



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

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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 t_d and time spent on the surface between dives, t_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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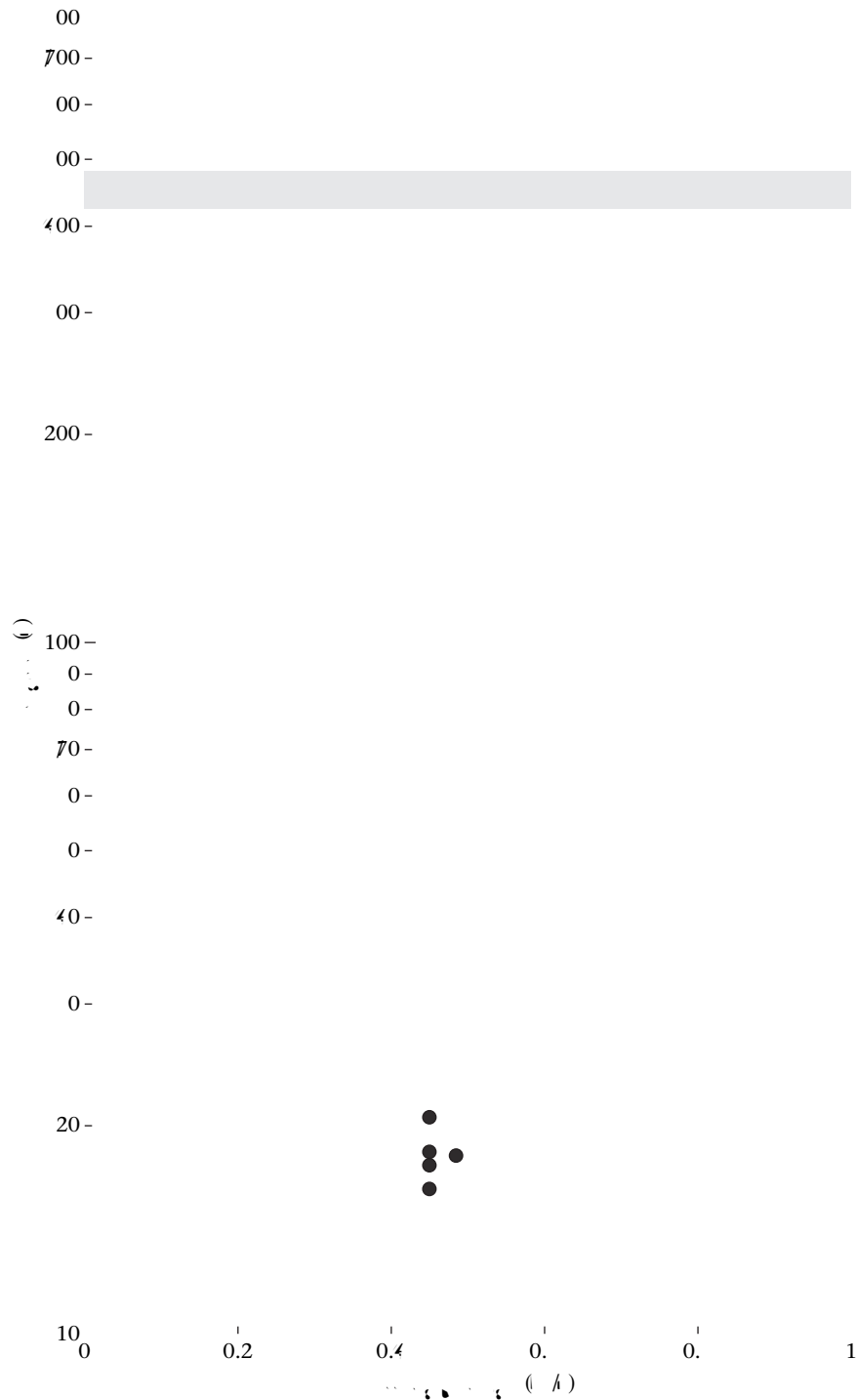
& McNamara 1985), departing the surface where oxygen is obtained (with assumed diminishing returns), to forage at depth, and subsequently returning to the surface. The marginal value theorem (Charnov 1976) is used to find the maximum 'long-term' foraging rate (Stephens & Krebs 1986), equivalent to maximizing the proportion of time at depth, for a given travel time τ . This allows pre),

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, *Haliaeetus urinator*, 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* (Heath et al. 2006). A noninvasive underwater video configuration allowed us to follow eiders through complete dive cycles over the same subtidal mussel beds. There

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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 complete-



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.

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

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.

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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