time lost to surface recovery. Although Walton et al. (1998) supported their model with field data on species from the alcid and cormorant families, no study using both field data and their model has since been published for estimating physiological parameters, such as the turnover rate of respiratory tract gases or the volume of oxygen reserves. These are essential for understanding diving performance but are difficult to measure.

Cormorants are foot-propelled pursuit-divers that dive to the water bottom to feed on benthic organisms, mainly fish, but also molluscs and annelids (Orta 1992). The so-called 'blue-eyed shag complex' (Van Tets 1976) is a group of closely related cormorant species living on the coasts and islands of the waters of the Southern Ocean between roughly 40°S and 70°S latitude (New Zealand, Patagonia, Antarctic Peninsula, sub-Antarctic islands) and comprising 13 species (Siegel-Causey 1988). Each species is considered to be geographically isolated from the others. Blue-eyed shags represent one of the main top predators to feed off the coastal benthic fish community (Casaux & Barrera-Oro 2006), fish from the Notothenioidei suborder, a group

that evolved specifically in the Southern Ocean (Eastman 2005). They are well known within the cormorant family for extreme dives (maximum recorded dive depth 145 m, Tremblay et al. 2005), a remarkable feat considering their body mass when compared to the other groups of avian divers. The mechanisms that enable these medium-sized birds with little blubber and partially wettable plumage (Grémillet et al. 2005) to sustain such behaviour in the cold sub-Antarctic or Antarctic waters remain poorly understood (Bevan et al. 1997; Cook & Leblanc 2007; Quintana et al. 2007).

We studied the diving behaviour of the blue-eyed shag species that lives in the Kerguelen Archipelago, the Kerguelen shag, *Phalacrocorax verrucosus*. By using time–depth recorders we examined first whether Kerguelen shags dived longer than their behavioural aerobic dive limit, using the method proposed by Kooyman et al. (1980). Second, our objective was to determine whether Kerguelen shags behaved according to the optimality model proposed by Walton et al. (1998). Among other parameters, we wished to establish the dive duration after which the respiratory tract oxygen reserves are considered to be depleted, to see whether birds targeted this particular dive duration ('optimal breathing'). We compared the results with those obtained by Tremblay et al. (2005) using time–depth recorders on another species of blue-eyed shag living 1400 km from the Kerguelen Archipelago, the Crozet shag, *Phalacrocorax melanogenis*, inhabiting the Crozet Archipelago and faced with very distinct oceanographic features. At Crozet, the marine shelf is spatially limited. In contrast, Kerguelen holds the largest marine shelf of the southern Indian Ocean with extensive fish availability (Duhamel et al. 2005). This allowed us to test the degree to which the environment can influence optimality. To investigate how these animals are able to dive so far, we constructed a physiological model for deep-diving blue-eyed shags. Using the optimality model framework and focusing in particular on the rate of oxygen consumption inferred from the dive parameters, we sought to estimate the body oxygen store volumes of blue-eyed shags. Finally, we were able to compare the resulting estimates with volumes that have been found for other diving vertebrates and consequently to examine the pertinence of the optimality model.

METHODS

Study Site, Procedure and Data Loggers

The Kerguelen Archipelago lies in the southern Indian Ocean at the limit of Antarctic waters. It consists of a large mainland surrounded by 300 islets and islands (total surface 7000 km²). The study colony was located on the mainland (Fig. 1), at Cap Cotter (49°03'S, 70°19'E), above a rocky shore lined with kelp beds and facing the open ocean.

During the 2002–2003 and 2003–2004 summer breeding seasons, 15 adult breeding Kerguelen shags were equipped with time–depth recorders (TDRs). Birds were captured at their nest, with a noose at the end of a 4 m fishing pole. At a safe distance from the nest and other individuals, experimental birds were measured and weighed,

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