Surface pauses in relation to dive duration in imperial cormorants; how much time for a breather?

Rory P. Wilson[1,*] and Flavio Quintana[2]

[1]*Institut für Meereskunde, Düsternbrooker Weg 20, D-24105 Kiel, Germany* and [2]*Centro Nacional Patagonico (Conicet) (9120) Puerto Madryn, Chubut, Argentina*

*Author for correspondence (e-mail: rwilson@ifm.uni-kiel.de)

Summary

Air-breathing animals diving to forage can optimize time underwater by diving with just enough oxygen for the projected performance underwater. By so doing they surface with minimal body oxygen levels, which leads to maximal rates of oxygen uptake. We examined whether imperial cormorants *Phalacrocorax atriceps* adhere to this by examining dive:pause ratios in birds diving for extended, continuous periods to constant depths, assuming that the oxygen used underwater was exactly replenished by the periods at the surface. Examination of the cumulative time spent in surface pauses relative to the cumulative time spent in diving showed that surface pauses increase according to a power curve function of time spent in the dive or water depth. In a simplistic model we considered the rate at which birds expended energy underwater to be constant and that the rate of oxygen replenishment during the surface pause was directly proportional to the oxygen deficit. We then worked out values for the rate constant for the surface pause before using this constant to examine bird body oxygen levels immediately pre- and post dive. The model predicted that imperial cormorants do not submerge with just enough oxygen to cover their projected dive performance but rather dive with substantial reserves, although these reserves decrease with increasing dive depth/duration. We speculate that these oxygen reserves may be used to enhance bird survival when rare events, such as the appearance of predators or discovery of large prey requiring extended handling time, occur. The form of the oxygen saturation curve over time at the surface means that the time costs for maintaining constant oxygen reserves become particularly onerous for long, deep dives, so the observed decrease in reserves with increasing dive duration is expected in animals benefiting by optimizing for time.

Key words: diving, imperial cormorant, *Phalacrocorax atriceps*, oxygen saturation curve, time optimization, surface interval between dives.

Introduction

There has been interest in how diving species partition their foraging time into that underwater and that at the surface since the early 20th century (Dewar, 1924). Diving animals only have access to oxygen *via* body stores while underwater and use subsequent periods at the surface to replenish these stores, and it is generally assumed that extended durations underwater necessitate extended periods at the surface to allow time for the extra oxygen to be taken on board. Consequently, a number of authors have attempted to examine the relationship between dive duration and subsequent pause duration at the surface (e.g. Cooper, 1986; Croxall et al., 1991; Wanless et al., 1993). The relationship between dive duration and subsequent pause duration is, however, complicated by three things. (1) The rate at which oxygen can be accumulated by a diving animal at the water surface is dependent on whether this animal has dived aerobically or anaerobically; conversion of lactate following anaerobic dives is a comparatively slow process (Butler and Jones, 1997), so that surface intervals following dives that have

exceeded the aerobic dive limit (*sensu* Kooyman, 1989) are extended (Butler and Jones, 1997). To determine the aerobic dive limit, some authors have attempted to look for a point of inflection in the dive duration *versus* pause duration regression (e.g. Horning, 1992) although, in fact, it has recently been pointed out that there are times when animals may work underwater partially anaerobically without incurring a significant time penalty (Carbone and Houston, 1996; Carbone et al., 1996). (2) The rate at which oxygen is likely to be taken into body tissues is not constant, being most likely directly related to the difference in oxygen partial pressure between body tissues and air (Butler and Jones, 1997). (3) It has long been assumed that pauses at the water surface reflect a simple recovery from the previous dive where depleted oxygen is replaced (e.g. Cooper, 1986). However, it has recently been shown that some diving animals prepare for the forthcoming dive for some of the time that they spend at the surface (Wilson, 2003), so that surface durations reflect a mixture of

time spent recovering from the previous dive and time spent preparing for the dive to come. Future dives are assessed according to their projected durations and, since dive durations may be highly variable between consecutive dives, it is hardly surprising that relationships between dive durations and surface durations show extreme variability (e.g. Cooper, 1986).

In an interesting consideration of the law of diminishing returns, Kramer (1988) pointed out that, since oxygen uptake rate at the surface was dependent on tissue deficit, maximum uptake rates should be achieved in animals that surface with oxygen reserves virtually exhausted. A consequence of this is that animals attempting to minimize time at the surface should not dive with body tissues saturated with oxygen, but rather only with that needed for the dive. This incorporates point (2) above and leads to the prediction of point (3), ultimately leading to the conclusion that diving animals need not have a systematic ideal single level of oxygen concentration in the body, but rather that the ideal pre-dive level must be highly variable if time is to be optimised (Wilson et al., 2003).

In view of the complexities discussed above, any attempt to understand the relationship between dive and surface duration should consider data where the diving animal is in steady state. That is to say that dive duration should be constant over a series of dives so that surface pauses may also stabilize, incorporating both the recovery and preparation components. The dive/pause relationship should also be determined for different batches of dives to different depths so that a general strategy, resulting from different amounts of oxygen being used, can be alluded to. Finally, since even within a constant dive duration regime, diving animals might show some variability in pre-dive levels of oxygen (this being mediated by more or less extended surface pauses), it would be helpful if dives were not considered singly but in a series as a cumulative surface duration plotted against a cumulative dive duration, the slope of this regression identifying the dive/pause relationship and automatically ironing out inconsistencies that might occur in particular surface pauses.

To this end, we used imperial cormorants *Phalacrocorax atriceps*, which are known to forage primarily benthically at a particular locality in Argentina (Sapoznikow and Quintana, 2003; Punta et al., 1993) where bottom topography changes only very slowly (F. Quintana, unpublished data). Since, in cormorants, the time for transit from the water surface to the seabed and back accounts for a substantial part of the time underwater (Wilson and Wilson, 1988; Croxall et al., 1991; see later), swim speed is constant (Wilson and Wilson, 1988) and bottom duration tends to increase in a predictable manner with increasing dive depth (Wilson and Wilson, 1988; Croxall et al., 1991; Grémillet et al., 1999; see later), we reasoned that use of these birds in this locality would give us the best chance of attaining the steady state conditions referred to above. This paper describes how imperial cormorants partition their time into dive and pause durations as a function of water depth and how the various strategies that they adopt might be used to optimize for time. Although this work considers imperial cormorants in detail, it potentially applies to all air-breathing diving animals and thus has broad implications for aquatic birds, mammals and reptiles.

Materials and methods

Fieldwork was conducted at Caleta Malaspina (45°11′S, 66°30′W), Bustamante Bay, Chubut, Argentina. This is an inlet of 34 km², with a maximum width of 4 km and a length of 10 km (Herrera, 1997). The imperial cormorants *Phalacrocorax atriceps* King (563 pairs) breed in a complex of islands at the mouth of the inlet (Yorio et al., 1998).

Time–depth recorders (TDR Mk7, Wildlife Computers, Woodinville, WA, USA) were deployed on 15 adult male imperial cormorants during the first 10 days of the chick-rearing period. The TDRs measured 10 cm×2 cm×1 cm and weighed 30 g, less than 1.5% of adult body mass. Devices were attached to the feathers in the centre of the back, using waterproof tape and two cable ties. The procedure was completed in less than 5 min and birds quickly returned to their nest. All birds carrying devices continued breeding normally during the study period. Depth data were recorded with a resolution of 0.5 m and recorded at 1 Hz. Birds were recaptured after several foraging trips (1–10, undertaken during periods of 1–5 days), the TDRs removed and the data downloaded.

Data obtained from the TDRs were analysed using the programme MTDIVE (Jensen Software Systems, Laboe, Germany). This programme displays the depth data against time graphically and then places cursors at the start and end of dives as well as at points of inflection in the dive profile, to indicate the initiation of the bottom phase where birds forage along the seabed. The appropriateness of the cursor positions was checked visually by the user before the data were written to an ASCII spreadsheet with the following parameters for each dive being determined: the time of initiation of each dive, the durations and rates of the descent, bottom and ascent phases as well as the maximum depth reached during the dive. Data were then processed using EXCEL, TABLECURVE and STATEASY software packages. Although all dives were analysed for determination of the rates of descent and ascent as well as the time spent in the bottom phase of the dive, dives were specifically selected for consideration of the ratio of the pause duration:dive duration *versus* dive duration (see earlier). Here, only those data were considered where birds had dived consistently to a specific depth, not varying by more than 10% for the duration of the bout considered, and where at least 20 dives had been conducted in succession (see rationale in the Introduction).

Results

Of the 15 birds fitted with devices, 14 were recovered in good condition having foraged extensively for periods of between 1 and 9.5 h over any single day. A single bird could not be recaptured although it continued tending for the brood. All other birds continued rearing chicks normally after removal of their devices.
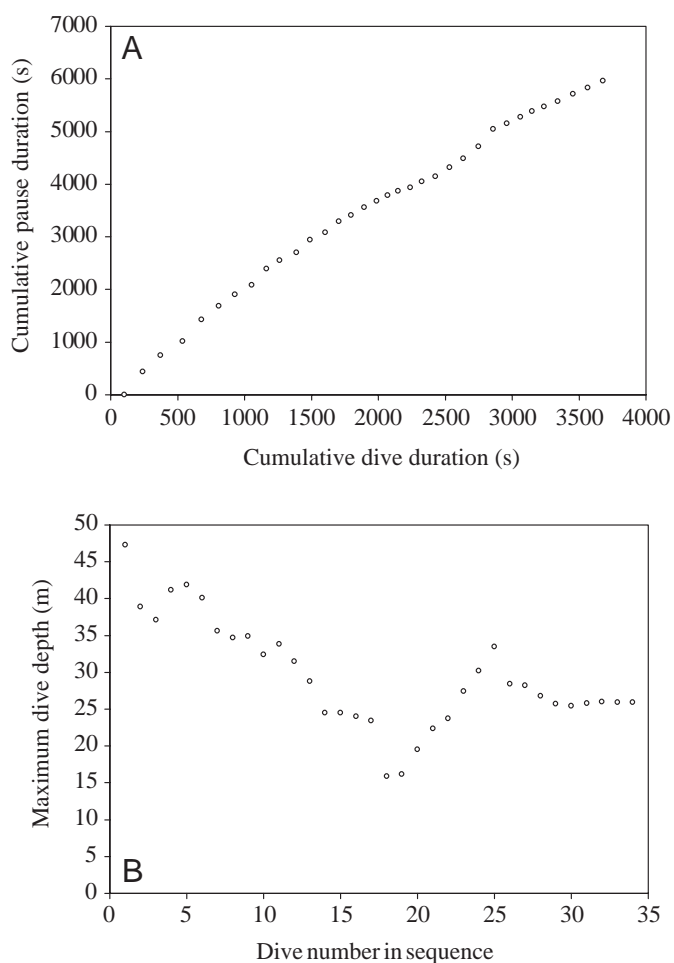
Fig. 1. (A) Example of the cumulative pause duration versus the cumulative dive duration for a dive sequence (B) of a single imperial cormorant foraging in water between 10 and 50 m deep. Note that the steeper slope of the gradient in deeper waters is not as obvious as it otherwise might be because the presentation of the cumulative values irons out a great deal of variability in single pause *versus* dive duration values.

3149 dives in total were analysed for standard dive parameters, and 47 bouts from 14 birds (no more than 5 per individual) for determination of the relationship between the ratio pause duration:dive duration and dive duration.

Consideration of the cumulative pause duration *versus* the dive duration in a dive sequence showed a steady increase in both parameters, provided that water depth during that sequence remained constant (Fig. 1). Where water depths were shallow the gradient flattened off, steepening again when dive depth increased (Fig. 1).

The time spent descending and ascending the water column during dives was strongly linearly correlated with depth (Fig. 2) with birds taking about 0.67 s to descend and ascend every 1 m of water depth, resulting in vertical travelling speeds of the order of about 1.5 m s^{-1}, irrespective of the maximum depth to which they dived. A similar, though less strong, correlation was apparent between the time spent on the bottom and maximum depth achieved during the dive, where birds
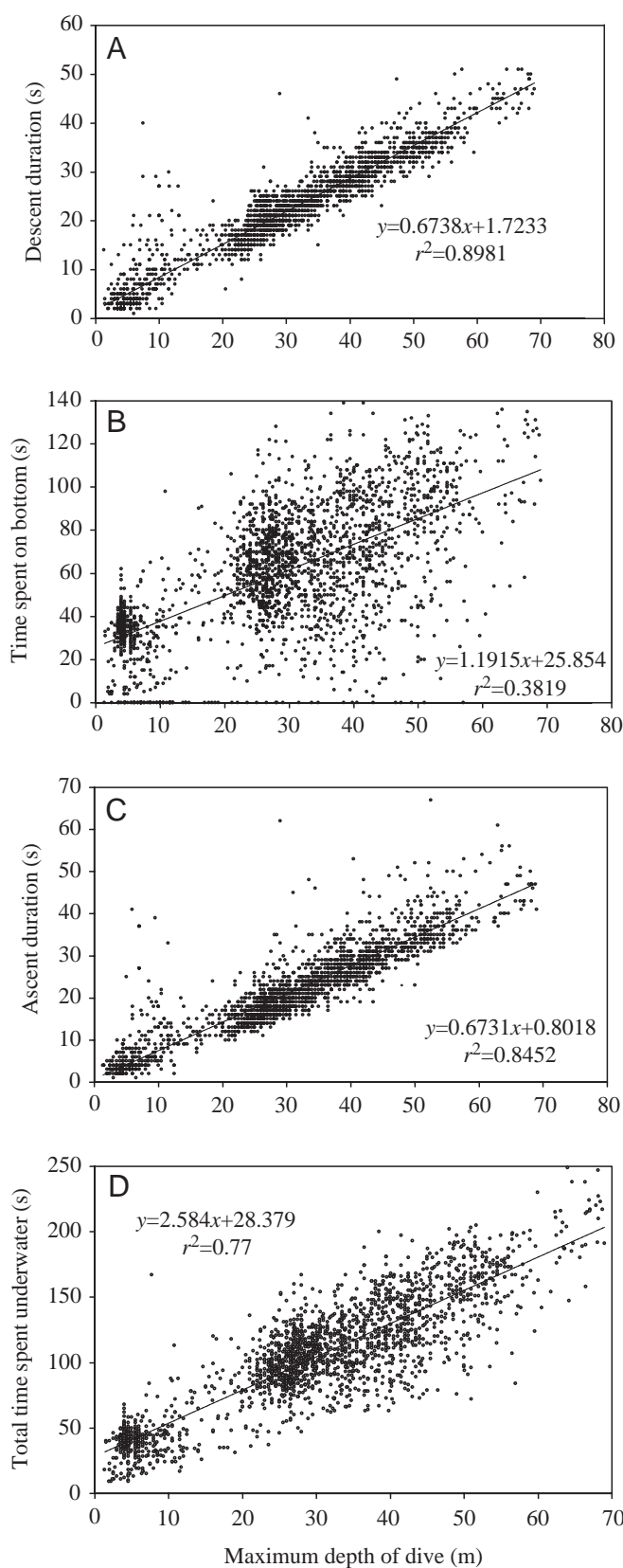

Fig. 2. Relationship between the time taken to (A) descend, (B) move along the bottom, (C) ascend and (D) complete the full dive, as a function of maximum depth reached during the dive for 14 imperial cormorants foraging in coastal waters off Argentina.

spent an average of 25 s plus approx. 1.2 s for every 1 m depth dived (Fig. 2B). Thus, taking all parameters together, birds diving deeper dived for longer periods (Fig. 2D). Longer periods underwater, however, resulted in longer periods spent at the surface; graphical examination of the regression of the slope of the cumulative pause duration divided by the cumulative dive duration (y-axis) as a function of dive duration (x-axis) showed that during deeper, longer dives, the pauses became proportionally longer with the best fit curve having the form $T_s=0.374+0.00558T_u+2.744\times10^{-7}T_u^3$ ($r^2=0.65$, $F=81.0$, $P<0.001$; residuals normally distributed (Shapiro–Wilk test), $W=0.98$), where T_s is the time at the surface (s) and T_u is the time spent underwater (s) (Fig. 3).

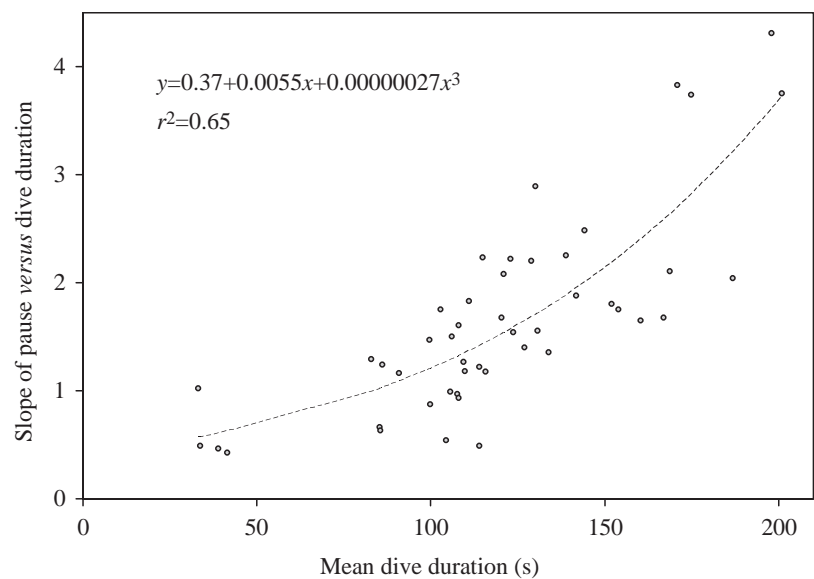$$y=0.37+0.0055x+0.00000027x^3$$
$$r^2=0.65$$

Fig. 3. Relationship between the ratio of the pause duration at the surface and the time spent underwater as a function of the time spent underwater during dives to constant depths (see text) for 14 imperial cormorants foraging in coastal waters off Argentina.

Discussion

The attachment of external devices to seabirds is known to affect aspects of their foraging ecology (e.g. Wanless et al., 1988; Taylor et al., 2001) so the results obtained in our study should be considered carefully. Although some device effects are likely (not least of which is the shyness of equipped birds to land at the nest site when we were present), the relatively small size of the units used and the fact that the behaviour of the birds carrying the devices was virtually identical to non-equipped conspecifics make us believe that the parameters recorded by us are a good approximation to normal foraging behaviour (cf. Croxall et al., 1991; Wanless et al., 1993; Grémillet et al., 1999).

Overall, the results obtained by us for the imperial cormorant accord with those presented for other species of cormorant: dive duration appears linearly related to maximum dive depth, rates of descent and ascent are roughly constant and the time spent on the bottom increases with increasing dive depth (e.g. Croxall et al., 1991; Wanless and Harris, 1991; Wanless et al., 1993; Grémillet et al., 1999).

For our cormorants, the relationships between the time taken for the descent, bottom phase, ascent and maximum depth reached during the dive means that the total time spent by birds underwater can be readily calculated as:

$$T_{tot} = 0.72D + 25 + 1.2D + 0.69D = 2.61D + 25 , \quad (1)$$

where D is depth (m). This compares very favourably with the overall linear regression for total time spent underwater *vs.* depth (Fig. 1D), where:

$$T_{tot} = 2.54D + 28 . \quad (2)$$

The energy used during the time underwater can be approximated by data derived from great cormorants *Phalacrocorax carbo* by Schmidt et al. (1995) where, at speeds of *ca.* 1.5 m s^{-1}, birds had a power consumption of 35 W kg^{-1}. We assume, for simplicity, that these power requirements are independent of depth or dive angle, although it is known that air in the plumage and respiratory spaces affects the work done by diving birds as a function of depth (Lovvorn et al., 1999; Sato et al., 2002). We note, however, that this effect is likely to be minimized in cormorants, which have less plumage air than any other bird (Wilson et al., 1992). Using the conversion factor of 1 litre of oxygen being needed for every 20.1 kJ (Schmidt-Nielsen, 1993) and assuming that birds weigh on average 2.5 kg (our unpublished data), we can calculate oxygen use (V_{O_2}) (in l) as a function of dive duration to be:

$$V_{O_2} = (35\times2.5\times T_u) / 20\,100 , \quad (3)$$

where T_u is the time spent underwater and the 35 refers to the mass-specific power consumption for birds swimming under water (Schmidt et al., 1995). Note that this term is purely linear.

During steady state diving such as that studied by us, this amount of oxygen is repaid at the surface during a pause duration (T_s) that is related to time underwater by:

$$T_s = T_u(0.37431 + 0.0055831T_u + 2.744\times10^{-7} T_u^3) . \quad (4)$$

Here, the term inside the parentheses is derived from the relationship between slope of the pause duration/dive duration as a function of dive duration (Fig. 3). Using Equation 3, the mean rate at which the oxygen is taken up by the bird during the surface pause is therefore:

$$\text{mean } dO_2/dt = (35\times2.5T_u) / 20100T_s = 0.00435T_u/T_s . \quad (5)$$

Here, we assume our foraging cormorants did not dive anaerobically (cf. Woakes and Butler, 1983; Butler and Woakes, 1984; Butler, 1998, 2000, in press; cf. Carbone and Houston, 1996; Carbone et al., 1996). There are a number of papers on the validity of this assumption for diving animals, a

major problem being that, with the exception of a study on tufted ducks *Aythya fuligula* (Woakes and Butler, 1983), no study has thus far been able to determine rate of oxygen uptake during diving itself. Authors have noted that empirical data suggest that some diving animals routinely exceed their aerobic dive limit (ADL; e.g. Croxall et al., 1991; Kato et al., 1992; Costa et al., 2001) and Kooyman (1989) even discusses how elephant seals *Mirounga* might link consecutive anaerobic dives together. However, extended bouts consisting of serial dives where animals routinely exceed their ADL, despite short inter-dive periods, are difficult to reconcile with rates of accumulated lactate removal. Reduced costs of transport, and therefore reduced oxygen uptake, associated with greater depths due to air compression (e.g. Costa and Gales, 2000; Williams et al., 2000; Sato et al., 2002, 2003) may partially explain the discrepancy, as may regional hypothermia (Culik et al., 1996; Handrich et al., 1997; Bevan et al., 2002; but see Ponganis et al., 2003). Although attempts have been made to quantify the contribution of anaerobic diving in field studies (e.g. Costa and Gales, 2000, 2003; Costa et al., 2001), ultimately, the extent to which dives are genuinely anaerobic will have to wait until measurements of blood lactate can be made for a definitive answer.

The expression in Equation 5 above gives the mean rate of oxygen uptake over the whole of the surface pause, incorporating both the dive and the observed pause durations. Although derivation of a mean value implies that the rate of gas exchange does not change over the considered pause duration this is not the case. At any one time within the pause period, irrespective of bird body oxygen concentration at the beginning or end of the pause, the rate of uptake of oxygen into the body is likely to be a direct function of the difference in partial pressure between the air ($Pair_{O_2}$) and the bird body tissues ($Pbird_{O_2}$). Note that this assumes that blood flow to the lungs is constant, mediated by constant tachycardia and appropriate blood shunting (Butler and Jones, 1997; Butler, 1998), so that at any one time:

$$dO_2/dt \, \mu \, (Pair_{O_2} - Pbird_{O_2}) = k(Pair_{O_2} - Pbird_{O_2}) \,. \quad (6)$$

Since, during steady state diving, the total oxygen uptake during the surface pause is equal to that expended during the period underwater, this is given by the integral of the rate of uptake of oxygen over the surface pause. Assuming that the rate of uptake is directly proportional to the deficit (Equation 6), the rate of oxygen uptake at any one time during the surface pause can be calculated together with the body oxygen concentrations at the start and end of the pause by adhering to the precise conditions of surface to dive ratios defined by our results (Equation 4) and by assuming that we can reasonably allude to energy expenditure during the dive (Equation 3). In order to do this, an appropriate constant, *k* (see Equation 6)*, or appropriate range of constants that conform to the figures used for oxygen levels, has to be determined. Then, a particular known dive duration resulting in a defined oxygen use can be equated to the surface pause of defined length (*via* Equation 4), during which the oxygen must be taken up by the

body according to Equation 6. Since the oxygen used during the dive must equal that repaid during the surface period, there is only one solution to this, which can be solved by iteration by setting pre-dive oxygen levels to a particular value and then seeing the extent to which this differs from that observed after mathematical treatment so that the initial value can be corrected accordingly. This process can be conducted over the range of dive durations.

For this we assume that the maximum amount of oxygen that can be contained within a cormorant body can be calculated *via* the metabolic rate of cormorants underwater (Schmidt et al., 1995) multiplied by the maximum dive duration. In fact, we assume that the maximum value observed by us (280 s) represents the 95% confidence limit, so that the full oxygen capacity of the body is given by 0.00435×295≈1.28 l. We note that this far exceeds that predicted using standard values for body oxygen concentrations derived from consideration of factors such as the amount of respiratory pigment (e.g. Mill and Baldwin, 1983; Chappell et al., 1993), the oxygen binding capacity (e.g. Lenfant et al., 1969; Kooyman, 1989), the saturation prior to dives (Stephenson et al., 1989a; Croll et al., 1992) and the volume of air in the respiratory tract (Lasiewski and Calder, 1971; Stephenson et al., 1989b; Wilson et al., 2003), but actually, for the model, precise figures are unimportant since we are only interested in relative, rather than absolute, changes in pre- and post-dive body oxygen levels. In order to access the rate of oxygen uptake at the surface we assume that this is proportional to the difference between maximum body oxygen levels (corresponding to saturation) and that observed at any one time. Note that our treatise does not specifically attempt to define the upper limit to oxygen reserves because the inconsistencies noted above from the literature, perhaps due to marked inter-specific differences, make such a procedure questionable. Rather, we stress that our presented derivations from the model are useful in indicating trends rather than absolute values, and that the robustness of our methodology can only be extended that far.

Use of our values necessitates that we use *k* = 0.005–0.015, depending on the initial pre-dive oxygen body levels chosen, with the lower rate constants precluding the occurrence of long dives since oxygen levels in the body cannot be replaced in the time at the surface defined by Equation 4. For any particular value of *k,* the points on the oxygen saturation curve that correspond to the pre- and post-dive levels can be defined (Fig. 4A). Consideration of these values with respect to dive duration shows that increasing dive durations result in increasing pre-dive body oxygen levels and decreasing post-dive body oxygen levels (Fig. 4B) (note that differing values of *k* do not affect the overall form of the pre- and post-dive oxygen levels in the body, merely shift the curves up or down). This does not substantiate Kramer's hypothesis that diving animals should only take down enough oxygen to complete their dive because, by so doing, the minimal body oxygen levels on return to the surface lead to maximized uptake rates and reduced (non-foraging) time. Rather, it would appear that oxygen reserves are important even if the extent of these
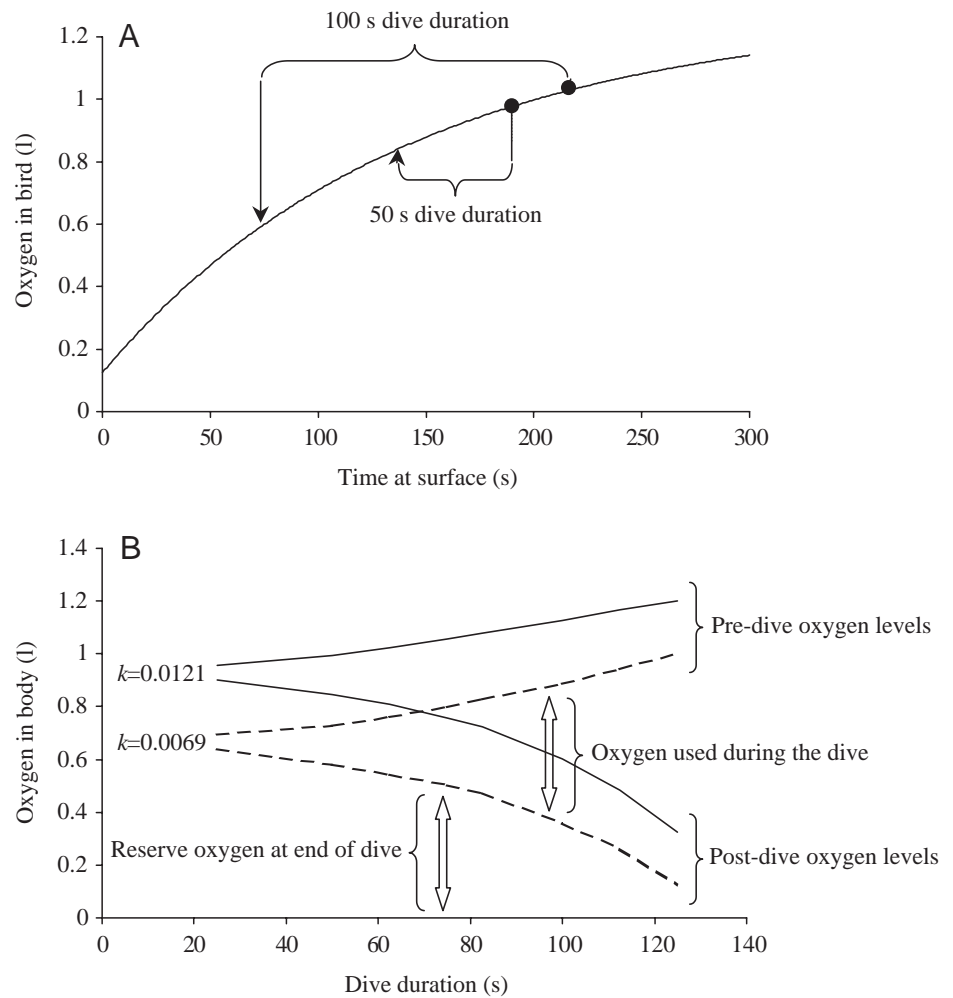
Fig. 4. (A) Simulated oxygen saturation curve for an imperial cormorant during time at the surface after dives. The arrows show the calculated pre- and post-dive oxygen concentrations for dives of two different durations. (B) Projected pre- (upper lines) and post- (lower) dive body oxygen concentrations as a function of steady state diving for dives of particular durations in the imperial cormorant. The value between the upper and lower curves shows the oxygen used during the dive, and the value between the lower curve and the x-axis shows the oxygen reserve carried by the bird. Varying values of the rate constant, k, shift the curves up or down.

reserves held by the birds decreases with increasing dive duration (Fig. 4B). Why should this be?

Obviously, in an absolute sense, oxygen reserves over and above those projected to be needed for the dive are beneficial since they could be used for predator avoidance (Heithaus and Frid, 2003) or extensive prey handling where a particularly large prey item was discovered. However, these reserves come at a price in terms of time invested at the surface, since they must be paid for during every recovery interval. Of particular importance is that, due to the logarithmic-type form of the oxygen saturation curve over time, the reserves are not linearly detrimental (in terms of time) but tend to be more onerous with increasing pre-dive oxygen levels (as is necessary for long dives). This might explain why the effective extra time invested in the reserves decreases with increasing dive duration (Fig. 5 – line labelled 'reserves first'). In other words, birds might benefit from having extra oxygen reserves during any particular dive, but the time that has to be invested in maintaining these reserves is a critical factor in determining their extent. In the dynamic state of the cormorants diving, if the reserves themselves are ignored (assuming that they are effectively never used), the real cost in terms of time for the birds diving with and without reserves is given by the ratio of

the recovery time for a bird with, compared to without, reserves (Fig. 5). Here it can be seen that birds diving for short periods without reserves would be three times more efficient in terms of time at the surface as birds diving with reserves although, due to decreasing reserves with increasing depth (Fig. 4B), they are only about twice as efficient for extended dive durations (Fig. 5). Ultimately, however, the extent of the reserves and the decrease in efficiency that they imply will be expected to be balanced out by the advantages accrued when they are used, and in this respect the extent of the reserves might vary according to local conditions, even on a day to day basis.

The model used here is simplistic in assuming, for instance, that energy expenditure is constant during the dive and independent of depth (cf. Wilson et al., 1992; Lovvorn et al., 1999; Sato et al., 2002) and, although cormorants have little plumage air (Wilson et al., 1992), this is unlikely to be completely true. Costa and Gales (2000) note, for example, that New Zealand sea lions *Phocarctos hookeri* expend less energy during deeper dives, presumably because they are able to spend more time gliding due to reduced upthrust following decreases in body air volume due to hydrostatic pressure. We also assume that the rate of oxygen uptake at the surface is directly

proportional to the oxygen deficit, when actually this will depend on the extent of tachycardia and blood shunting at the surface (e.g. Butler, 1998, 2000). However, the trends are well defined so that a substantial deviation from our assumptions will be needed to invalidate them. The major element in our model that affects the outcome is the form of the recovery duration/dive duration regression (cf. Fig. 2). There is considerable literature on dive recovery durations in a general sense (e.g. Harcourt et al., 1994; Campagna et al., 1995; Boyd and Croxall, 1996) but relatively little in relation to dive performance. Nonetheless, in a paper summarizing data from 19 cormorant species, Cooper (1986) considered the relationship between inter-dive duration and dive duration to be linear although depths were generally shallow and dive durations short. Both Croxall et al. (1991) and Wanless et al. (1993) note that long dive durations result in overly long subsequent surface pauses. Kramer (1988) postulated that recovery duration should increase as a power function of dive duration and this is ultimately close to that observed by us (cf. Fig. 2), although Wanless et al. (1993) found a better fit using an exponential function. In fact, the difference is really only one of degree and, given the scatter in data, it is hard to be equivocal about which is really the best fit. Although accelerating surface pause durations with respect to dive durations are often used to invoke anaerobic metabolism (e.g. Ydenberg, 1988; Wanless et al., 1993) this is not necessarily the case since the oxygen saturation curve over time is not linear (Butler and Jones, 1997), so that as diving animals use an increasing proportion of their overall oxygen stores, recovery durations are expected to accelerate with respect to dive duration (Kramer, 1988). Resolution of the extent of anaerobic metabolism (cf. Carbone and Houston, 1996; Carbone et al., 1996) will be critical in any consideration of this type and, ultimately, the question can only be definitively resolved by direct measurement of oxygen and/or lactate levels in foraging birds. Perhaps recent advances in this field (e.g. Parkes et al., 2002; Halsey et al., 2003) indicate that it may not be long before this happens.
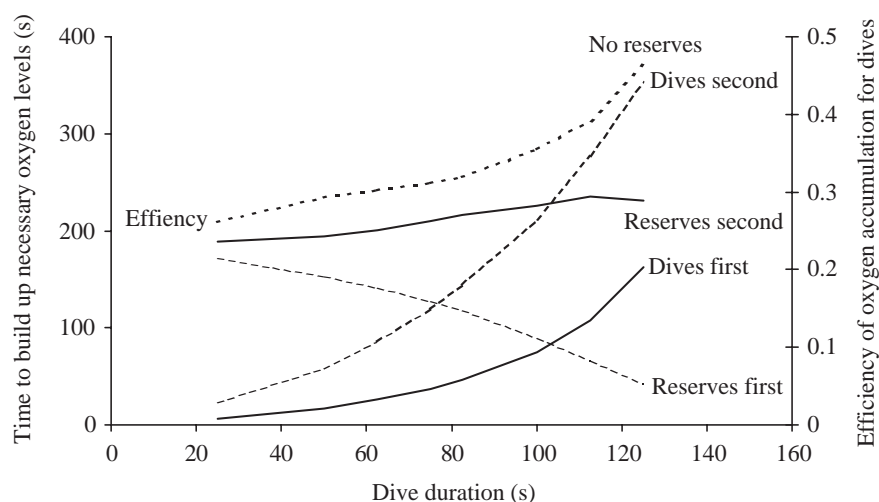
Fig. 5. Necessary time invested by an imperial cormorant to cater for oxygen acquisition at the surface as a function of dive duration, starting from a body oxygen concentration of zero. We assume that the bird must acquire oxygen for two processes; (i) diving and (ii) as a reserve, and that the acquisition of the oxygen for the two processes occurs in distinct phases. This condition is given by the output of the model (see text), which projects that birds do not actually normally use their reserves and therefore must acquire oxygen for the dive at a slower rate than they would otherwise do if they had no reserves. For comparison the figure details two options: oxygen is acquired for the projected dive first (solid line, 'dives first') followed by acquisition of the reserves (solid line, 'reserves second' – cf. Fig. 4B) and (the most likely situation) that oxygen is acquired for the reserves first (broken line, 'reserves first') followed by oxygen for the dive (broken line, 'dives second'). Since, however, the reserves are not normally used, the drop in efficiency for cormorants diving with reserves, compared with those diving without (top dotted line), is given by the time necessary to build up necessary oxygen levels from a body oxygen concentration of zero (the solid 'dives first' line) divided by the time necessary to build up necessary oxygen levels from a body oxygen concentration equivalent to that used in reserves (the broken 'dives second' line).

References

Bevan, R. M., Butler, P. J., Woakes, A. J. and Boyd, I. L. (2002). The energetics of gentoo penguins, *Pygoscelis papua*, during the breeding season. *Funct. Ecol.* **16**, 175-190.

Boyd, I. L. and Croxall, J. P. (1996). Dive durations in pinnipeds and seabirds. *Can. J. Zool.* **74**, 1696-1705.

Butler, P. J. (1998). The exercise response and the 'classical' diving response during natural submersion in birds and mammals. *Can. J. Zool.* **66**, 29-39.

Butler, P. J. (2000). Energy cost of surface swimming and diving of birds. *Physiol. Biochem. Zool.* **73**, 699-705.

Butler, P. J. (in press). Metabolic regulation in diving birds and mammals. *Resp. Physiol.*

Butler, P. J. and Jones, D. R. (1997). The physiology of diving of birds and mammals. *Physiol. Rev.* **77**, 837-899.

Butler, P. J. and Woakes, A. J. (1984). Heart rate and aerobic metabolism in Humboldt penguins *Spheniscus humboldti* during voluntary dives. *J. Exp. Biol.* **108**, 419-428.

Campagna, C., Le Boeuf, B. J., Blackwell, S. B., Crocker, D. E. and

Quintana, F. (1995). Diving behaviour and foraging location of female southern elephant seals from Patagonia. *J. Zool. Lond.* **236**, 55-71.

Carbone, C. and Houston, A. I. (1996). The optimum allocation of time over the dive cycle: an approach based on aerobic and anaerobic respiration. *Anim. Behav.* **51**, 1247-1255.

Carbone, C., De Leeuw, J. and Houston, I. (1996). Adjustments in the diving time budgets of tufted duck and pochard: is there evidence for a mix of metabolic pathways. *Anim. Behav.* **51**, 1257-1268.

Chappell, M. A., Shoemaker, V. H., Janes, D. N., Bucher, T. L. and Maloney, S. K. (1993). Diving behavior during foraging in breeding Adélie penguins. *Ecology* **74**, 1204-1215.

Cooper, J. (1986). Diving patterns of cormorants (Phalacrocoracidae). *Ibis* **128**, 562-569.

Costa, D. P. and Gales, N. J. (2000). Foraging energetics and diving behaviour of lactating New Zealand sea lions *Phoarctos hookeri*. *J. Exp. Biol.* **203**, 3655-3665.

Costa, D. P. and Gales, N. J. (2003). Energetics of a benthic diver: Seasonal foraging ecology of the Australian sea lion, *Neophoca cinerea*. *Ecol. Monogr.* **73**, 27-43.

Costa, D, P., Gales, N. P. and Goebel, M. E. (2001). Aerobic dive limit: How often does it occur in nature? *Comp. Biochem. Physiol.* **129A**, 771-783.

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

Croxall, J. P., Naito, Y., Kato, A., Rothery, P. and Briggs, D. R. (1991). Diving patterns and performance in the Antarctic blue-eyed shag *Phalacrocorax atriceps*. *J. Zool. Lond.* **225**, 177-199.

Culik, B. M., Pütz, K., Wilson, R. P., Allers, D., Lage, J., Bost, C.-A. and Le Maho, Y. (1996). Diving energetics in king penguins (*Aptenodytes patagonicus*). *J. Exp. Biol.* **199**, 973-983.

Dewar, J. M. (1924). *The Bird as a Diver*. Witherby, London.

Grémillet, D., Wilson, R. P., Storch, S. and Gary, Y. (1999). Three-dimensional space utilization by a marine predator. *Mar. Ecol. Progr. Ser.* **183**, 263-273.

Halsey, L., Butler, P. J. and Woakes, A. J. (2003). Testing optimal foraging model for air-breathing divers. *Anim. Behav.* **65**, 641-653.

Handrich, Y., Bevan, R. M., Charrassin, J. B., Butler, P. J., Pütz, K., Woakes, A. J., Lage, J. and LeMaho, Y. (1997). Hypothermia in foraging king penguins. *Nature* **388**, 64-67.

Harcourt, R. G., Schulman, A. M., Davis, L. S. and Trillmich, F. (1994). Summer foraging by lactating female New Zealand fur seals (*Arctocephalus forsteri*) off Otago Peninsula, New Zealand. *Can. J. Zool.* **73**, 678-690.

Heithaus, M. R. and Frid, A. (2003). Optimal diving under the risk of predation. *J. Theoret. Biol.* **223**, 79-92.

Herrera, G. O. (1997). Dieta reproductiva de la gaviota de Olrog Larus atlanticus en la provincia del Chubut. Undergraduate thesis, Universidad Nacional de la Patagonia San Juan Bosco. Puerto Madryn, Argentina.

Horning, M. (1992). Die Ontogenese des Tauchverhaltens beim Galapagos-Seebären *Arctocephalus galapagonensis* (Heller 1904). PhD thesis, University of Bielefeld, Germany.

Kato, A., Croxall, J. P., Watanuki, Y. and Naito, Y. (1992). Diving patterns and performance in male and female blue-eyed cormorants *Phalacrocorax atriceps* at South Georgia. *Mar. Orn.* **19**, 117-129.

Kooyman, G. L. (1989). *Diverse Divers*. Berlin, Springer-Verlag.

Kramer, D. L. (1988). The behavioral ecology of air breathing by aquatic animals. *Can. J. Zool.* **66**, 89-94.

Lasiewski, R. C. and Calder, W. A. (1971). A preliminary allometric analysis of repiratory variables in resting birds. *Resp. Physiol.* **11**, 152-166.

Lenfant, C., Kooyman, G. L., Elsner, R. and Drabek, C. M. (1969). Respiratory function of the blood of the Adélie penguin (*Pygoscelis adeliae*). *Am. J. Physiol.* **216**, 1598-1600.

Lovvorn, J. R., Croll, D. A. and Liggins, G. A. (1999). Mechanical *versus* physiological determinants of swimming speeds in diving Brünnich's guillemots. *J. Exp. Biol.* **202**, 1741-1752.

Mill, G. K. and Baldwin, J. (1983). Biochemical correlates of swimming and diving behavior in the Little penguin, *Eudptula minor*. *Physiol. Zool.* **56**, 242-254.

Parkes, R., Halsey, L. G., Woakes, A. J., Holder, R. L. and Butler, P. J. (2002). Oxygen uptake during post dive recovery in a diving bird, *Aythya fuligula*: implications for optimal foraging models. *J. Exp. Biol.* **205**, 3945-3954.

Ponganis, P. J., Van Dam, R. P., Levensen, D. H., Knower, T., Ponganis, K. V. and Marshall, G. (2003). Regional heterothermy and conservation of core temperature in emperor penguins diving under the ice. *Comp. Biochem. Physiol.* **135A**, 477-487.

Punta, G., Saravia, J. and Yorio, P. (1993). The diet and foraging behavior of two Patagonian cormorants. *Mar. Ornithol.* **21**, 27-36.

Sapoznikow, A. and Quintana, F. (2003). Foraging behavior and feeding locations of imperial cormorants and rock shags breeding in sympatry in Patagonia, Argentina. *Waterbirds* **26**, 184-191.

Sato, K., Naito, Y., Kato, A., Niizuma, Y., Watanuki, Y., Charrassin, J.-B., Bost, C.-A., Handrich, Y. and Le Maho, Y. (2002). Buoyancy and maximal diving depth in penguins: do they control inhaling air volume. *J. Exp. Biol.* **205**, 1189-1197.

Sato, K., Mitani, Y., Cameron, M. F., Siniff, D. B. and Naito, Y. (2003). Factors affecting stroking patterns and body angle in diving Weddell seals under natural conditions. *J. Exp. Biol.* **206**, 1461-1470.

Schmidt-Nielsen, K. (1993). *Animal Physiology: Adaptation and Environment*. Cambridge: Cambridge University Press.

Schmidt, D., Grémillet, D. and Culik, B. (1995). Energetics of underwater swimming in the Great Cormorant (*Phalacrocorax carbo sinensis*). *Mar. Biol.* **123**, 875-881.

Stephenson, R., Turner, D. L. and Butler, P. J. (1989a). The relationship between diving activity and oxygen storage capacity in the tufted duck (*Aythia fuligula*). *J. Exp. Biol.* **141**, 265-275.

Stephenson, R., Lovvorn, J. R., Heieis, M. R. A., Jones, D. R. and Blake, R. W. (1989b). A hydromechanical estimate of the power requirements of diving and surface swimming in the lesser scaup (*Aythya affinis*). *J. Exp. Biol.* **147**, 507-519.

Taylor, S. S., Boness, D. J. and Majluf, P. (2001). Foraging trip duration increases for Humboldt penguins tagged with recording devices. *J. Avian Biol.* **32**, 369-372.

Wanless, S., Harris, M. P. and Morris, J. A. (1988). The effect of radio transmitters on the behavior of common murres and razorbills during chick rearing. *Condor* **90**, 816-823.

Wanless, S. and Harris, M. (1991). Diving patterns of full-grown and juvenile rock shags. *Condor* **93**, 44-48.

Wanless, S., Corfield, T., Harris, M. P., Buckland, S. T. and Morris, J. A. (1993). Diving behaviour of the shag *Phalacrocorax aristotelis* (Aves: Pelecaniformes) in relation to water depth and prey size. *J. Zool. Lond.* **123**, 11-25.

Williams, T. D., Davis, R. W., Fuiman, L. A. M., Francis, J., Le Boeuf, B. J., Horning, M., Calabokidis, J. and Croll, D. A. (2000). Sink or swim: strategies for cost-efficient diving by marine mammals. *Science* **288**, 133-136.

Wilson, R. P., Hustler, K., Ryan, P. G., Noeldeke, C. and Burger, A. E. (1992). Diving birds in cold water: do Archemedes and Boyle determine energy costs. *Am. Nat.* **140**, 179-200.

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

Wilson, R. P. (2003). Penguins predict performance. *Mar. Ecol. Progr. Ser.* **249**, 305-310.

Wilson, R. P., Simeone, A., Luna-Jorquera, G., Steinfurth, A., Jackson, S. and Fahlman, A. (2003). Patterns of respiration in diving penguins: Is the last gasp based on an inspired tactic? *J. Exp. Biol.* **206**, 1751-1763.

Woakes, A. J. and Butler, P. J. (1983). Swimming and diving in tufted ducks, *Aythya fuligula*, with particular reference to heart rate and gas exchange. *J. Exp. Biol.* **107**, 311-329.

Ydenberg, R. C. (1988). Foraging by diving birds. *Proc. Int. Orn. Congr.* **19**, 1831-1842.

Yorio, P., Frere, E., Gandini, P. and Harris, G. (1998). Atlas de la distribución reproductiva y abundancia de aves marinas del litoral patagónico Argentino. *Plan de Manejo Integrado de la Zona Costera Patagónica*. Patagonia, Argentina: Fundación Patagonia Natural and Wildlife Conservation Society.