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Respiratory Physiology & Neurobiology 154 (2006) 268–283

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Optimal diving behaviour and respiratory gas exchange in birds[☆]

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Accepted 23 January 2006

Abstract

This review discusses the advancements in our understanding of the physiology and behaviour of avian diving that have been underpinned by optimal foraging theory and the testing of optimal models. To maximise their foraging efficiency during foraging periods, diving birds must balance numerous factors that are directly or indirectly related to the replenishment of the oxygen stores and the removal of excess carbon dioxide. These include (1) the time spent underwater (which diminishes the oxygen supply, increases carbon dioxide levels and may even include a build up of lactate due to anaerobic metabolism), (2) the time spent at the surface recovering from the previous dive and preparing for the next (including reloading their oxygen supply, decreasing their carbon dioxide levels and possibly also metabolising lactate) and (3) the trade-off between maximising oxygen reserves for consumption underwater by taking in more air to the respiratory system, and minimising the energy costs of positive buoyancy caused by this air, to maximise the time available underwater to forage. Due to its importance in avian diving, replenishment of the oxygen stores has become integral to models of optimal diving, which predict the time budgeting of animals foraging underwater. While many of these models have been examined qualitatively, such tests of predictive trends appear fallible and only quantifiable support affords strong evidence of their predictive value. This review describes how the quantification of certain optimal diving models, using tufted ducks, indeed demonstrates some predictive success. This suggests that replenishment of the oxygen stores and removal of excess carbon dioxide have significant influences on the duration of the surface period between dives. Nevertheless, present models are too simplistic to be robust predictors of diving behaviour for individual animals and it is proposed that they require refinement through the incorporation of other variables that also influence diving behaviour such as, perhaps, prey density and predator avoidance.

Keywords: Birds, diving, behaviour, physiology; Optimality, optimal models, optimal foraging, testing models; Respiration, gas exchange, oxygen stores, carbon dioxide stores, buoyancy

1. Introduction

A considerable amount of research into the foraging behaviour of organisms is based upon the concept that they forage optimally in terms of energy gain within certain constraints, such as those imposed by their physiology. In particular, such research has formed

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[☆] This paper is part of a special issue entitled "Frontiers in Comparative Physiology II: Respiratory Rhythm, Pattern and Responses to Environmental Change", Guest-Edited by W.K. Milsom, F.L. Powell and G.S. Mitchell.

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1569-9048/$ – see front matter © 2006 Published by Elsevier B.V.
doi:10.1016/j.resp.2006.01.012

the foundation for the development of analytical tools known as optimality models, which are used to produce testable predictions in order to study behavioural and physiological adaptations (Alexander, 1982).

A number of studies have considered how diving birds might maximise energy gain during foraging, generally selecting a particular parameter to be optimised, for example time (Wilson and Wilson, 1988), ability to ingest prey (Draulans, 1982) or diet (Ball, 1994). However, air breathing divers must periodically interrupt their foraging to return to the surface to breathe, and the energy costs of diving are often greatly influenced by positive buoyancy caused by the air in their respiratory system (Wilson et al., 1992). Thus, the replenishment of used oxygen and the removal of accumulated carbon dioxide are particularly important components of foraging in aquatic birds. The optimisation of these aspects of respiratory gas exchange in diving birds is likely to require trade-offs between a number of conflicting factors. These include the rate and amount of respiratory gas exchange that takes place at the water surface and the energetic implications of this both during the surface period and during the subsequent dive. Furthermore, the optimal balance will differ depending upon the characteristics of the dives being undertaken. Perhaps because respiratory gas exchange is such a fundamental, and complex, feature of avian diving, it has become the central element for many optimal foraging studies of aquatic birds. The present paper reviews empirical studies and models of diving behaviour, all based on the concept of optimal foraging in diving birds that focus on different aspects of respiratory gas exchange. The development of these models and their varying degrees of validity are discussed alongside an examination of the advancements in our understanding of the physiology and behaviour of diving birds that have been underpinned by optimal foraging theory and the testing of optimality models.

2. Buoyancy during diving

Potentially, diving is energetically costly for many species of birds because a large proportion of the oxygen they have available when they dive is stored in the respiratory system, and this makes their bodies positively buoyant. As diving birds travel through the water column, at least at shallow depths, they must work against their positive buoyancy in order to remain underwater. The increase in hydrostatic pressure at greater depths (approximately 1 atm for every 10 m descent into the water column) compresses the air sacs thus reducing the buoyancy of the bird and the energy required to remain at the new depth. As the volume of a gas is inversely proportional to its pressure, when a bird descends 10 m from the surface, the pressure doubles and so the volume of gas present in a bird is halved, thus reducing its buoyancy. However, a descent of a further 20 m, to a depth of 30 m, is required to double the pressure and thus halve the volume again, and so on. Below a certain depth, birds become negatively buoyant and tend to sink.

Thus the energetic costs resulting from positive buoyancy are generally greater in birds that dive shallowly (Stephenson, 1994). For example, for lesser scaup, *Aythya affinis*, diving to 1.5 m, buoyancy accounted for 62% of the mechanical cost of descent and 87% of the cost of remaining at 1.5 m while foraging. To maximise the duration of a dive and hence the time available to forage, diving birds are faced with an intriguing trade-off between maximising the volume of oxygen in their stores and minimising their buoyancy during the dive (Halsey et al., 2005b). Thus it seems reasonable to suppose that avian divers will not always dive with maximum oxygen stores, but there will be a trade-off between oxygen stores and buoyancy depending upon the characteristics of the dives they are undertaking (e.g. the depth and duration).

Tufted ducks, *Aythya fuligula*, apparently respond to changes in dive depth purely by adjusting their dive time budgeting (Halsey et al., 2005b). However, some other species of birds do seem to respond to diving to different depths by manipulating their body air volumes through changes in their ventilatory behaviour. Sato et al. (2002) report evidence that king penguins (*Aptenodytes patagonicus*) and Adélie penguins (*Pygoscelis adeliae*) inhale less air when diving more shallowly. Wilson and Zimmer (2004) recorded Magellanic penguins inhaling just enough air to achieve a low positive buoyancy at the depth of the bottom phase of a dive. If it is assumed that the direction of cause and effect in such data indicates conation by these birds about the dive they are about to undertake, then they are exhibiting an impressive degree of fine-tuning to their behaviours. This is presumably to ensure that time and energy are used efficiently both underwater and at the surface to maximise time spent foraging. Such fine-tuning might indicate that these birds are indeed predisposed to forage optimally. However, to date there are no optimal foraging models adapted for air breathing divers (often termed ‘optimal diving models’) that consider buoyancy. Instead, optimal diving models have focussed on the rates of exchange of the respiratory gases at the surface between dives.

3. Optimal diving models and tests of their qualitative predictions

A number of optimal diving models that incorporate the dynamics of oxygen uptake between dives are based on the marginal value theorem (Charnov, 1976). This model was initially used to investigate the optimal rate of energy gain of foragers that exploit a patchy food resource and depress the availability of the food for themselves over time in each patch visited (Fig. 1). The distinctive curve incorporated into the original model by Charnov (1976) is an exponential decay representing the progressively diminishing food resource over time in a patch. Thus as the forager spends more time in the patch, it experiences a diminishing acquisition of food as it depletes the food at the patch. Given that foragers have to spend time both travelling between patches and foraging at those patches, the model predicts how they should allocate their time. The highest rate of resource gain is shown from the line that runs from the travel duration and is tangential to the food acquisition curve. The optimal duration spent at each food patch can be found by dropping a perpendicular from the point where the line touches the curve. Other lines that intercept the curve after less or more food is gained produce a lower rate of resource gain (Fig. 1a; see legend for more details) while different travel durations produce different optimal foraging durations (Fig. 1b).

The marginal value theorem is an effective and popular basis for models of optimal foraging, as illustrated by its application to the investigation of many behavioural traits. For example, Cowie (1977) used the marginal value model to study the exploitation of patchily distributed prey by great tits. Other behaviours, such as avian migration, have also been investigated using the marginal value theorem (Hedenström, 2000). In applying the marginal value theorem to the acqui-

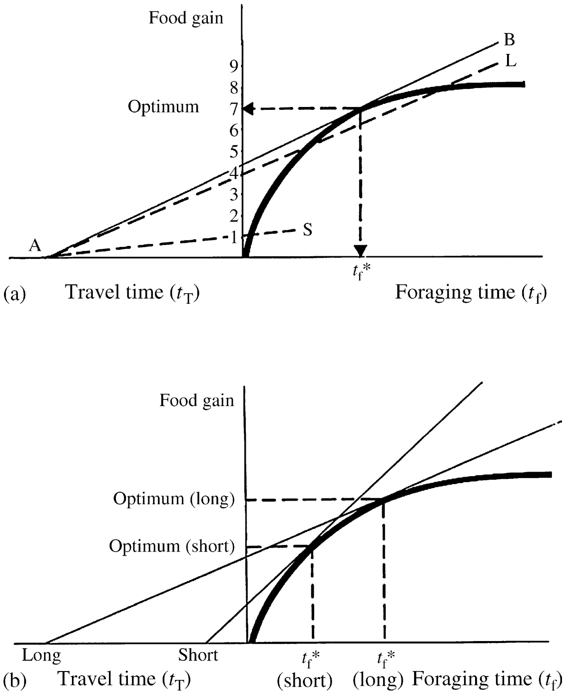

Fig. 1. Marginal value model (Charnov, 1976)—graphical representation of the marginal value theorem, which finds the optimal time for an animal to forage in a distant food patch, t_f^*, in order to maximise average rate of food intake (adapted from Krebs and Kacelnik (1991)): The forager spends time travelling between and foraging within patches. Within each patch, the forager experiences diminishing returns over time and so the curve of cumulative food gain (thick line) shows an exponential decay. To the left of the origin is the time taken to travel to the next patch (t_T), while to the right is the time spent foraging at the patch (t_f). (a) Calculation of t_f^* is achieved by constructing a line (AB) from t_T which touches the curve (the tangent). In this example, 7 units of food have been gained within t_f^*. The dashed lines (AL and AS) have been formed by drawing lines from A that meet the curve at alternative points. These represent time spent at the food patch that results in different amounts of food being gained. AL is associated with a longer foraging time whereby more food is gained during the visit to the patch compared to AB (approximately 8 units), while AS is associated with a shorter foraging time whereby less food is gained (approximately 1 unit). Given that the slopes of the tangent AB and of the lines AL and AS are calculated as y/x, each slope therefore represents the rate of food gain over the period of time associated with foraging at this patch (i.e. t_T plus t_f). The tangent AB has the highest gradient of any line that can be drawn from A to touch the cumulative gain curve and therefore represents the highest rate of food gain possible. (b) Long and short travel durations to a patch produce different optimal foraging durations (t_f^* long and t_f^* short, respectively) at that patch.

sition of oxygen at the surface of the water by diving animals, the spatially localised source of oxygen above the water surface is treated in the same manner as the patchy food resource in the original model of Charnov (1976) (Houston and McNamara, 1985). Such optimal diving models predict how diving animals might allocate their time over a dive cycle (a dive and the subsequent surface period) assuming that the net rate of oxygen gain from each surface visit is maximised so as to minimise the duration at the surface and therefore maximise the time spent underwater. Given that diving animals forage underwater, these models are in fact optimal foraging models. If a linear relationship between duration at the surface and oxygen gained is assumed, diving animals would be predicted to fill their oxygen stores completely and then remain underwater until those oxygen stores were low. This would minimise the proportion of time spent travelling underwater to the food site and thus maximise the proportion of time spent foraging.

However, Kramer (1988) presented an optimal diving model (Kramer's model) incorporating an exponential decay curve, as in the marginal value model, arguing that such a curve is representative of the replacement of oxygen by diving animals when at the surface between dives (Fig. 2). Kramer (1988) reasoned that the rate of oxygen gain would decrease as a function of time at the surface because the differences in partial pressure of oxygen in the lungs and blood will decrease over time, thus producing a progressively lower rate of diffusion. A comparison of Figs. 1 and 2 underlines the similarity between Kramer's model and the marginal value model. In the case of Kramer's model, the curve now represents the replacement of the oxygen stores of the body over time at the surface. This curve is not simply a measure of the volume of oxygen taken up to replace that used during the previous dive since a proportion of the oxygen taken up is used for ongoing metabolic processes in the bird. Thus in the present article, curves representing the total amount of oxygen taken up will be referred to as oxygen uptake curves while curves representing oxygen taken up to replenish the oxygen stores will be referred to as oxygen loading curves.

A number of important points and predictions arise from Kramer's model concerning ventilatory behaviour and the distance to the under water food site. Firstly, when the bird is at the surface, the optimal volume of oxygen to store is likely to be less than the maximum possible because of the diminishing gain experienced over time. From this it follows that, as distance to the food resource increases (i.e. travel duration increases), surface durations should also increase and the volume of oxygen carried in the stores should be greater (Fig. 2). Kramer's model also predicts that the amount of oxygen remaining at the end of a dive should be unaffected by the distance travelled during a dive. This leads on to further predictions that dive durations should also increase as distance to the food resource (usually dive depth) increases. Kramer (1988) cites a number of studies, the majority of which report behavioural data on diving animals, which tend to support the qualitative predictions of the model. Many

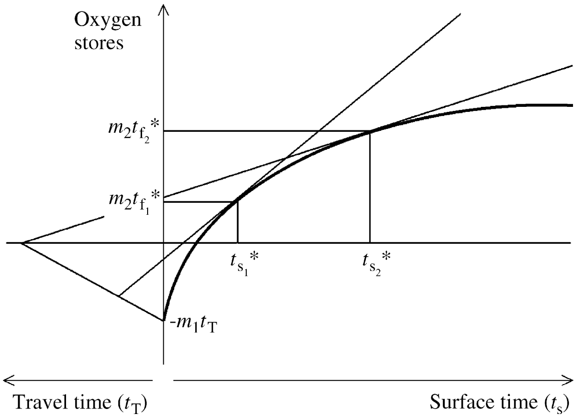

Fig. 2. Kramer's model (Kramer, 1988)—graphical representation of the marginal value theorem adapted to find the optimal surface time for an air breathing diver (adapted from Halsey et al. (2003b), with permission from Elsevier). The y-axis represents oxygen stores. The line from travel time, t_T, to $-m_1t_T$ represents a constant rate of reduction of the oxygen stores during t_T, where m_1 is the rate of oxygen consumption during travelling. The curve represents the oxygen obtained over time at the surface (t_s). The oxygen stores are exhausted where the curve starts at the abscissa i.e. at the start of the surface period. The portion of the curve below the ordinate represents the replacement of the oxygen used during travelling and that above the ordinate represents the replacement of oxygen used at the foraging site. Different optimal surface durations (t^*_{s1} and t^*_{s2}) are found by constructing a tangent starting at different values of t_T (similar to those shown in Fig. 1b). t^*_s is the optimal surface time in terms of maximising the rate of oxygen gain over the duration of the dive and surface period, which therefore maximises the proportion of time spent foraging. The value of y where the tangent touches the oxygen loading curve (m_2t_{f1} and m_2t_{f2}) represents the amount of oxygen available at the foraging site i.e. after accounting for an amount, m_1t_T, that is used during travel.

subsequent studies include observational data that test some of the predictions of Kramer's model (e.g. Lea et al., 1996; Jodice and Collopy, 1999) and are more mixed in their level of support for the model. For example, Jodice and Collopy (1999) found that the surface duration of marbled murrelets, *Brachyramphus marmoratus*, increased with dive duration, as predicted by Kramer's model while, contrary to the prediction of the model, dive duration did not increase with dive depth.

Thus, Kramer's model is concerned with maximising the delivery of oxygen to the underwater foraging area which, therefore, maximises the proportion of the total dive cycle that the animal spends at the foraging site. Houston and Carbone (1992) developed Kramer's model by explicitly plotting time at the food patch (foraging duration) against time at the surface. Just as with the change in the volume of the oxygen stores (Fig. 2), the change in the time at the food patch decreases with time at the surface (Fig. 3). In the latter case, the tangent now gives the time at the surface (s^*) that maximises the proportion of the dive cycle at the food patch and the resulting time at the food patch is t^*. A possible problem with this model is that Houston and Carbone (1992) assumed that divers return to the surface when they are on the verge of completely exhausting their oxygen reserves.

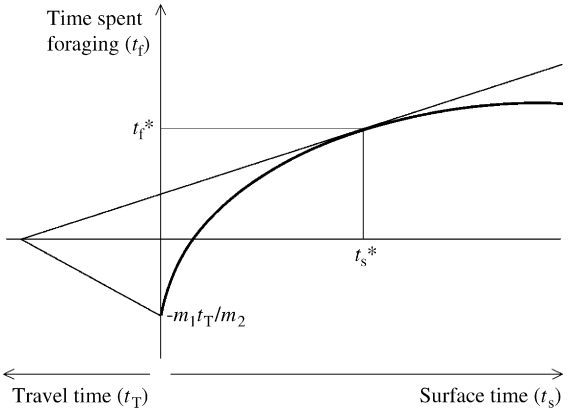

Fig. 3. Houston and Carbone's model (Houston and Carbone, 1992)—graphical representation of a modification to Kramer's model, where the y-axis is the time spent foraging (t_f) (adapted from Halsey et al. (2003b), with permission from Elsevier). The line from travel time, t_T, to $-m_1t_T/m_2$ shows the oxygen used during t_T. Foraging time is decreased by the duration m_1t_T/m_2, where m_1 is the rate of oxygen consumption during travel and m_2 is the rate of oxygen consumption during the foraging period (cf. Houston and Carbone, 1992). Thus for shorter travel times, assuming the same rate of oxygen consumption, $-m_1t_T/m_2$ would be greater and the oxygen loading curve would effectively be moved up the abscissa. The tangent construction represents the time at the surface (s^*) that maximises the proportion of time spent foraging and the resulting time at the surface is t_s^*.

Most researchers who wish to estimate the maximum aerobic dive duration of a species will calculate the aerobic diving limit (cADL), which is defined as the usable oxygen stores of the diver divided by the average rate at which the diver consumes oxygen while underwater. Thus Houston and Carbone's model assumes that divers have reached their cADL at the point that they return to the surface (Fig. 4). However, it is highly unlikely that an animal would routinely, if ever, reach such an extreme depletion of these reserves (Butler, 2004). Rather, long duration divers most likely start to experience an increasing reliance on anaerobic metabolism after a certain duration underwater, but still retain some accessible oxygen to supply the nervous system, heart and also, at least to some extent, the muscles involved in locomotion (Butler, 2004).

The diving lactate threshold (DLT), originally called the aerobic dive limit (ADL) by Kooyman et al. (1983), is the dive duration at which post-dive blood lactate concentration increases (Butler and Jones, 1997). This

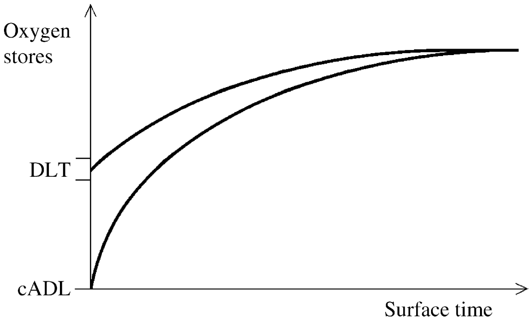

Fig. 4. Both Kramer's model and Houston and Carbone's model assume that the usable oxygen stores are exhausted as the animal surfaces at the end of a dive, i.e. at the end of the ascent phase of travelling. Thus the animals surface when they have reached their calculated aerobic dive limit (cADL). However, most birds and mammals seem to surface from most of their dives before reaching their diving lactate threshold (DLT), which was originally called the aerobic dive limit (ADL), when usable oxygen is still available. Unlike the cADL, the DLT cannot be calculated, but for comparison, an indication is given of the approximate position of the DLT on the abscissa of a plot of the size of the oxygen stores against time at the surface after a dive (see also Fig. 2). See text for further discussion of DLT and cADL.

occurs when reliance on anaerobic metabolism is such that lactate is created faster than it can be removed and thus it accumulates (Butler, 2004). It seems likely that diving birds rarely exceed their DLT during dives (Butler and Jones, 1997). In the one species of bird for which this has been investigated thoroughly, the emperor penguin, *Aptenodytes forsteri*, the measurement of post-dive lactate concentration in the blood gave a DLT of approximately 7 min. Nonetheless, these birds are able to dive for at least twice this duration (Ponganis et al., 1997), indicating that there is still usable oxygen in the stores at the DLT. A behavioural study, based on the dive duration to surface duration ratio, estimated that only dives over 8 min in duration exceeded the DLT (Kooyman and Kooyman, 1995), which represent less than 5% of dives. The reason that few dives exceed the DLT is because an increased reliance on anaerobic metabolism reduces foraging efficiency. Either surface durations subsequent to such dives must be of unusually long duration to allow for removal of the lactic acid and/or many relatively short dives must be performed in order for the animal to oxidise the accumulated lactate as quickly as possible (Butler and Jones, 1997).

It is probable that if Houston and Carbone's model assumed that divers return to the surface when they reach their DLT (Fig. 4) rather than when they reach their cADL, that the predictions of the model would be unaffected. This is because the important consequence of this assumption, in either form, is that a diver is returning to the surface with the same level of oxygen stores after each dive, independent of the nature of the dive. Carbone and Houston (1994) tested many of these predictions in the laboratory with pochards (*Aythya ferina*) and in general, the trends were similar to the qualitative predictions of the model. For example, foraging duration was independent of food concentration while surface duration tended to increase with travel time. Guillemette et al. (2004) also tested some of these predictions, on eider ducks (*Somateria mollissima*) in the wild, and found that on average the data were qualitatively supportive of the model.

Carbone and Houston (1996) produced two further models that build upon those of Houston and Carbone (1992). These attempted to account for the more complex, and quite possibly hypothetical, situation of divers routinely using both aerobic and extensive anaerobic metabolism during submergence i.e. routinely staying submerged beyond the DLT. In these cases, the surface period includes recovery from the accumulation of blood lactate above pre-dive levels. These models produce new predictions including more complex relationships between dive depth/duration, foraging duration and surface duration. The majority of studies suggest that the repeated dives with relatively short surface periods that characterise most diving bouts by birds are only possible if they are predominantly aerobic in nature (Butler and Jones, 1997). However, the model propounded by Ydenberg and Clark (1989), based on western grebes (*Aechmorphus occidentalis*), offers persuasive evidence that diving birds might make more extensive use of anaerobic pathways under certain circumstances. The model suggests that anaerobic diving is favoured when the prey of choice exists in dense and mobile concentrations that take time to locate, since such elongated dives allow fuller exploitation of the prey mass before the bird surfaces and loses contact with the prey. The provisos for such a scenario are, however, considerable: (1) carbohydrates must be available as the substrate for anaerobic metabolism (Butler, 2004); (2) the subsequent surface period would need to be relatively long to allow for removal of the accumulated lactate ions and protons and/or there is a series of subsequent, relatively short, dives during which oxygen is oxidised (Fedak and Thompson, 1993). Nonetheless, the possibility remains that overall foraging efficiency might be increased in specific situations.

Other optimal diving models building upon the seminal models of Kramer (1988) and of Houston and Carbone (1992) have also been developed. These are still based on replenishment of the oxygen stores at the surface, although they incorporate additional variables (Table 1 summarises these later models, along with some studies that have tested the predictions of the models on birds). For example, Mori (1998) noted that in the original models, the diving animal was assumed to dive to the depth of the food resource and its behaviour was adjusted around this fixed depth. However, food is not always at one fixed point in the water column but rather varies in density with depth. In such cases, assuming that food is gained more quickly where it is denser, divers would be expected to maximise foraging efficiency not just by maximising the time at the foraging site but also by maximising time in combi-

Table 1

A summary of the findings from certain studies, which have qualitatively tested the predictions of optimal diving models developed from the models of Kramer (1988) and Houston and Carbone (1992)

Model(s)	Tested by	Species	Field/laboratory	Prediction tested	Confirmed?
Models that have been tested					
Carbone and Houston (1996) Switch model	Carbone et al. (1996)	Pochard (*Aythya ferina*), tufted duck (*Aythya fuligula*)	Laboratory	Surface duration increases non-linearly with dive depth	Yes
				There is a step increase in surface duration at a certain travel duration (dive depth)	Yes
				There is a step increase in foraging duration at a certain travel duration (dive depth)	No
Carbone and Houston (1996) Mixed metabolism model	Carbone et al. (1996)	Pochard (*A. ferina*), tufted duck (*A. fuligula*)	Laboratory	Patterns in foraging duration with dive depth are non-linear	Partially
				Surface duration increases non-linearly with dive depth	Yes
				There will be two sudden upturns in surface duration as dive depth increases	No
				The relationship between surface duration and dive duration will increase abruptly at a certain depth	Yes
Walton et al. (1998)	Walton et al. (1998)	Shag (*Phalacrocorax aristotelis*), Black guillemot (*Cepphus grylle*), Common guillemot (*Uria aalge*)	Field	The existence of a non-monotonic relationship between the ratio of dive to surface duration, with the ratio peaking at a particular dive duration	Yes for first two species and no for third species
Mori (1998)	Mori (1998)	Cormorants (*Phalacrocoracidae*), auks and alcids (*Alcidae*), penguins (*Sphenisidae*)	Field (results from other studies)	Larger divers make deeper and longer dives and longer surface durations	Partially
Models that have yet to be tested					
Mori et al. (2002)[a]	–			Dive duration increases with dive depth Dive duration increases with patch quality	
Heithaus and Frid (2003)	–			If risk of predation at the surface increases with surface duration, surface duration should be less than the optimal to maximise energy intake	
				If risk of predation at the surface decreases with surface duration, surface duration should be more than the optimal to maximise energy intake	

Adapted from Green et al. (2005).

[a] Mori et al. (2002) do provide some data on Brünnich's guillemots but these data do not adequately test predictions from this model.

nation with greatest food density. Thus the model of Mori (1998) predicts the optimal depth at which a diver should forage. The model of Mori et al. (2002) incorporates patch quality as a parameter of energy intake to try to account for the fact that divers remain submerged for varied durations when diving to the same depth. Heithaus and Frid (2003) modelled diving behaviour in terms of risk of predation at the surface. This added factor was predicted to influence the optimal surface duration by increasing surface duration when predation risk is low or absent and decreasing surface duration when predation risk is high.

Table 1 shows that tests of the models that are developed from Kramer's model and predictions of Houston and Carbone's model produce mixed conclusions about their validity. Often the trends from the behavioural data used to test the qualitative predictions of these models are in support of the models, however, on a noteworthy number of occasions the data do not support the predictions. Possible reasons for the lack of support for certain model predictions are that the assumptions upon which they are based are not entirely valid or are incomplete. For example, the nature of the most fundamental aspect of all these models, namely the oxygen loading curve, is assumed from only simple physiological premises. While these might seem reasonable, the fine detail of the oxygen loading curve has an important effect on the gross predictions of diving optimality models (Ruxton et al., 2000) and as such, errors in the assumptions about the shape of the oxygen loading curve are likely to produce spurious or inaccurate predictions.

A case in point is the study by Walton et al. (1998) who attempted to refine the shape of the oxygen loading curve specifically for avian divers, and thus fine-tune for birds the predictions of Houston and Carbone's model (Walton et al. model). Walton et al. (1998) replaced the smooth oxygen loading curve of birds with a biphasic curve, where the first phase was steeper than the second (Fig. 5). They argued that oxygen must enter the caudal air sacs of the bird before becoming available for gas exchange. Therefore, the steeper part of the curve represents oxygen being taken up into the respiratory tract and air sacs, where most avian divers store about 50% of their usable oxygen (Keijer and Butler, 1982; Stephenson et al., 1989a,b; Croll et al., 1992), and the shallower part corresponds to slower replenishment of the haemoglobin and myoglobin stores (Fig. 5).

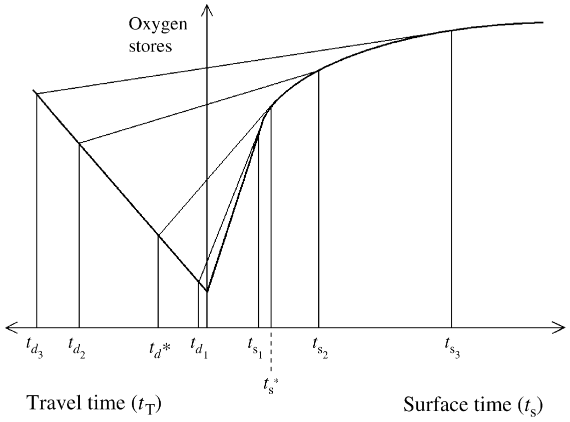

Fig. 5. Walton et al. model (Walton et al., 1998)—Kramer's model adapted specifically for birds by attempting to account for the effect of avian respiratory physiology on the shape of the oxygen loading curve (adapted from Parkes et al. (2002)). When maximising the dive to surface ratio, t_s^* represents optimal surface time and t_d^* the optimal dive time. t_{d1-3} and t_{s1-3} represent a selection of dive times and corresponding surface times, respectively. A range of short dive times (from t_{d1} to t_d^*) have similar t_s (t_{s1} to t_s^*) due to the prominent disfigurement of the oxygen loading curve, while a range of long dive times (from t_d^* to t_{d3}) have values of t_s (t_s^* to t_{s3}) that increase disproportionately. This results in an increase, peak and then decrease in the dive time to surface time ratio as dive duration increases (see text).

Kramer's model and Houston and Carbone's model tend to predict a decline in the ratio between dive duration and surface duration as dive duration increases. However, the model by Walton et al. (1998) predicts a slightly more complex relationship, which they pointed out is observed in a number species of diving bird.

The data of Dewar (1924) obtained from a wide range of avian divers typify this relationship, whereby for relatively short dives, the dive to surface ratio increases with increasing dive duration, reaches a peak and then decreases with further increases in dive duration. Also, Walton et al. (1998) themselves observed such peaks in two out of the three species of diving seabird that they studied (Fig. 6). The model of Walton et al. (1998) predicts this peak in dive to surface ratio because for a range of relatively short dives, the optimal surface periods will increase only slowly with increasing dive duration up to a critical point (Fig. 5). Beyond this dive duration, the tangential line denoting optimal surface duration touches the oxygen gain curve at the shallower, second phase of the curve and thus longer

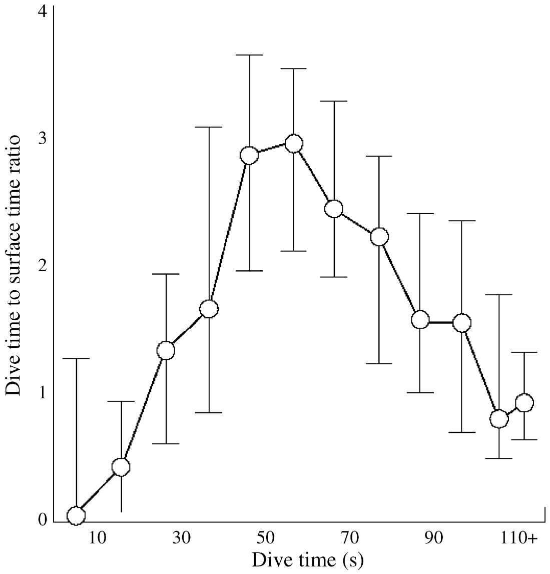

Fig. 6. The ratio of dive time to surface time against dive time in black guillemots, *Cepphus grylle*, for categories of dive time (median +25 and −75 percentiles) (adapted from Walton et al. (1998), with permission from Elsevier).

dive durations have corresponding surface durations that increase at a disproportionately high rate relative to the dive duration.

However, the physiological basis of the model of Walton et al. (1998) is probably incorrect, since it is likely that some inspired air reaches all the way to the cranial air sacs within one breath (Powell, 2000), thus reaching the lungs on the first inspiration (Parkes et al., 2002). Furthermore, a biphasic oxygen loading curve is not in fact necessary for the dive:pause ratio to be non-monotonic (Houston, 2000). When models such as that of Walton et al. (1998) appear to be good predictors, even though they contain incorrect assumptions, the benefit of optimality models to investigate behaviour and physiology is inevitably questioned. In fact, what the study by Walton et al. (1998) shows is the fallibility of testing predictive trends of models and consequently that confirmations of the *qualitative* predictions of a model can only be considered to provide weak support for the model's validity. Far more weight can be placed on testing the *quantitative* aspects of optimality models and, in doing so, investigating the links between behaviour and physiology (Stearns and Schmid-Hempel, 1987).

4. Testing the quantitative predictions of optimal diving models

Parkes et al. (2002) began the process of testing the quantitative predictions of optimal diving models by determining the oxygen uptake curve for tufted ducks. As the tufted duck is the only species of aquatic bird that has been the subject of a comprehensive, quantitative analysis of its respiratory physiology and behaviour, the following section of this article will inevitably concentrate on this species. Parkes et al. (2002) used a respirometry technique developed by Woakes and Butler (1983), coupled with a fast response oxygen analyser and semi-automated data recording system, to calculate oxygen uptake over periods as short as 0.25 s, despite the system having a much longer response time. This is a higher frequency than the fastest respiratory rate for this species (Butler and Woakes, 1979) and as such, accurate oxygen uptake curves were recorded.

Parkes et al. (2002) found that there was always a particularly rapid phase of oxygen uptake in tufted ducks for approximately the first 3 s after a dive and then a subsequent slower phase. Furthermore, rather than the curve being a fixed entity, its shape and size were dependent on the duration of the preceding dive (Fig. 7). Specifically, the rate of oxygen uptake was significantly higher during the first 3 s at the surface after longer dives (>16 s) than after shorter dives (<16 s), while the rate of oxygen uptake after the first 3 s did not vary with dive duration but was always slower than that during the initial period. After longer dives, the recovery period showed a biphasic oxygen uptake. Indeed the shape of the actual oxygen uptake curve following the longer dives is similar to that predicted by the model of Walton et al. (1998), but this is probably the result of

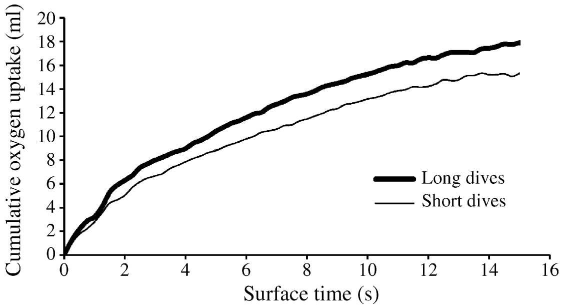

Fig. 7. Comparison of the oxygen uptake curve for tufted ducks after short dives and long dives (adapted from Parkes et al. (2002)).

an initially higher respiratory frequency rather than of the anatomy of the avian lung (Parkes et al., 2002). Furthermore, the inflection in the curve may be sufficiently close to the start of the surface period, and the volume of oxygen consumed during the dive may be high enough, that the tangent of Kramer's model routinely touches the curve beyond the inflection (Houston, 2000). Thus the presence of the inflection rarely affects the predictions of the model (Parkes et al., 2002).

Having quantified the oxygen uptake curve for tufted ducks, Parkes et al. (2002) found that it was more complicated than that portrayed in optimal diving models. The exact shape of the curve and how it changes as a function of diving duration is likely to have important implications for the quantitative predictions of optimal diving models. Looking again at Kramer's model (Fig. 2), it is clear that elements of it can indeed be tested empirically. The negative value of the oxygen stores at the ordinate represents the amount of oxygen consumed during travel to and from the site of food resource while the positive value of the oxygen stores where the tangent intercepts the oxygen loading curve represents the oxygen consumed at that site. A perpendicular line dropped to the abscissa from the tangent at the point of interception denotes the optimal surface duration.

The energy costs of diving ducks during different phases of the dive have been calculated by Stephenson et al. (1989b), Lovvorn et al. (1991) and Stephenson (1994) and these can be easily converted into rates of oxygen consumption (although with certain important assumptions; Walsberg and Hoffman, 2005). Halsey et al. (2003b) combined quantification of the oxygen loading curve for tufted ducks and the estimation of energy costs for a similar species (lesser scaup, *A. affinis*) to test the quantitative predictions of Kramer's model. Tufted ducks also have the advantage in this instance of being short duration divers which require only short surface periods. This is an advantage because optimal diving models based on the marginal value theorem produce stronger effects of dive depth and duration on surface durations for shorter dives, in particular when the replenishing of the oxygen stores occurs very rapidly (Kramer, 1988). Thus, diving ducks are ideal species with which to test the quantitative predictions of such models.

Halsey et al. (2003b) employed a similar methodology to that of Parkes et al. (2002) in order to obtain high resolution measures of the rates of oxygen reloading of tufted ducks between dives. Along with recording the diving time budgets of the ducks for each dive, they also manipulated the energetic costs of the dive with either the presence or absence of stones obstructing the food on the feeding tray (food obstructed and food unobstructed, respectively). The presence of the stones increased the foraging effort of the ducks and therefore the oxygen consumption during a dive. For the mean of six ducks, surface duration and estimated oxygen consumption while at the feeding tray were compared to those values predicted by Kramer's model. Statistically, albeit in part because the variations around the means were large, the model successfully predicted surface duration both when the food was obstructed and unobstructed, and oxygen consumption during the foraging part of the dive when the food was unobstructed. For example, the model predicted a surface duration of 12.6 s for tufted ducks when the food was unobstructed, while the recorded mean surface duration for six birds was 12.3 ± 1.4 s.

This empirical testing also proved useful in exploring Houston and Carbone's model more closely. An element of the time budget data recorded by Halsey et al. (2003b) agreed with a prediction of Houston and Carbone's model, in that surface duration did not increase after dives when food was obstructed despite oxygen consumption being greater. However, similar to the findings of Parkes et al. (2002), the rate of oxygen reloading over the first few seconds subsequent to a dive when food was obstructed was higher than that during the same period of time following dives when food was unobstructed. Thus, contrary to the model of Houston and Carbone (1992), which assumes that the oxygen loading curve is fixed and that surface durations of a particular length will always allow the same gain in oxygen, for tufted ducks at least, oxygen is gained more quickly per unit time after more energetically costly dives. Also, the assumption in Houston and Carbone's model leads to the prediction that more energetically costly dives will be shorter because oxygen consumption will be higher, but this was not found to be the case by Halsey et al. (2003b). In fact, the opposite was true since the ducks spent longer at the feeding tray when the food was obstructed, presumably to compensate for the decrease in foraging rate due to the presence of the stones.

Between the longer and more energetic dives when the food was obstructed, the ducks took up oxygen at a higher rate. This could be interpreted as indicating that the ducks surfaced with lower oxygen stores after more energetically costly dives and that oxygen loading at the surface was quicker as a result of the greater difference in partial pressure of oxygen between the lungs and the blood. However, Houston and Carbone's model assume that divers reach the surface with the same volume of oxygen stores after every dive. If this is correct, it suggests that for the ducks to gain oxygen more quickly when at the surface between more energetically costly dives, they had to increase their ventilatory effort. This would result in the ducks diving with greater oxygen stores to compensate for the increased consumption of oxygen during the dive.

Indeed, Halsey et al. (2003a,b) obtained evidence to support the idea that tufted ducks vary their ventilatory effort when replenishing their oxygen stores. The ducks were found to take up oxygen more slowly during longer surface durations after dives of a fixed duration, suggesting that the rate of oxygen gain could be varied by the ducks independently of variation in the oxygen partial pressure in the lung. Furthermore, after accounting for the differences in partial pressures of oxygen throughout the cardio-respiratory system after two dives of different energetic cost, the shapes of the two curves were still statistically different. If indeed the ducks can actively increase the rate of oxygen loading between dives, perhaps by an increase in respiratory frequency and/or tidal volume and associated tachycardia (Butler and Woakes, 1979), then not only are they decreasing surface durations and increasing foraging durations but they are also increasing energy costs while at the surface. This represents a degree of complexity to optimal diving over and above that which is considered by optimal diving models.

5. Beyond the oxygen loading curve

The fact that Halsey et al. (2003b) showed that, on average, Kramer's model predicted optimal surface duration for dives of different energetic costs as well as oxygen consumption for less costly dives, is compelling evidence that the model is incorporating at least some of the important factors which influence diving behaviour. It is also persuasive evidence that these important factors include replacement of the oxygen stores. However, despite the incorporation of the oxygen loading curve as the centrepiece of these optimal diving models, it is not clear that oxygen is indeed the respiratory gas most influential on diving behaviour.

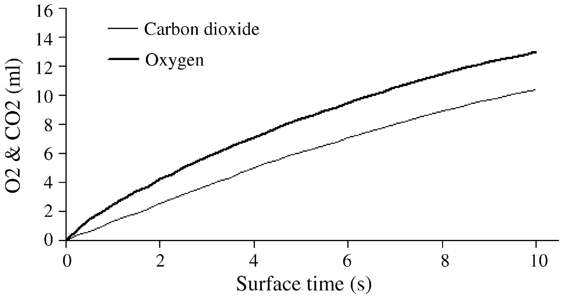

Fig. 8. Comparison of the oxygen uptake curve and carbon dioxide output curve for tufted ducks after dives of between 10 and 20 s (adapted from Halsey et al. (2003a)).

The shape of the carbon dioxide output curve for tufted ducks is similar to that of the oxygen uptake curve (Fig. 8) and thus it is quite possible that using either curve in an optimal diving model would predict similar optimal surface durations. In terms of the surface element of diving behaviour, Halsey et al. (2003a) found that both the oxygen stores and the carbon dioxide stores were close to, but not quite, fully replenished at the termination of a surface period, thus indicating that, for diving ducks at least, neither respiratory gas has a more prominent influence on surface duration than the other.

With regards to the diving part of the dive cycle, it is often assumed that the decision to terminate a dive is determined solely by the level of an animal's oxygen stores, but this may not always be the case (Butler, 2000; Thompson and Fedak, 2001). Behavioural studies, based on dive duration to surface duration ratios, suggest that not only tufted ducks (Woakes and Butler, 1983; Stephenson et al., 1986; Halsey et al., 2005a,b) but also, for example, Adélie penguins (*P. Adeliae*; Chappell et al., 1993), marbled murrelets (*B. marmoratus*; Jodice and Collopy, 1999) and emperor penguins (*A. forsteri*; Knower Stockard et al., 2005) all terminate most of their dives some time before they reach their DLT. The conclusion from these observations is that these species of bird have a reasonably large propor-

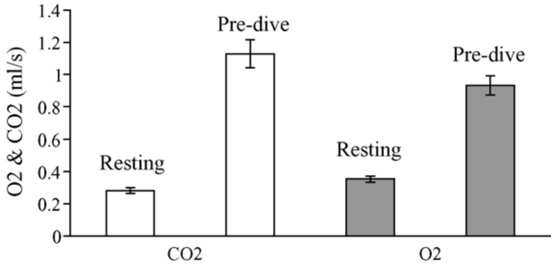

Fig. 9. Mean values ± standard error for rate of carbon dioxide output and rate of oxygen uptake in tufted ducks at rest on water and during the pre-dive hyperventilation before a diving bout (adapted from Halsey et al., 2003a).

tion of their usable oxygen remaining in their stores at the end of a dive. This is somewhat paradoxical for in the case of tufted ducks, they have a number of oxygen related adaptations to diving such as a high oxygen storage capacity (Keijer and Butler, 1982; Stephenson et al., 1989a,b), regional redistribution of blood (Bevan and Butler, 1992) and distinct tolerance of hypoxia (Grubb et al., 1977; Kiley et al., 1985; Lutfullah et al., 2005). Nonetheless, there is a possible advantage for tufted ducks maintaining a safety margin in terms of these stores (Halsey et al., 2005a,b), in the event that they become trapped under ice in winter when they try to reach the surface (Butler, 2004) or are confronted by a predator (see also Wilson and Quintana, 2004).

Studies on diving birds provide evidence for the prominent influence of carbon dioxide on durations of apnoea. Halsey et al. (2003a) found that in tufted ducks, more carbon dioxide is exchanged than oxygen during the few breaths of hyperventilation before the start of a bout of dives (Fig. 9) and this was also the conclusion arrived at by Wilson et al. (2003) for Humboldt penguins, *Spheniscus humboldti*. Jones et al. (1982) found that during forced dives, arterial chemoreceptors caused an increase in hind limb vascular resistance when stimulated by high partial pressures of carbon dioxide and low partial pressures of oxygen, but not by hypoxia alone. Furthermore, while in the laboratory, tufted ducks and double-crested cormorants reduce their dive durations and/or increase their surface durations when diving from gas mixes of up to 5% carbon dioxide (Butler and Stephenson, 1988; Enstipp et al., 2001; Borg et al., 2004; Halsey et al., 2005a). Finally, a complex model of the cardio-respiratory control of diving, albeit based on a marine mammal, supports this empirical evidence in indicating that carbon dioxide, not oxygen, is the key variable determining dive duration (Stephenson, 2005).

The most significant point here with regards to optimal diving behaviour is that species which terminate a dive before their DLT is reached are not foraging optimally if oxygen is considered to be the primary physiological constraint. This is because divers that do not remain submerged until their DLT are not staying at the foraging site for as long as possible given the oxygen they have in their stores, nor are they replenishing their oxygen stores over the steepest possible part of the oxygen loading curve (without also accumulating lactate). As emphasised by Green et al. (2005), such species are instead replenishing oxygen consumed during the dive over a shallower and therefore less effective part of the oxygen loading curve (and removing carbon dioxide over a shallower part of the carbon dioxide washout curve).

It is highly doubtful that the respiratory gases are the only variables that influence the diving behaviour of aquatic birds. Halsey et al. (2003a) point out that feeding duration in diving birds, which is usually correlated with dive duration, is probably also influenced by a plethora of other factors such as food density (Halsey et al., 2003b), particle selection time (Draulans, 1982), rate of food ingestion (Stephenson et al., 1986), giving up times when attempting to locate food (Hustler, 1992) and predation risk (Heithaus and Frid, 2003). The possibility that tufted ducks usually terminate dives before they experience any discomfort (e.g. an uncomfortable urge to breathe) is another factor that must also be considered (Gabrielsen, 1986; Halsey et al., 2003a). Furthermore, the influence of all these factors is likely to change depending upon the environmental and social situation of the bird (Guillemette et al., 2004). In the laboratory, tufted ducks seem to work harder when foraging for food with conspecifics than when alone and this may well represent a greater focus on maximising rate of food assimilation when in competition with other birds (Halsey et al., 2006). Thus when foraging in groups in the wild, concerns of predation risk may have a reduced influence on diving behaviour while the increased effort of the dives, depleting the oxygen stores and increasing carbon dioxide levels more, may increase the emphasis on the respiratory gases in influencing surface durations and dive durations.

6. Future directions for optimal diving models

An important facet of optimality theory is the development of models with improved predictive validity, often through an increase in complexity. Current optimal diving models have some merit as qualitative predictors of diving behaviour since they can often predict the behaviour of diving birds in laboratory conditions. However, their predictive limitations are also apparent. A test of these models that seems to expose their deficiencies most clearly and thus can aid in uncovering which variables should be added to improve their predictions, is a comparison of observed and predicted values for *individual* animals. For example, when Halsey et al. (2003b) tested the quantitative predictions of Kramer's model using average values taken from several ducks, the model generally showed good predictive validity. However, when the model was tested with individual tufted ducks it was a poor predictor of both energy consumed during the foraging phase of the dive and surface duration. Since models such as Kramer's are an attempt to describe the diving behaviour of an average, i.e. typical, bird, perhaps it is not surprising that at the level of the individual animal models are less accurate than at the species level. Individuals can vary considerably and thus at the individual level, the model may not always incorporate all of the variables that are influential in determining diving behaviour. When considering mean values across several birds however, the individual differences, i.e. the idiosyncrasies, between birds are averaged out.

Indeed, both laboratory based (Carbone and Houston, 1994) and field based (Ball, 1994; Green et al., 2003; Guillemette et al., 2004) studies of birds foraging have reported considerable differences between individuals. Halsey et al. (2003b) suggest that the foraging strategies seemed to vary between ducks in terms of foraging duration, surface duration and rate of oxygen consumption over the dive cycle, and that these may be connected to the rate of oxygen loading at the surface. Guillemette et al. (2004) considered that the individual differences in diving time budgets recorded between common eiders might be associated with differing physiological states, such as body mass (Walker and Boersma, 2003) and volumes of the plumage and respiratory system, all of which affect buoyancy (Lovvorn et al., 1991; Stephenson et al., 1989a,b). Finally, the number of dives per bout varied enormously between each tufted duck in the study by Halsey et al. (2003b), which may indicate that the time scale over which the birds optimally forage differs, with perhaps some birds diving optimally at the unit of a diving bout rather than at that of a single dive. To develop more robust optimal diving models, their complexity must be increased through the judicious addition of more of these influential factors. It would also be useful, and more realistic, if some indication of the degree of uncertainty of the predictions could be incorporated into the models.

However, certain factors already discussed in the present review that might influence diving behaviour such as predator avoidance, maintaining a safety margin of usable oxygen and optimising over a diving bout rather than over a single dive, expose a potential problem with optimality theory in considering short-term optimisation criteria. Assuming organisms are attempting to maximise their lifetime reproductive success, which will involve a large number of short-term behaviours, it can be argued that if diving animals are behaving optimally at all, that this optimality is based upon long term, rather than short term, strategies. Optimal behaviour based upon long-term strategies may produce discrete short-term behaviours that roughly approximate to optimal behaviour over short-term criteria such as foraging. However, scrutiny of foraging behaviour may reveal it to be sub-optimal over the short term, as appears to be the case with the foraging of individual tufted ducks (Halsey et al., 2003b). For example, long-term optimisation strategies forged by natural selection will probably include behaviour in all species to limit the chances of predation or misadventure such as becoming trapped under ice. For these reasons, optimal diving models are probably best considered as working hypotheses to explore how far rates of respiratory gas exchange and other influential factors can explain what diving birds do, rather than providing the last word in explaining diving behaviour (cf. Stamp Dawkins, 1995). Nevertheless, optimal diving models clearly provide an important tool for exploring the physiology, as well as the ecology of diving behaviour, predominantly through tests of the extent to which phenomena associated with respiratory gas exchange dominate the control of diving behaviour.

7. Conclusions

A cycle of testing and refinement of optimal diving models can be criticised because this cyclical process may in fact lead to the definition of optimal foraging itself being refined until it approximates more and more closely to the observed behaviour, regardless of whether that behaviour is actually optimal or not (Ollason, 1980). Nevertheless, the discrepancies between the qualitative predictions of models and observations of diving behaviour reported by some studies (e.g. see Table 1) serve to promote investigation into other diving variables that might improve the realism of these models, such as predator avoidance and variations in food density in the water column. Furthermore, the concept of optimality has aided research that considers the role played by the respiratory gases in the time budgeting and energetics of diving birds without considering optimality models per se. Such investigations inevitably enhance our understanding of the behaviour and physiology of diving animals over and above aiding in the development of a sufficiently sophisticated model that makes credible quantitative predictions. Given that optimal diving models have been present in the literature for over 15 years, their value to the study of diving behaviour and physiology can arguably be discussed in terms of what has been learnt since their introduction.

There have perhaps been two main advances in our understanding of diving physiology and behaviour since the advent of optimal foraging models for air breathing divers. The first has been the increased interest in the extent to which the physiology of diving animals might constrain their underwater foraging behaviour. For example, from this approach, much has been learnt about the ability of some diving birds to anticipate the nature of the next dive by adjusting their buoyancy (in a trade-off with the volume of their oxygen stores) and therefore improving their time and energy budgets while foraging. The discovery that some diving birds do indeed make such physiological adjustments depending on the depth and duration of their diving serves to highlight those species that do not (e.g. tufted ducks) and raises interesting questions about why these differences exist. Further, it has been implicitly assumed by many researchers for a long time that diving behaviour is centred on the consumption and subsequent reloading of the oxygen stores. However, considering diving birds as optimal foragers has highlighted the fact that many such species regularly terminate a dive with considerable oxygen stores remaining. This has promoted investigations into other possible influences on diving behaviour that might explain this possible paradox, such as levels of carbon dioxide in the body and the density of food in the foraging area. Many researchers tend to assume that most avian divers do not perform many dives beyond the DLT because either a long duration at the surface must then be spent to remove the lactate or else a number of subsequent dives must be well within the DLT to oxidise the lactate (Fedak and Thompson, 1993). However, optimal diving models that include the possibility of an increased reliance on anaerobic respiration as dives progress have shown that such a strategy might be advantageous in situations where the premature termination of a dive would otherwise allow motile prey to escape.

The second main advance has been the knowledge obtained from the quantification of certain optimal diving models. The focus on the physiology and behaviour of diving required to test such models in this way has uncovered important details about the diving strategies of particular species of diving birds, most notably the tufted duck. In particular, changes in the oxygen loading curve and carbon dioxide washout curve in response to differences in diving energetics (due to dive duration and the ease with which food is obtained), and how these variations relate to changes in diving behaviour, have been studied. The associated effects of the changes in these uptake and output curves on surface duration, respiratory costs and also buoyancy, have also been investigated. Together, they underline the fact that the physiological and behavioural aspects of avian diving strategies have not yet been studied in a co-ordinated manner, nor has their complexity yet been fully appreciated.

Acknowledgement

The authors received support from the Natural Environment Research Council (grant number NER/A/S/2000/01074) during the writing of this review.

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