



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

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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).

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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,

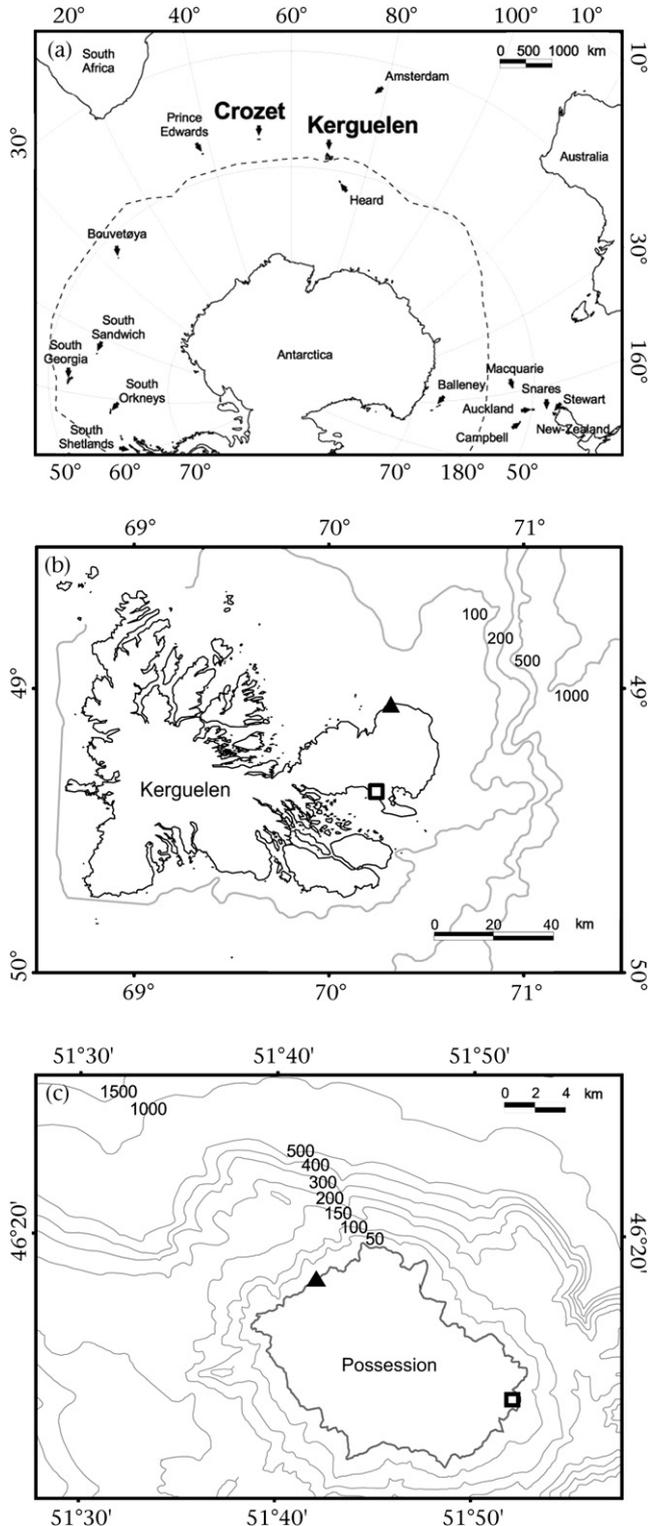


Figure 1. (a) General location of the Kerguelen and Crozet Archipelagos in the Southern Ocean in relation to the Polar Front (dotted line). (b) Map of the Kerguelen Archipelago, with the location of the study colony of Kerguelen shags, *Phalacrocorax verrucosus* (black triangle). The Port-aux-Français Station is represented by the white square. Kerguelen waters vary from 2 to 6 °C between winter and summer. (c) Map of Possession Island, Crozet Archipelago. The black triangle is the location of the study colony of Crozet shags, *Phalacrocorax melanogenis* (Tremblay et al. 2005). The Alfred Faure Station is represented by the white square. Crozet waters vary between 4 and 8 °C between winter and summer.

and TDRs were attached on the cover feathers of the chest with Tesa tape secured with cyanoacrylate glue (Loctite 401). To reduce handling stress, the head of each bird was covered with a hood. The birds were then released towards the nest (maximum total handling time 10 min). Birds were recaptured after a variable period lasting from between one foraging trip to 2 days, and the equipment was removed.

This study was approved by the ethics committee of the French Polar Institute (Institut Paul Emile Victor – IPEV). The TDRs were MK9 models (Wildlife Computers, Woodinville, Washington, U.S.A.). They measured $6.7 \times 1.7 \times 1.7$ cm and weighed 30 g (1.1–1.2% of the bird's body mass). Their tips were streamlined to reduce drag. The loggers were programmed to record depth and light every 1 s and external temperature every 5 s. Depth and temperature resolution were ± 0.5 m and ± 0.05 °C. Light (relative scale) was linearly related to log lx. Logger memory was 2.03 MB.

Analysing Dive Data

We calculated dive parameters using software designed by us for dive analysis (e.g. Tremblay & Cherel 2003). Dive data consist of a succession of depth values over time (Fig. 2). A dive is characterized by a descent phase, a bottom phase and an ascent phase. We defined dive depth as the maximum depth reached during the dive. Dive duration was defined as the time difference between the moment of emergence at the sea surface and the preceding event of submergence. In accordance with the depth resolution of the TDRs, a dive was considered as taking place only when it was ≥ 1 m. Bottom time was expressed as the time spent in the zone below 80% of maximum dive depth (Kato et al. 1999).

A surface postdive interval (PDI), enabling recovery, separates one dive from the next. In cases where blue-eyed shags flew from the sea surface to the sea surface between two successive dives, the PDI of the first dive was considered to have ended when the flight began. Flight periods were detected by using published techniques for describing behaviour associated with the use of ventrally attaching TDRs on flying avian divers (Tremblay et al. 2003, 2005).

Behavioural Aerobic Dive Limit (bADL)

The aerobic dive limit is the dive duration after which there is a sudden increase in blood lactate concentration, caused by an elevation in anaerobic metabolism. We estimated the bADL by plotting all data points of dive duration in relation to PDIs according to Kooyman et al. (1980). The bADL occurs when there is an abrupt slope change in this relation, and PDIs begin to rise exponentially with dive durations, reflecting the increase in blood lactate concentration. This change point is determined visually on a graphic bottom contour plot of the data. A bottom contour plot is used because the minimum values of PDIs corresponding to the longest values of dive durations are the most relevant physiologically (they represent the physiological limits of the species).

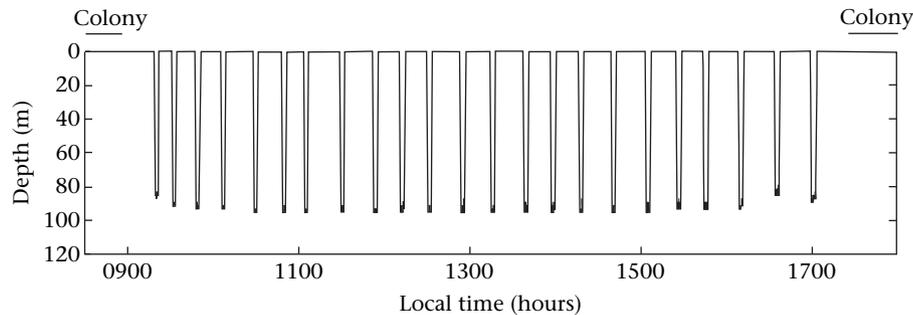


Figure 2. Example of a complete daily sequence of dive profiles from a breeding male Kerguelen shag.

Optimal Breathing

Walton et al. (1998) proposed that the PDI oxygen gain curve for birds has a biphasic shape caused by a change in the curve slope for dives longer than a given dive duration, generating a peak in the dive to PDI ratio. Such a dive to PDI ratio is called nonmonotonic. Walton et al. (1998) suggested this pattern was due to the unique respiratory physiology of birds, which possess both lungs and air sacs. According to these authors, because of the specific structure of the respiratory tract of birds, a small parabronchial lung and large air sacs comprising a large proportion of the total body oxygen (O_2) storage capacity, the dive to PDI ratio peaks for dives lasting the time it takes to consume the volumes of O_2 contained in the respiratory tract of birds. Consequently, such dives have the proportionately shortest PDIs. This is because the surface recovery time corresponds only to the turnover time of the respiratory gases. Dives shorter than this duration correspond to a use of O_2 from the respiratory reserves. Longer dives correspond to a use of O_2 from the blood haemoglobin and skeletal muscle myoglobin stores. Eventually, when dive durations reach the bADL, haemoglobin and myoglobin stores are theoretically close to total depletion and metabolism switches towards anaerobiosis.

Using the Walton et al. (1998) model, we calculated the dive to PDI ratio and plotted it in relation to dive duration. The peak value in the ratio and the corresponding dive duration were estimated graphically. To maximize foraging time spent underwater relative to the time spent on the surface recovering (time lost to foraging), divers should target dive durations with the highest dive duration to PDI ratio. We therefore examined how this prediction fitted with the frequency distribution of dive durations from the data. Hereafter, by optimal dive duration, we mean the dive duration that corresponds to the peak in the dive to PDI ratio. Optimal PDI refers to the corresponding recovery period. We emphasize that our use of the word optimal refers only to the optimality that is conferred on the diver in terms of maximizing its submergence period, and thus its potential foraging time.

Modelling Oxygen Consumption and Body Oxygen Reserves

The theoretical dive duration that achieves depletion of respiratory O_2 (optimal dive duration) is the dive duration

at the peak in the dive to PDI ratio. After depletion of respiratory O_2 , the additional dive duration that achieves depletion of haemoglobin + myoglobin respiratory O_2 is the bADL minus the optimal dive duration. The surface time taken to achieve complete turnover of respiratory tract gases, or respiratory O_2 replenishment time (optimal PDI), can be calculated as the optimal dive duration divided by the peak in dive to PDI ratio. Once respiratory O_2 is replenished at the surface, the time to complete haemoglobin + myoglobin O_2 replenishment is equal to the bADL divided by the dive to PDI ratio at the bADL (estimated graphically), minus the optimal dive duration.

Hence, the theoretical volume of body O_2 reserves can be calculated as the O_2 depletion times for the different body compartments multiplied by the VO_2 , the theoretical O_2 consumption rate for diving. To evaluate the VO_2 (ml/min per kg), we estimated the basal metabolic rate (BMR) of cormorants by fitting a curve on all the usable data in the literature obtained from respirometry measurements (Henneman 1983; Sato et al. 1988; Bryant & Furness 1995; Schmid et al. 1995; Grémillet et al. 2003; Enstipp et al. 2005, 2006). Measurements by Ricklefs & Matthew (1983) and Ancel et al. (2000) were not used to because they represented an outlying value and a measurement from birds resting on water, respectively. We obtained the following equation: $BMR = 6.33 \times M^{-0.63}$ ($R^2 = 0.61$, $N = 7$, $P = 0.038$), where body mass (M) is in kg and BMR is in W/kg. To estimate the factor (\times BMR) needed to calculate a deep-diving metabolic rate, we used a value based on measures by Enstipp et al. (2006) on double-crested cormorants, *Phalacrocorax auritus*, diving to 10 m in various water temperatures. We extrapolated the curve and obtained a value of deep-diving metabolic rate equal to $6.2 \times$ BMR in 5°C waters (temperatures encountered by Kerguelen shags in summer during deep dives). Since $BMR = (20.1 \times VO_2)/60$ (Schmidt-Nielsen 1983), the VO_2 for deep-diving Kerguelen shags is equal to $(6.2 \times BMR \times 60)/20.1$.

RESULTS

Dive Depth, Dive Duration and Bottom Time

We recorded 541 dives for the Kerguelen shag, occurring during 25 foraging trips. Dive depths were distributed according to three main depth zones: dives around 10 m deep, dives around 40 m deep and dives around 90 m

deep (Fig. 3a). The maximum recorded dive depth was 108.5 m.

Maximum recorded dive duration was 321 s. Dive duration increased with maximum dive depth, then started levelling off for dives near 300 s long (Fig. 3c). Concurrently, bottom times reached a peak near 200 s for dives 90 m deep before decreasing for dives reaching greater depths (Fig. 3e). The maximum recorded bottom time was 241 s.

PDI and Dive to PDI Ratio

In the bottom contour plot of the relation between PDI and dive duration for the Kerguelen shag, we detected a variation in the scattergram for dives lasting around

4 min (240 s; Fig. 4a). This was considered to be the bADL. Dive durations were distributed according to three modes (mode 1 near 50 s, mode 2 near 140 s, mode 3 near 280 s); 26% of dives lasted longer than the bADL (Fig. 4c).

The dive to PDI ratio peaked around 2.4 for dives lasting about 65 s (Fig. 4e), before decreasing for longer dives. Dive to PDI ratio at the bADL was estimated to be 0.8.

Application of the Model

From the above analysis, the optimal dive duration was found to be 65 s. Once respiratory O₂ was expended, the remaining dive duration to complete depletion of haemoglobin + myoglobin O₂ was then 175 s. The optimal PDI was 27 s. After the respiratory O₂ was replenished, the

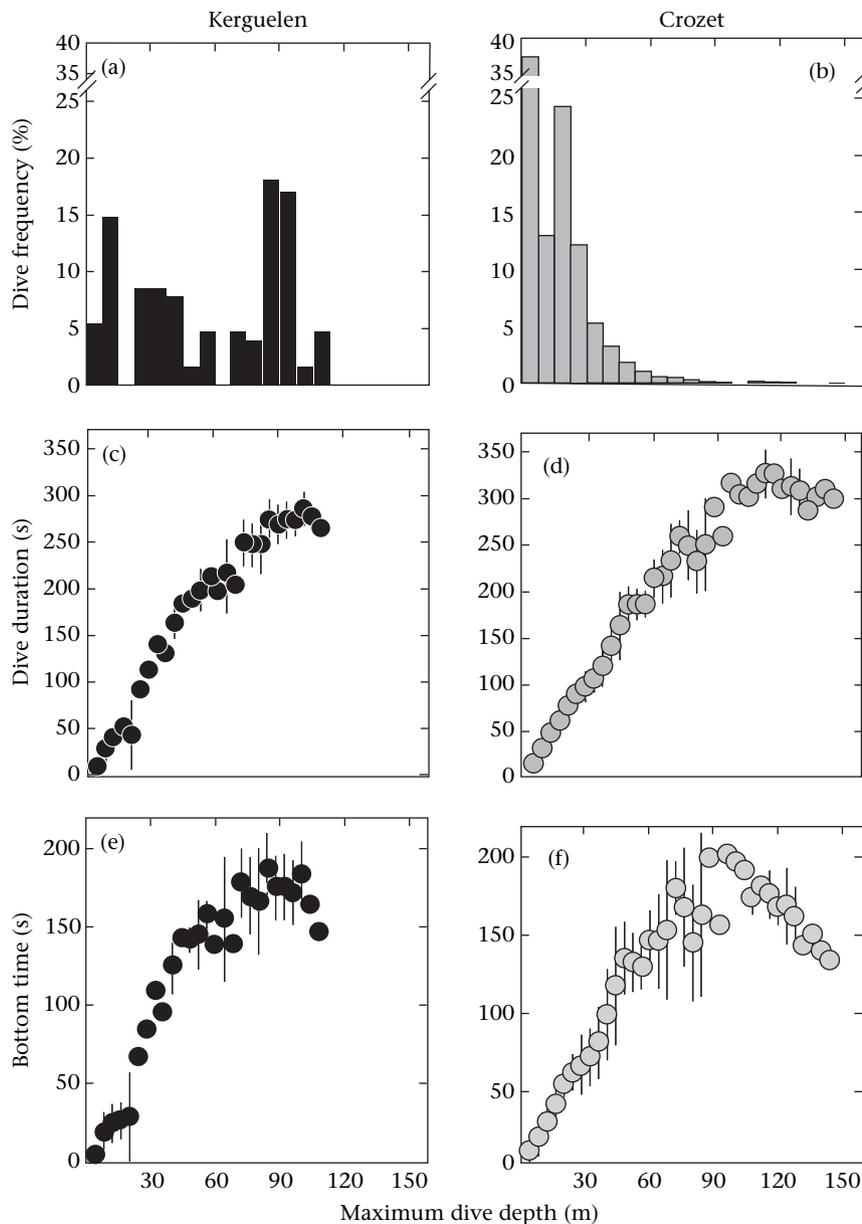


Figure 3. (a, b) Dive frequency, (c, d) dive duration and (e, f) bottom time in relation to maximum dive depth in the Kerguelen shag and the Crozet shag (redrawn from Tremblay et al. 2005). Values are individual means averaged by depth class.

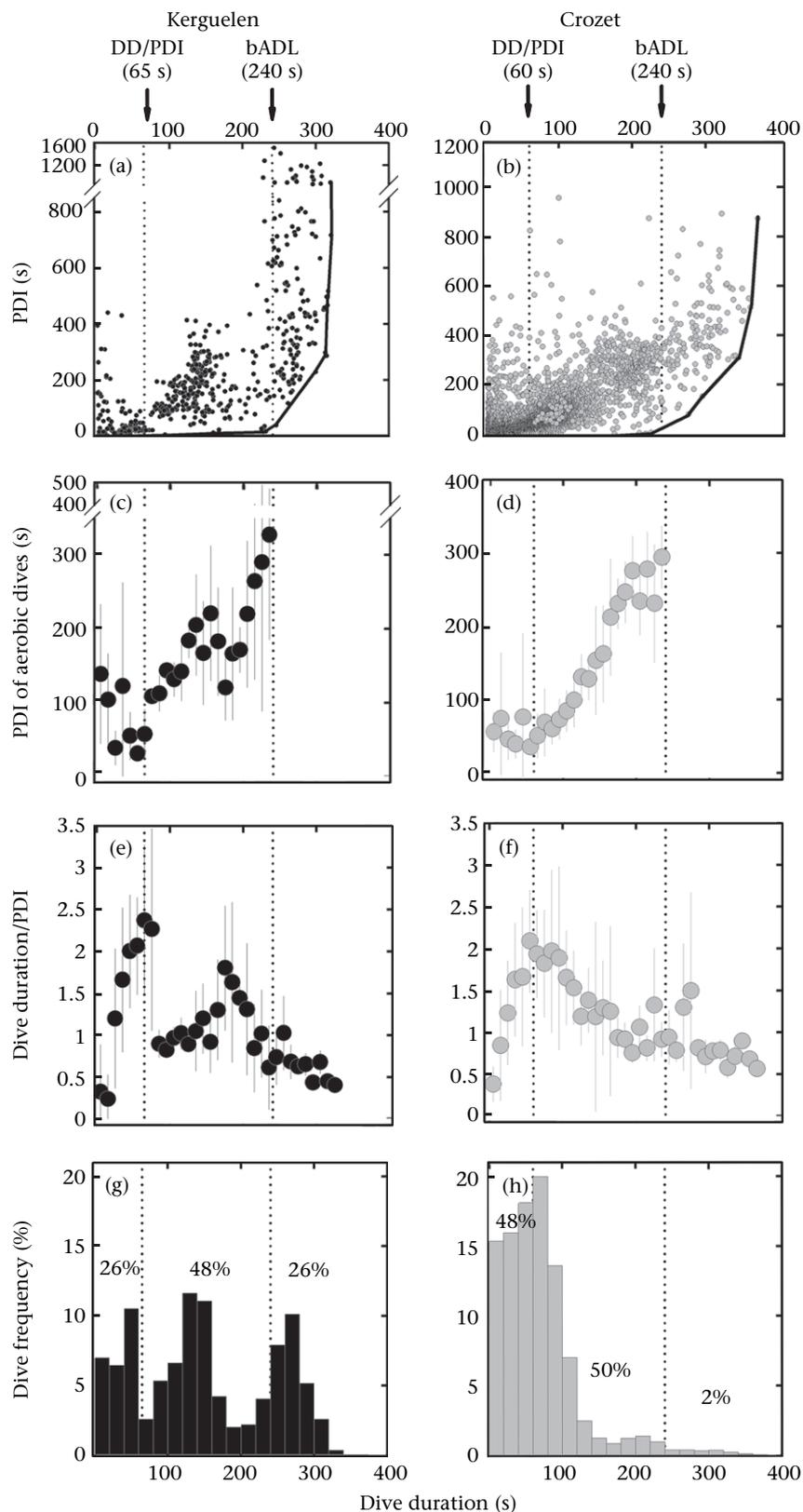


Figure 4. Postdive interval (PDI) and dive to PDI ratio in relation to dive duration in the Kerguelen shag and the Crozet shag (redrawn from Tremblay et al. 2005). Dotted lines indicate the maximum dive duration to PDI ratio (DD/PDI) and the behavioural aerobic dive limit (bADL). (a, b) PDI. (c, d) The PDI of aerobic dives. Values are individual means averaged by dive duration class. (e, f) Dive duration to PDI ratio. Values are individual means averaged by dive duration class. (g, h) Frequency distribution of dive durations. The percentages of dives in each dive duration class are shown.

surface time to achieve haemoglobin + myoglobin O₂ replenishment was 273 s.

The BMR of a 2.45 kg Kerguelen shag was estimated at 3.6 W/kg, or 10.7 ml O₂/min per kg. Deep-diving metabolic rate was thus calculated as 66 ml O₂/min per kg. Assuming total body O₂ reserves are depleted in 4 min (bADL), we estimated the volume of body O₂ as equal to 647 ml or 264 ml/kg. Assuming respiratory tract O₂ is depleted in 65 s, we assessed respiratory O₂ reserves as equal to 71 ml/kg or 174 ml. Haemoglobin + myoglobin O₂ stores could thus be calculated as 264 – 71 = 193 ml/kg or 473 ml. Finally, assuming a proportion of 20.95% of O₂ in atmospheric air, we calculated the full air volume of the respiratory tract as equal to 830 ml.

DISCUSSION

To Breathe or Not to Breathe: Optimality or Plasticity?

The detailed study of Kerguelen shag dive parameters showed these were extremely close to those of the blue-eyed Crozet shag (Tables 1, 2, Figs 3, 4). In both species, dive durations increased with maximum dive depth before levelling off around 300–350 s, and bottom times reached a peak near 200 s before decreasing for deeper dives. Because the time used for vertical transit (descent and ascent) increases with dive depth, shags can only dive deeper than the depth where dive durations start levelling off, to the detriment of time spent at the bottom. In other words, shags can dive deeper than 100 m, but this does not result in increased dive durations. They have reached their physiological limits. These converging limits are also expressed by the noticeable overlap between the species for the values of bADL and the position of the peak in dive to PDI ratio.

Body size can influence diving performances, with large species capable of diving longer than smaller ones because they load greater O₂ stores and have a lower mass-specific metabolic rate (Schmidt-Nielsen 1983; Schreer & Kovacs 1997). However, in the present case, Kerguelen shags and Crozet shags were similar in weight. Differences in sea water temperature between Crozet and Kerguelen

Table 1. Mean body mass ± SE and main dive parameters for the Kerguelen shag and the Crozet shag (from Tremblay et al. 2005)

Parameter	Kerguelen shag	Crozet shag
Body mass (g)	2454±254	2326±250
Maximum dive depth (m)	108.5	145
Maximum dive duration (s)	321	371
Dive duration at dive duration plateau (s)	300*	350*
Dive depth at onset of dive duration plateau (m)	100*	120*
Maximum bottom time (s)	241	241
Bottom time peak (s)	200*	200*
Dive depth at bottom time peak (m)	90*	90*

*Estimated graphically.

Table 2. Dive and surface times to deplete and replenish O₂ stores from the respiratory tract system and the blood haemoglobin + muscle skeletal myoglobin reserves in the Kerguelen shag and Crozet shag

	Kerguelen shag	Crozet shag
Dive and surface times		
Optimal dive duration (s)	65*	60*
Optimal PDI (s)	27	29
Time to deplete haemoglobin+myoglobin O ₂ (s)	175	180
Time to replenish haemoglobin+myoglobin O ₂ (s)	273	271
Parameters used in calculations		
Peak in dive to PDI ratio	2.4*	2.1*
bADL (s)	240*	240*
Dive to PDI ratio at bADL (s)	0.8*	0.8*

Values were calculated with the parameters in the bottom half of the table (PDI = postdive interval; bADL = behavioural aerobic dive limit). *Estimated graphically.

might affect at-sea energy expenditure. However, the difference is only 2 °C; this should not bring about a major difference in the metabolic rate (Enstipp et al. 2006). It appears that these two species, living in different environments, are similarly designed and have similar constraints, with their physiologies leaving little opportunity for differences between them.

However, there was a significant divergence in foraging behaviours. These concerned the frequency distribution of dive durations (Fig. 3). At Kerguelen, dive depths were distributed according to three categories, corresponding approximately to dives 50, 140 and 280 s long. As a consequence, Kerguelen shags dived repeatedly beyond their bADL (26% of dives). Crozet shags, on the other hand, rarely dived longer than their bADL (2% of dives; reanalysed from Tremblay et al. 2005). The majority of their dives were distributed around 60 s, thus close to the peak in dive to PDI ratio. Hence, the behavioural strategy of Crozet shags fits with optimal breathing, with birds targeting dives that bring the greatest amount of time directly dedicated to diving, and thus to foraging, versus surface recovery time. This corresponds to a strong mode of dive depth distribution in the 20 m depth zone (Fig. 3).

Knowledge about the distribution of prey abundance is lacking in both localities (Duhamel et al. 2005). Perhaps prey distribution at Crozet enabled shags to dive to depths compatible with breathing optimality. In a theoretical situation where benthic resources are distributed homogeneously in relation to depth, optimal breathing would certainly appear to be the most advantageous strategy. We know that the mean foraging range of Crozet shags is between 1 and 2 km (Tremblay et al. 2005). At Kerguelen, higher abundance or quality of prey from deeper waters could have motivated shags to dive in waters close to 90 m deep (Fig. 3), thus regularly exceeding the bADL and spending time and energy flying to and from distant foraging grounds (the closest 100 m isobath is 20 km from the colony, Fig. 1). This suggests that benthic resources were probably not uniformly distributed at Kerguelen,

but instead were irregularly dispersed (patches). Blue-eyed shags are thus capable, regardless of the extent to which they are physiologically programmed, of adjusting their behaviour to environmental variation, an example of behavioural plasticity.

There was no clear evidence for the Kerguelen shag or the Crozet shag of a relation between dive duration and PDI for dives less than or equal to 1 min, with such dives triggering recovery times close to optimality. According to Walton et al.'s (1998) model, shags thus targeted surface periods necessary for complete turnover of respiratory gases, entirely replenishing the body O₂ reserves before diving again. Because the dive to PDI ratio peaked at similar values corresponding to similar dive durations in the Kerguelen and Crozet shags, we can infer that neither species had a higher level of O₂ resource depletion upon surfacing after sequential diving. In the same way, no difference between these variables was observed by Walton et al. (1998) for European shags, *Phalacrocorax aristotelis*, during 3 consecutive years, suggesting that different cormorant species may be alike in this respect. These authors suggested that this behaviour is suitable as an ideal strategy when a large proportion of underwater time is allocated to searching for prey. When a prey item is located, dive duration can be extended for prey manipulation or searching for other prey, because body O₂ stores have been previously filled to their maximum.

To conclude, the dive to PDI ratio of the Kerguelen shag also peaked slightly for dives lasting around 200 s (Fig. 4). These correspond roughly to dives reaching a maximum depth of 60 m. This depth zone corresponds to the zone of neutral buoyancy in blue-eyed shags (Cook et al., 2008). Diving at a depth where the buoyancy upthrust force and gravity cancel each other out might be an ideal strategy for swimming over food beds with the least expenditure of energy. In such a situation, maintaining perfect control of roll, pitch and yaw while hunting would be relatively easy, consequently leading to reduced O₂ consumption, and therefore shorter recovery periods. However, this depth zone was not particularly targeted by either the Kerguelen or the Crozet shag.

Deep Diving in Blue-eyed Shags

The Kerguelen shag upholds the reputation of blue-eyed shags for deep diving, as its performances are well within the upper limits found in the cormorant family (Cooper 1986) and typical of those encountered in species of blue-eyed shags from other localities (Casaux & Barrera-Oro 2006).

It is important to point out that blue-eyed shags carry out dives in the cold sub-Antarctic waters for a total of more than 6 h a day during the breeding season (e.g. Wanless et al. 1995; Tremblay et al. 2005). In comparison, breeding great cormorants, *Phalacrocorax carbo*, from Greenland spend only 1 h per day foraging at sea (Grémillet et al. 2001). The shallower dives observed in species from outside the blue-eyed shag complex may not represent the species' physiological limits, but simply reflect ecological factors, such as prey abundance. Building comparative models including foraging success (prey units and food load), clutch

size, chick growth rate, time and energy budgets and the energetic value of prey will help answer this question.

Nevertheless, blue-eyed shags may be better adapted than their cousin species to endure the conditions of anoxia, high hydrostatic pressure and cold that prevail during deep dives in the Southern Ocean. A graphic extrapolation of bottom times in relation to dive depth (Fig. 3) suggests these shags could theoretically dive to 200 m if they spent 0 s at the bottom of the dive. Or, if we assume a mean swim speed of 1.5 m/s (Schmid et al. 1995), a vertical descent and ascent, and 0 s spent at the bottom, these shags could theoretically dive to 290 m. Although such values are theoretical and do not take into account the fact that shags are benthic divers (a bottom period is necessary for hunting), nor the fact they might not actually be able to withstand the problems potentially arising at such depths caused by the hydrostatic pressure (barotraumatism, nitrogen narcosis), they are indicative of the diving capacities of these animals and suggest potential large body O₂ stores.

There are few studies reporting how the dive to PDI ratio, or even the dive efficiency (bottom time/[dive + PDI]), is related to dive duration in other avian divers. Values of optimal dive duration and optimal PDI for blue-eyed shags were close to those encountered in certain species of alcids (Table 3), but they differ markedly from values for European shags which were smaller by half. This suggests potentially greater respiratory O₂ reserves in blue-eyed shags than in their European relatives. Unfortunately, available estimates of these volumes for cormorant species are scarce (Wilson & Quintana 2004) to nonexistent.

Diving Performances: Using Behaviour to Understand Physiology

We used a simple model to estimate body O₂ reserves of Kerguelen shags and showed how it is possible to use dive data to estimate O₂ depletion and replenishment rates, and estimate oxygen stores, adding to the model on avian breathing by Walton et al. (1998). None the less, a certain number of reservations should be noted.

First, we are aware that because of the graphical method used for determining the bADL (Kooyman et al. 1980), our estimate should be set within a range of dive duration values rather than considered as a precise and absolute figure. The definition of the aerobic dive limit is itself subject to debate (Butler 2001). The onset of anaerobic metabolism is certainly triggered earlier in the dive, although it would be used at a lower rate. We used the bADL to calculate total body O₂ stores, but O₂ is still present until the end of the dive as certain organs are purely aerobic. Yet, we suggest that O₂ reserves become severely depleted once dive duration passes the bADL and that the rate of consumption occurring afterwards is considerably lower than before. Hence, we may have underestimated total O₂ stores, but we believe the error in overestimating by using the maximum dive duration is larger than the error in underestimating by using the bADL.

Table 3. Optimal dive duration and optimal postdive interval (PDI) in several species of avian divers (alcids, cormorants, penguins)

Species	Source	Body mass (kg)	Optimal dive duration (s)	Optimal PDI (s)	Respiratory volume (ml)	Diving metabolism (ml O ₂ /min per kg)
Black guillemot, <i>Cephus grylle</i>	Walton et al. 1998	0.4	50	18	103	65
Atlantic puffin, <i>Fratercula arctica</i>	Wanless et al. 1988	0.5	15	2	133	223
Common murre, <i>Uria aalge</i>	Wanless et al. 1988	0.9	75	29	256	48
Common murre, <i>Uria aalge</i>	Walton et al. 1998	0.9	70	20	256	51
European shag, <i>Phalacrocorax aristotelis</i>	Walton et al. 1998	2.0	35	17	627	113
Crozet shag, <i>Phalacrocorax melanogenis</i>	Present study	2.3	60	29	734	67
Kerguelen shag, <i>Phalacrocorax verrucosus</i>	Present study	2.4	65	27	787	62
Rockhopper penguin, <i>Eudyptes chrysocome</i>	Tremblay & Cherel 2003	2.3	90	30	734	45

Values of body mass come from Schreer & Kovacs (1997), blue-eyed shags excluded (present study). The respiratory tract (lung + air sacs) volume V (ml) can be estimated from the allometric equation $V = 0.126 \times M^{1.12}$ where M (g) is the body mass (Duncker & Güntert 1985). A simple theoretical diving metabolic rate can be calculated as the consumption of the total volume of O₂ contained in this volume of air (20.95%) during the optimal time of submergence. Comparison between species should be done acknowledging that different environmental conditions between the studies (dive depth, water temperature) and different propulsion systems between the species (foot-propelled versus wing-propelled) will influence diving metabolism.

Second, we used Walton et al.'s (1998) model to estimate the turnover rate of respiratory tract air gases (and consequently all of which follows). This model has been discussed as being a reductionist mathematical model (Houston 2000; Parkes et al. 2002; Green et al. 2005; Halsey & Butler 2006) and it is true that it does not incorporate potential subtle physiological processes, such as possible unused O₂ reserves trapped in certain parts of the air sac system, for example. It has also been argued that the presence of the particular morphological feature of birds (lungs plus air sacs) was not essential to produce a nonmonotonic dive to PDI ratio. This pattern could be generated independently, for example by the action of the aerobic and anaerobic metabolic pathways functioning simultaneously during submergence (Houston & Carbone 1996), or through behavioural adjustments, such as varying breathing frequency during surface recovery periods (Parkes et al. 2002). Yet, this model predicts a peak in the dive to PDI ratio in avian divers (as found in blue-eyed shags) and proposes a physiological explanation for its presence: the end of the air tract O₂ reserve. In addition, to our knowledge this peak is observed in avian divers, but not in other taxa (Walton et al. 1998).

Third, our estimation of air tract volume comes from dives that occur in the 10–30 m depth zone. Respiratory air volume adjustments in relation to dive depth can occur in cormorants to reduce the effect of buoyancy (Cook et al., 2008). Thus, our estimate of air tract volumes should be valid for shallow dives, but is probably slightly smaller than what birds load for deep dives. Lastly, our estimates of the BMR and the deep diving metabolic rate come from studies on other species and under other conditions.

The aspect of our model most open to criticism, but also the most interesting feature, comes from the results themselves. On the one hand, we calculated the volume of the body O₂ reserves as equal to 264 ml/kg. This is three to six times the value of the usable body O₂ reserves per kg estimated for seabirds or sea mammals (Butler 2001). On

the other hand, the estimate of the respiratory tract air volume is realistic. This volume V (ml) can be predicted knowing body mass M (g) as $V = 0.126 \times M^{1.12}$ (Duncker & Güntert 1985; for lung volume see Maina & King 1984; Duncker & Güntert 1985). For a 2.45 kg Kerguelen shag, the result is equal to 787 ml, a value close to our own estimate of 830 ml.

These singular results have several consequences. First, we obtain the same respiratory tract volume (and thus diving metabolic rate) when we estimate this volume using our model or when we calculate it with the allometric equation. Since our estimate of the respiratory volume is the final output of our model, and is therefore based on all other estimates, our evaluation of the deep-diving metabolic rate of the Kerguelen shag appears credible. Although this agreement between methods is not an actual test of Walton et al.'s (1998) model, it naturally leads to the suggestion that a theoretical diving metabolic rate for avian divers might easily be predictable. This could be done by simply using the respiratory tract volume given by the allometric equation and considering that metabolism is represented by consumption of the total proportion of O₂ (20.95%) contained in this volume of air during the optimal time of submergence. This would offer the possibility to those studying diving energetics of other species to compare their findings with these values. To date, these theoretical diving metabolic rates can be predicted for species for which data on optimal dive duration are already present in the literature (Table 3). In this case, results obtained for most species are roughly distributed between 45 and 65 ml O₂/min per kg, a range that is rather small (only two species show values above 100 ml O₂/min per kg). We stress the fact that these results come from studies carried out in different environmental conditions and that a species' diving metabolism is determined, among other things, by its body mass, plumage and blubber isolation capacity, dive depth, propulsion system and water temperature.

Second, either previous estimates of body oxygen stores in seabirds and sea mammals are considerably underestimated, or O₂ consumption falls drastically in the Kerguelen shag after respiratory stores (71 ml O₂/kg) are depleted, with other metabolic pathways taking over. Phosphocreatine, for example, is a possible source of phosphorus for ATP, different from the main oxidative pathway (Butler & Jones 1997). The glycolytic pathway of anaerobiosis brings quick energy with lactic acid as a waste product. Although seabirds and sea mammals generally prefer to execute aerobic dives (Butler & Jones 1997), evidence within the cormorant family for an exponential increase in PDIs in relation to dive durations, suggesting the aerobic dive limit is exceeded, has been recorded in blue-eyed shag species (Schreer et al. 2001; Tremblay et al. 2005; present study). Increasing evidence thus suggests that blue-eyed shags may frequently use anaerobic metabolism to prolong dive duration and this may explain how they are capable of diving to such depths. Concurrently, heart rate and body temperature are important determinants of metabolic rate. A strong reflex bradycardia on diving has been detected in South Georgian blue-eyed shags, *Phalacrocorax georgianus*, with heart rates capable of falling to 40 beats/min (Bevan et al. 1997). Such an intense response (2–3 times lower than resting heart rate) would significantly reduce O₂ consumption. Bevan et al. (1997) also measured strong local hypothermia, with abdominal temperatures of diving shags sometimes descending to 28 °C, corresponding to a drop of 12 °C compared to surface values at the beginning of a dive bout. This would save energy both in terms of the Q₁₀ effect and thermoregulatory costs. To date, there are few publications in this area on cormorants. Yet, considering the available literature (Enstipp et al. 2001; Grémillet et al. 2005), it appears that blue-eyed shags may show the greatest bradycardiac and hypothermic responses to diving in the family. In addition, blue-eyed shags are notorious for lacking wing-spreading behaviour, an absence of display that may be symptomatic of certain thermoregulatory strategies (Cook & Leblanc 2007).

To summarize, oxygen stores in seabirds and sea mammals normally range between 40 and 85 ml/kg (Butler 2001). If Kerguelen shags possess similar values of body O₂ stores to other divers, most of their reserves should be depleted after 1 min of active submergence because they consume 60–70 ml/kg of O₂ during the first minute. Because the onset of the bADL occurs after 4 min of diving, a black box of 3 min remains unclear. The reason could be that our estimate of the deep-diving metabolic rate of Kerguelen shags may be too high. However, if our estimate is correct, Kerguelen shags could have means for drawing energy from nonoxidative metabolic pathways during the very early phase of the dive, thus saving O₂. In this context, and this may be the most important conclusion of our study, future work should seriously focus on the possibility that avian divers use a 'mixed' diving metabolism, a simultaneous mix of aerobic and anaerobic pathways starting early in the dive (Carbone & Houston 1996), rather than a 'switching' diving metabolism, that is, one pathway at a time, with the switch to anaerobiosis occurring when O₂ stores are depleted. The ensuing new

definition of the bADL would be the dive duration after which there is a noticeable drop (but not a halt) in the proportion of total metabolism that is aerobic, and a concomitant rise in the proportion that is anaerobic. Naturally, this would be expected to occur right after the respiratory system ceases to supply the blood with O₂, which we can consider to be at the peak in the dive to PDI ratio, at the optimal dive duration. In such a model, the effects of a mixed metabolism and the influence of the parabronchial lung become superimposed. In blue-eyed shags, the metabolism would be able to turn on a low proportion of O₂ after this bADL (near 1 min), because the proportion of anaerobic metabolism is sufficient. The total O₂ stores necessary for this would fit better with previous estimates in diving endotherms (Butler 2001).

Conclusion

In the light of all this, using our model to explain so many complex physiological processes could be asking too much. It is a simple model that we deliberately pushed to its limits to explore certain parts of the process. Yet, we cannot reject it entirely, particularly if we consider how difficult it is to measure energetics of free-ranging animals directly. Walton et al.'s (1998) model is not validated by the present study; however, neither is it refuted. Nevertheless, it is clear that it is limited in its explanatory power, as it raises more questions than it provides answers. Our work is primarily based on behavioural data. In the future, a complete understanding of the adaptations of the Kerguelen shag to deep diving will require a serious physiological approach.

Blue-eyed shags appear to be excellent study models, not only for exploring fields in behavioural ecology but also for testing avian respiratory models. We suggest that behavioural data can provide considerable amounts of information to those who wish to do such modelling, and should therefore be given regular and careful examination. The present study supports the use of comparative research to study closely related species in different geographical areas (or the detailed study of a population and its environment in the same locality over several years; Kato et al. 2001). In particular, using the same methods of investigation and similar analyses provides more detailed results, which are more readily interpretable. We stress the point that a cross-sectional study in a single locality gives us only a static picture of a situation, whereas animals, although limited physiologically, are actually capable of adjusting to a wide range of environments.

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