



Can dive cycle models predict patterns of foraging behaviour? Diving by common eiders in an Arctic polynya

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There has been wide empirical and theoretical interest in how diving animals allocate time between obtaining oxygen at the surface and foraging at depth. Assuming diminishing returns in oxygen gain at the surface, classic diving models predict that time on the surface should increase, while time spent foraging at depth should first increase and then decrease as travel time increases. Controlled laboratory experiments have indicated partial support for predictions of diving models; however, their usefulness in understanding patterns of diving behaviour in the wild is still in question. We assessed the applicability of diving models to foraging patterns of common eiders, *Somateria mollissima sedentaria*, wintering in the Canadian Arctic. Underwater footage was used to quantify time foraging at depth and duration of surface pauses in relation to changes in travel time induced by strong tidal currents. Consistent with predictions of diving models, bottom foraging time decreased with increasing travel time, while total dive duration was relatively constant at 58.47 ± 5.32 s, close to the estimated aerobic dive limit for this species. However, durations of surface pauses were not associated with diving parameters, as anticipated from diving models. Durations of surface pauses were highly variable (183.05 ± 158.06 s) and often considerably longer than necessary to replenish oxygen stores. While the duration of surface pauses predicted by diving models in relation to travel time may be an optimal strategy when obtaining oxygen at the surface is the predominant constraint to foraging, a variety of processes operating at different timescales can influence behavioural patterns in the wild. Preliminary analysis considering the rate of digestive processing suggests that foraging patterns of eiders could be simultaneously influenced by several different rate constraints. Therefore, while static modelling approaches are an important heuristic tool for elucidating mechanisms underlying diving behaviour, dynamic approaches, which can incorporate variables concerning multiple physiological and environmental states, will probably be required to fully understand complex foraging patterns observed in the wild.

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Diving is an important mode of foraging for a variety of aquatic air-breathing animals. In addition to more typical foraging considerations (e.g. characteristics of prey and patches), diving animals must account for the capabilities and limitations of their respiratory system when making foraging decisions. In particular, diving animals face

a trade-off between time spent breathing at the surface and time spent foraging at depth, so behaviours that maximize energy intake should be strongly selected for (Kramer 1988; Ydenberg 1988).

Static diving models have been used to explore the relations between time allocated to foraging at depth f and time spent on the surface between dives, s (Kramer 1988; Houston & Carbone 1992), obtaining oxygen (or exchanging other respiratory gases; Halsey et al. 2003a; Green et al. 2005). In the literature, these models and their derivatives are frequently referred to by a variety of names, including 'diving models', 'dive cycle models', 'oxygen balance models' or 'optimal breathing models'. The approach treats the diving animal as a central-place forager (Houston

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& McNamara 1985), departing the surface where oxygen is obtained (with assumed diminishing returns), to forage at depth, and subsequently returning to the surface. The marginal value theorem (Charnov 1976) is used to find the maximum 'long-term' foraging rate (Stephens & Krebs 1986), equivalent to maximizing the proportion of time at depth, for a given travel time τ . This allows predictions to be made about the length of time a diving animal should spend replenishing oxygen stores on the surface s^* and how long it should spend foraging at depth f^* in relation to the travel time between these environments (typically investigated as a function of depth).

The dive cycle models make several general predictions. First, foraging time f^* should initially increase and then decrease as travel time τ increases (Fig. 1). Second, total dive duration ($d = f + \tau$) is predicted to increase as a decelerating function of travel time, to the point where total dive duration is limited by the maximum oxygen stores of the animal (although anaerobic metabolism has also been considered). Third, durations of surface pauses s^* are predicted to increase exponentially with travel time (see Houston & Carbone 1992).

These models assume a single patch type and a linear relationship between prey acquisition and time in the foraging patch, so that foraging time and dive duration will not be related to prey concentration/patch quality at depth. The diving models have also been extended to include scenarios of nonlinearity in intake rate, as well as heterogeneity in patch quality due to differences in prey abundance/profitability and risk of predation (e.g. Thompson & Fedak 2001; Mori et al. 2002; Heithaus & Frid 2003; Houston et al. 2003). Other models have

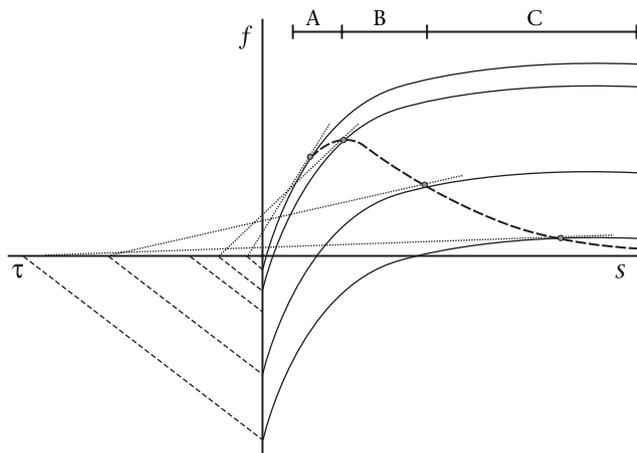


Figure 1. Schematic illustration of the dive cycle models over a range of travel times τ (after Houston & Carbone 1992). As travel time increases, the oxygen gain curve (solid) shifts downward, decreasing foraging time f as a function of the rate of oxygen consumed while travelling to the patch. The tangent line (dotted) to the oxygen gain curve indicates the optimal duration of surface pauses s^* and foraging time at depth f^* for each τ . The dashed curve tracks the change in s^* and f^* as τ increases, illustrating the general prediction that f^* should first increase and subsequently decrease as a function of travel time. For ease of discussion, this curve is divided into three regions representing (A) the initial increase in f^* , (B) the subsequent decrease in f^* and (C) the exponential increase in s^* and diminishing f^* under long τ . See text and Houston & Carbone (1992) for details.

considered dives that exceed the aerobic dive limit through the use of anaerobic metabolism (Carbone & Houston 1996); however, such a transition is generally rare (Butler 1988; Boyd 1997). The shift to anaerobic metabolism is probably more continuous than that predicted by these models (Butler 2004) and it should only be expected when prey are of adequately high energy content and/or are ephemeral (e.g. Ydenberg & Forbes 1988; Ydenberg & Clarke 1989). We do not consider these special cases. Instead, we focus on the fundamental features of the most basic set of dive cycle models, as outlined above.

Some empirical support exists for particular aspects of the basic diving models, primarily based upon controlled laboratory studies of captive birds diving in tanks (Carbone & Houston 1994; Carbone et al. 1996; Halsey et al. 2003b). Consistent with model predictions, both foraging time and total dive duration have been observed to increase over a narrow range of short travel times (Fig. 1, region A). However, dive tank depth has been inadequate to test the most general feature of the dive cycle models that foraging time first increases and subsequently decreases with increasing travel time (maximum tank depths: 3 m, Carbone & Houston 1994; 5 m, Carbone et al. 1996; 1.7 m, Halsey et al. 2003b). Also consistent with model predictions, field observations often show an increase in total dive time with increasing depth (Dewar 1924; Wilson & Wilson 1988; Croxall et al. 1991; Williams et al. 1992; Croll et al. 1992; Clowater & Burger 1994; but see Cairns 1992; Watanuki et al. 1996; Jodice & Collopy 1999).

Empirical support for predictions regarding durations of surface pauses remains unclear. Consistent with the diving models, many field studies have reported a positive and sometimes accelerating relationship between the duration of surface pauses and total dive time (Stonehouse 1967; Wanless et al. 1988; Cairns 1992; Clowater & Burger 1994; Monaghan et al. 1994; Jodice & Collopy 1999; Goudie 1999; Wilson & Quintana 2004; Heath et al., in press). For some avian species, dive:surface pause ratios tend to peak at short dive durations, which could be a function of avian respiratory physiology (i.e. air sacs; Walton et al. 1998). In contrast, the relation between depth (a surrogate for travel time) and duration of surface pauses appears to be weak in both birds and mammals (Kramer 1988). In dive tank experiments, the duration of surface pauses were observed to roughly increase with travel time/depth; however, the predicted acceleration in the duration of surface pauses with increasing travel time has not been observed (Carbone & Houston 1994). The time-scale over which the duration of surface pauses is examined, however, could partially bias results in a number of dive tank studies. In an attempt to control for potential bout structure, researchers have excluded from analyses those dive cycles in which surface durations were longer than 20 s (Carbone & Houston 1994; >28 s excluded by Halsey et al. 2003b; >35 s by Carbone et al. 1996). Therefore, only high rates of foraging were considered, which potentially confounds testing predictions of rate-maximizing models. Parkes et al. (2002) and Halsey et al. (2003b) found that tufted ducks, *Aythya fulgula*, could adjust their respiratory frequency by hyperventilating, and therefore, load oxygen stores more rapidly than has

been previously considered. Oxygen uptake curves showed a diminishing return of oxygen gain over time, consistent with a basic assumption of diving models; however, the models did not accurately predict the duration of surface pauses of individual birds (Halsey et al. 2003b). Diving models also assume that oxygen balance is the primary factor influencing surface duration and behavioural patterns. While oxygen balance is probably an important constraint, other physiological and ecological processes, such as digestion (Guillemette 1998) or endurance (Kramer & McLaughlin 2001; Heath et al., in press), operate at different timescales and could have an important influence on patterns of surface durations in the field.

We assessed the applicability of diving models to diving and foraging patterns of free-ranging birds. Around the Belcher Islands in Hudson Bay, Canada, common eiders, *Somateria mollissima sedentaria*, winter in persistent open water habitats maintained by strong tidal currents, in a marine environment otherwise covered in sea ice. Called 'polynyas', these habitats are essentially Arctic oases for marine wildlife. Within polynyas, the velocity of currents varies predictably over the tidal cycle and increases the time it takes eider ducks to dive to the bottom to forage on mussels, *Mytilus edulis* (Heath et al. 2006). A noninvasive underwater video configuration allowed us to follow eiders through complete dive cycles over the same subtidal mussel beds. Therefore, prey availability and depth (and therefore buoyancy costs) were relatively constant over the tidal cycle, and travel time for a given dive was primarily influenced by increased costs of drag in faster currents (Heath et al. 2006). Mussels are sessile prey, and multiple individuals are swallowed underwater by eiders, approximating model assumptions of a constant prey-energy-intake rate per second of time foraging (Houston & Carbone 1992). Similar to a flume tank, these spatially simplistic habitats therefore provided a unique opportunity to experimentally investigate the influence of travel time on time allocation over the dive cycle, from a population of free-ranging diving birds. Laboratory investigations using dive tank experiments have shown the predicted initial increase in foraging time under short travel times (Fig. 1, region A). We were particularly interested in investigating the predicted decrease in time foraging at depth under longer travel times (Fig. 1, region B/C) and related increases predicted in the duration of surface pauses. We discuss the benefits and limitations of existing diving models, and consider how multiple rate constraints operating simultaneously at different timescales may influence behavioural patterns in the wild.

METHODS

Field Site

In collaboration with Inuit from the community of Sanikiluaq, Nunavut, we studied the diving and foraging behaviour of common eiders wintering at Ulutsatuk polynya, located in the land-fast sea ice in the Belcher Islands, Hudson Bay (see Gilchrist & Robertson 2000). At this location, strong tidal currents flow between the entrance to

Omarolluk Sound, keeping the sea ice from freezing and therefore providing a persistent open water habitat for wildlife, including common eiders. Information provided by our Inuit collaborators indicated that this was an important wintering site for common eiders and an ideal location to study foraging behaviour. Further details are provided in Gilchrist & Robertson (2000) & Gilchrist et al. (2006).

Tidal Currents

Current velocities were quantified by deploying a Nortek Aquadopp 3D current meter with a directional fin in the middle of the water column (~5.5 m) on a mooring line anchored between the ocean bottom and the sea ice above, and within 3–10 m of where eiders were diving. This device uses three acoustic beams to measure Doppler velocity to an accuracy of 1% of the measured value ± 0.5 cm/s sampled at 23 Hz and averaged over 10-min intervals throughout the duration of the study. Therefore, by reference with time of day, we could determine an accurate average current velocity associated with each dive made by eiders.

Diving Behaviour

An underwater video camera was deployed at the edge of the polynya using a unique support system that allowed panning and tilting the camera through three dimensions by a surface operator (Heath et al. 2006). This allowed us to follow eiders through complete dives at a constant depth of 11.3 m. Dives were recorded over 8 days in March 2002 and 2003 by opportunistically following unmarked eiders departing from the surface. This probably represents a random sample of diving by eiders wintering at Ulutsatuk polynya (approximately 100 individuals). From digital video footage, we recorded descent, at depth and ascent durations. Departure from the surface was quantified as the frame in which the bill of the bird broke the surface of the water. The time at which the bird reached the bottom was determined by a change in the body axis to a horizontal direction, which was also accompanied by cessation of wing flaps. Departure for the surface occurred when the bird stopped working against its positive buoyancy, upon which the body axis shifted to an angle greater than horizontal and the bird passively rose to the surface. Surfacing was quantified as the frame when the tail of the bird broke the surface, leaving a characteristic splash pattern. The video footage was recorded at 30 frames per second (fps), allowing calculation of durations that were accurate to within 0.10–0.03 s. Subsequent durations of surface pauses were recorded by following birds (using video footage or by surface observation) and recording the latency to the subsequent dive.

Our previous research indicated that, during descent, wing stroke frequency remained constant while effective swim speed (relative to the moving water) showed a slight increase with current speed. Descent speed (relative to the bottom) showed a strong nonlinear decrease with increasing current speed (Heath et al. 2006). Therefore, descent duration and the number of wing flaps required to descend

to depth increased with current speed, indicating that both time and energy costs of descent probably increase with current speed (Heath et al. 2006). Current speed may therefore represent a more appropriate indicator of travel costs than just travel time alone. We therefore investigated dive cycle model predictions of foraging time and duration of surface pauses in relation to current speed. This approach allows implicit consideration of potential changes in metabolic rate and/or the rate of oxygen consumption during travel time in increasing currents. For completeness, we also present results in relation to travel time alone.

Statistics

Regression analysis was used to evaluate relations between behaviours, current velocity and travel time. Because diving costs are nonlinearly related to speed (Lovvorn 2001), and our previous research indicated that relationships between travel time and tidal currents are nonlinear (Heath et al. 2006), we used either linear or nonlinear (quadratic or logarithmic) regressions according to which curve explained the most variation in the data. Log base e (ln) transformation was used to evaluate nonlinear logarithmic relationships with linear regression. For completeness, we also present the R^2 values for linear regression to indicate the extra variation explained by nonlinear analysis.

RESULTS

Total travel time (descent plus ascent) increased nonlinearly with increasing current velocity (Fig. 2; quadratic regression: $F_{2,75} = 22.48$, $P < 0.0001$, $R^2 = 0.37$; linear = 0.29; quadratic regression equation: $\text{travel} = 16.61 + 3.49 (\text{current}) + 11.16 (\text{current} - 0.35)^2$). Consistent with predictions of dive cycle models considering longer travel times (Fig. 1, region B/C), the time that eiders spent feeding on the bottom decreased as a function of current velocity (Fig. 2; quadratic regression: $F_{2,139} = 10.37$, $P < 0.0001$, $R^2 = 0.13$; linear regression: $R^2 = 0.11$; quadratic regression equation: $\text{bottom} = 43.31 - 6.78 (\text{current}) - 12.85 (\text{current} - 0.35)^2$). Bottom duration (ln) also decreased as travel time increased (logarithmic regression: $F_{1,74} = 28.90$, $P < 0.0001$, $R^2 = 0.28$; linear regression: $R^2 = 0.20$; regression equation: $\ln(\text{bottom}) = 4.30 - 0.03 (\text{travel})$).

Total mean \pm SD dive duration (bottom plus travel) was relatively constant at 58.47 ± 5.32 s and did not change with current velocity (Fig. 1; regression: $F_{1,74} = 0.31$, $P = 0.578$, $R^2 = 0.004$) or travel time (regression: $F_{1,74} = 0.04$, $P = 0.842$, $R^2 = 0.001$). Surface pause durations were highly variable ($\bar{X} \pm \text{SD} = 183.05 \pm 158.06$ s) and were not related to current velocity (regression: $F_{1,59} = 0.22$, $P = 0.639$, $R^2 = 0.004$; Fig. 1) or travel time (regression: $F_{1,48} = 0.13$, $P = 0.719$, $R^2 = 0.003$).

DISCUSSION

Time Allocation Underwater

Previous observations of diving birds have provided only partial and incomplete support for predictions of the

dive cycle models, particularly that time at depth f initially increases with increasing travel time τ in shallow dive tanks (Fig. 1, region A; Carbone & Houston 1994; Carbone et al. 1996). Here we have empirically demonstrated that, given a sufficient increase in travel time, time spent on the bottom significantly decreases, as predicted theoretically (i.e. Fig. 1, region B). Together these results provide strong support for the most general prediction of the dive cycle models (Houston & Carbone 1992).

Dive duration of eiders in our study did not vary in relation to current velocity or travel time. This result is expected from dive cycle models once oxygen stores are utilized to near capacity. Dive duration was relatively constant across current velocity at a mean \pm SD of 58.5 ± 5.3 s, which closely corresponds to the estimated aerobic dive limit (ADL) for common eiders (~ 60 s, MacCharles 1997; 51 s, Hawkins et al. 2000), and is similar to maximum dive durations of eiders observed foraging at similar depths in the Gulf of St Lawrence (Ydenberg & Guillemette 1991). Observations of free-ranging phocid seals similarly indicate that dive durations are consistently close to the estimated ADL (Thompson & Fedak 2001). This constancy in dive duration for eiders suggests that, even at slack currents, eiders that dive to 11.3 m for mussels use the majority of their oxygen stores. As travel time and the number of wing flaps to descend to depth increase with current velocity, energy expenditure may increase with current velocity (Heath et al. 2006). Therefore, a dive of similar duration could require the use of more oxygen in faster currents, and given fixed oxygen stores, dive duration would be expected to decrease in faster currents. We did not observe this decrease in dive duration, although it could have occurred in very fast currents, but was not statistically detectable (e.g. dive durations in fast currents in Fig. 2 were mostly below the average dive duration). It is also possible that, in faster currents, eiders use their oxygen stores closer to capacity than during weak currents (and/or increasingly use anaerobic pathways) partly to compensate for reduced foraging time. They could also increase respiratory frequency before diving to increase their oxygen stores in fast currents (e.g. see Parkes et al. 2002). Detailed energetic and physiological studies would be required to fully evaluate these possibilities.

Oxygen Balance and the Duration of Surface Pauses

It is difficult to evaluate whether the duration of surface pauses in previous dive tank studies supported rate-maximizing predictions of diving models, because long surface durations were excluded from analysis. In contrast to predictions of diving models, observed durations of surface pauses in our study were not related to any components of diving behaviour (Fig. 2). Halsey et al. (2003b) also found that mean surface duration of individual tufted ducks were not predicted by optimal diving models (although model predictions were more accurate at predicting surface duration averaged over multiple birds). Furthermore, the breathing rate and oxygen uptake of tufted ducks occurred rapidly, and breathing rate could

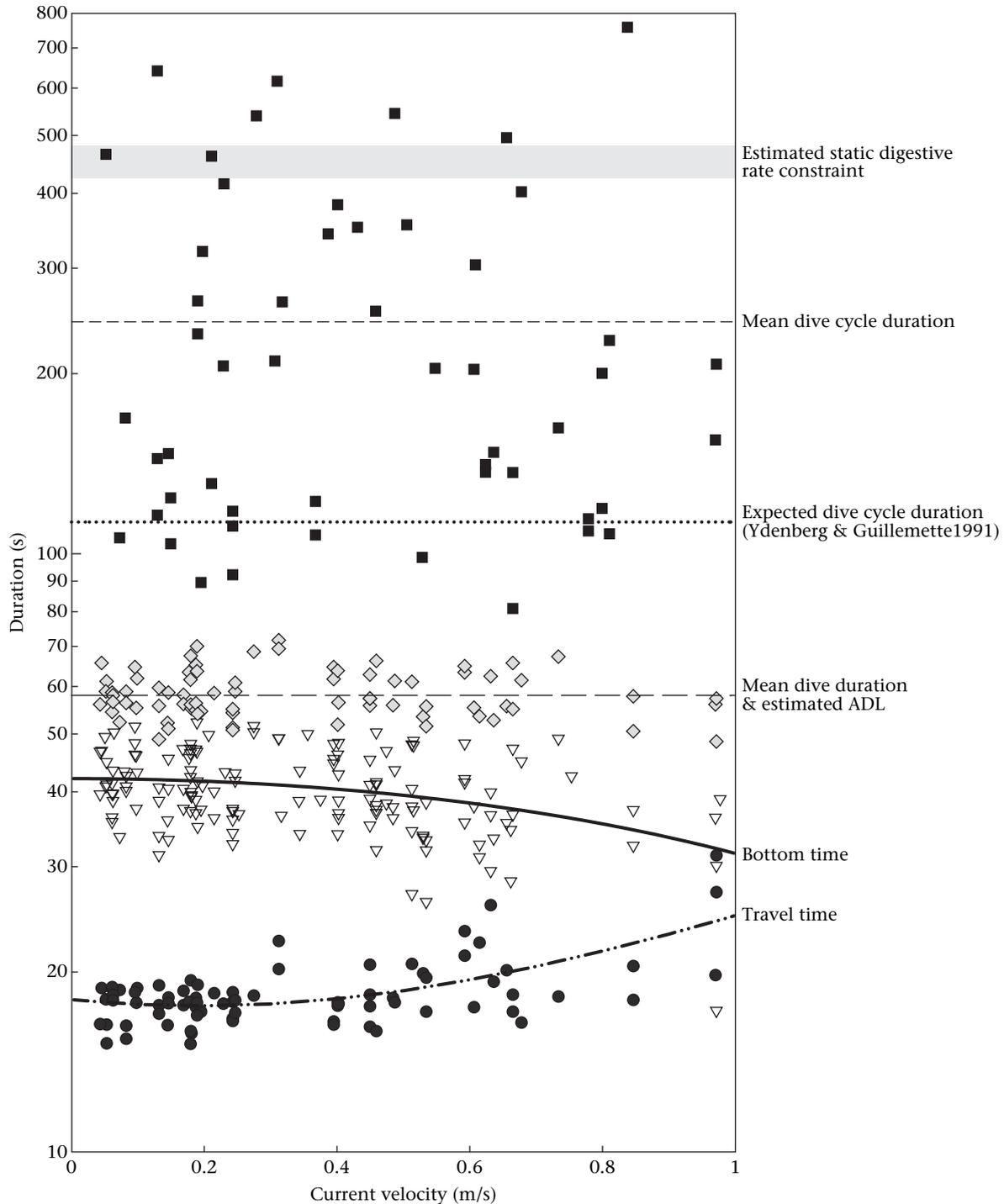


Figure 2. Relationship between travel time (●; descent plus ascent), bottom time (▼), dive duration (◇) and dive cycle duration (■: dive + surface pause) in relation to current velocity (m/s) for common eiders diving to forage on mussels at a constant depth of 11.3 m. An estimated dive cycle duration based on a digestive processing rate constraint is indicated by the shaded grey area (see text).

be adjusted by the animal as needed (Parkes et al. 2002; Halsey et al. 2003b). A number of alternative mechanisms have been suggested for observed variation in the duration of surface pauses, including synchrony among conspecifics, predation risk and vigilance (Schenkeveld & Ydenberg 1985; MacCharles 1997; Heithaus & Frid 2003). Eiders wintering at our study site did not dive

synchronously or have well-defined foraging bouts. Durations of surface pauses were extremely variable and often of sufficiently long duration to cast doubt about the role of any of these potential mechanisms. Some surface durations were in the range predicted by the regression curve of Ydenberg & Guillemette (1991), although the average surface duration was considerably higher than this value

(Fig. 2). These findings suggest that, while oxygen balance appears to be important in explaining time allocation underwater (i.e. the decrease in bottom duration), given the extensive duration of surface pauses, long-term foraging rate does not appear to be maximized over the constraint of loading oxygen stores at the surface.

Energetic Limits to the Diving Models

The models of Houston & Carbone (1992) also considered the influence of gross rate of energy gain on time spent foraging, although this did not have a major influence on model predictions, particularly when intake rate was constant. However, as travel time increases, the dive cycle models eventually make the biologically unrealistic prediction that foraging divers will spend a very long (and eventually infinite) amount of time on the surface in order to spend an increasingly (and eventually infinitely) short amount of time in the patch (Fig. 1, region C). Obviously, diving will not be profitable when long travel times provide no time to forage at depth within aerobic limitations. Even if energy intake is constant while foraging at depth, at some point the energetic costs of the dive cycle will be greater than the energy gained. More precisely, this will occur when

$$e(f^*) < f^* e_f + \tau^* e_\tau + s^* e_s$$

where $e(f^*)$ is gross energy intake as a function of foraging time f , and e_f , e_τ and e_s are the energetic costs of foraging f , travelling τ , and pausing on the surface s , respectively. Most eiders stop foraging when tidal currents are in excess of 0.8 m/s (unpublished data), which closely corresponds with accelerating increases in travel time and decreases in bottom time observed in our study (Fig. 2). Energetic balance could therefore be an important factor producing an upper limit on the parameter range for which the dive cycle models are applicable. Consideration of energy balance could be particularly important in applying diving models in the wild. For example, dive cycle models have previously been used to investigate the best depth at which to forage (Mori 1998). Similarly, our results indicate that foraging will be most profitable at this site when diving in slack currents, corresponding to the shortest travel time and the longest bottom time, and therefore, the greatest expected net energy gain per dive.

Multiple Rate Constraints

Dive cycle models may be useful in predicting the duration of surface pauses in situations when, for example, environmental conditions dictate maximized rates of foraging at the timescale of individual dive cycles. This constraint could be important when individuals exploit high-energy and/or ephemeral prey, or when they intermittently dive at high rates during structured foraging bouts. However, our results indicate that the dive cycle models may not generally be useful in predicting the duration of surface pauses and therefore patterns of foraging by diving birds in the wild. Recent literature

suggests that replenishing oxygen stores on the surface occurs over extremely short timescales (e.g. oxygen stores of tufted ducks can be filled to capacity within 10–15 s; Parkes et al. 2002). Processes occurring over longer timescales than oxygen balance could therefore have a greater influence on foraging patterns. For example, harlequin ducks, *Histrionicus histrionicus*, wintering in coastal Newfoundland, Canada reduced short-term foraging rate by increasing the duration of surface pauses just before dusk; however, this corresponded with an increase in the number of dives per foraging bout and therefore an increase in long-term foraging effort (Heath et al., in press). It was hypothesized that a trade-off between time allocation in dive cycles and foraging bouts could be influenced by fatigue. Supporting this conjecture, observations of cyclical increases and decreases in foraging effort (Ydenberg & Forbes 1988; Ydenberg & Guillemette 1991; Heath et al., in press) and a variety of literature on intermittent locomotion and exercise indicates that trade-offs may occur between behaviour in the short and long term. Owing to longer-term constraints such as fatigue, a reduction in short-term rate of locomotion can lead to an increased rate of work over the longer term (Weinstein 2001; Kramer & McLaughlin 2001). Therefore, if other factors besides oxygen balance are important over longer timescales, short-term currencies such as maximizing the proportion of time spent at depth per dive may not accurately reflect longer-term fitness. Note that the 'long-term' foraging rate terminology used by Stephens & Krebs (1986) refers to specific details of how rate calculations are made, whereas the assumption in static models is that the process being optimized (e.g. dive cycle, patch choice) occurs an infinite number of times. Such static modelling approaches only consider a single rate process or timescale, and the assumption that foraging currencies scale to long-term fitness is fundamental but rarely tested.

Given the extensive durations of surface pauses observed in our study, oxygen balance and endurance are unlikely to be the primary factors determining foraging patterns of eiders at this site. However, other longer-term constraints such as digestion could be important. Mussels are swallowed whole and must be ground in the muscular gizzard, a process which could produce a constraint on energy intake for eiders (Guillemette 1994, 1998; see also Zwartz et al. 1996). Based on esophagus contents from eiders at our study site and those wintering in Greenland, eiders obtain an estimated meal size of 4.1–4.7 g wet mass of mussels per dive (S. Jamieson, personal communication). Brinkman et al. (2003) have suggested a processing limit of 0.67 g/min, which leads to an estimated static digestive processing rate constraint of 367–421 s per surface duration (425–479 s per dive cycle). As seen in Fig. 2, most dive cycles were shorter than these dive cycle durations, suggesting that they are reasonable estimates. However, there was large variation in dive cycle duration, and a number of dive cycles were considerably longer than these estimates of a digestive processing constraint. Of course, static estimates do not consider how foraging rate may vary as a function of how full the gullet is, which could explain some of the variation in the observed durations of surface pauses, and is a topic that we are

investigating in forthcoming research (see also Zwarts et al. 1996). Allocation of time underwater would still be expected to correspond with predictions of the diving models, however, longer surface durations required for digestion could mean that oxygen stores are fully reloaded before each dive. With oxygen stores at capacity, maximizing foraging rate for sessile prey like mussels would require diving until the aerobic dive limit (or more accurately, their diving lactate threshold; Butler 2004) was reached. An increase in travel time would correspond with a forced decrease in the duration of foraging at depth, as predicted by diving models and observed in this study. Therefore, maximization of foraging rate could be a more dynamic process in response to both rates of digestion and oxygen balance, and interactions between these rate constraints could be important in determining foraging patterns in the field.

Summary

In conclusion, we suggest that while the existing dive cycle models are an important tool for understanding the trade-offs between time on the surface and time at depth when oxygen balance is the predominant constraint on dive cycle activity patterns, factors operating over other timescales can also influence observed behavioural patterns. As these models only consider a single rate, our results suggest that caution should be used when assuming that such foraging currencies scale to fitness and when applying predictions of these models to assess foraging patterns in the wild. As in other areas of ecology, our findings suggest that a multiscale approach will be required to understand observed behavioural patterns. Dynamic approaches that can keep track of multiple physiological and environmental states and that can be investigated over different timescales are likely to provide the next important step for understanding the behavioural patterns and elucidating the fascinating issues that diving animals face when foraging.

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