



Increasing energy expenditure for a deep-diving bird alters time allocation during the dive cycle

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How foraging animals respond to changes in energy costs is poorly understood. Energy costs are especially important for central-place foragers because they determine transit costs as well as foraging costs. For example, oxygen consumption during diving determines the minimum surface pause for a given oxygen store, dive depth and dive duration. A theoretical model based on the marginal value theorem suggests that dive duration should decrease and surface pauses should remain constant when energy expenditure during foraging increases, because divers balance oxygen gains and losses over a dive cycle for a given time at the surface. We tested this hypothesis by increasing hydrodynamic drag on Brünnich's guillemots, *Uria lomvia*, using wooden blocks attached to their backs. Handicapped guillemots decreased dive duration without altering surface pauses, as expected. This occurred because they increased surface pauses for a given dive depth and duration. The relationship between dive depth and duration and that between bottom time and dive duration did not differ for handicapped and unhandicapped guillemots. Dive duration did not increase and dive depth only slightly increased with sequential dives within a bout. The change in dive depth decreased with the number of dives in the bout and an index of patch quality, suggesting that guillemots maintained a constant dive depth when a high-quality prey patch was encountered. Although increasing energy expenditure altered the relationship between surface pauses and dive duration, it had little effect on time allocation within a dive (transit time, bottom time).

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The energy costs associated with foraging vary continually for wild animals as environmental conditions and prey-capture demands change. These costs can result in physiological changes (i.e. increase/decrease in energy output) without any alteration in behaviour, or they can result in behavioural changes. For example, when the cost of flight was increased through experimental manipulation, birds altered their behaviour with very little change

in energy expenditure (Nudds & Bryant 2002; Hambly et al. 2004). In contrast, energy costs for bats tripled when wing loading was doubled experimentally (Hughes & Rayner 1991).

For central-place foragers, such as diving birds, energy costs are especially important because they determine transit costs as well as foraging costs. Diving birds are central-place foragers. After foraging at depth, they need to return to the surface to replenish oxygen stores (Gaston 2004). The time spent replenishing oxygen stores increases rapidly with dive duration (Thompson & Fedak 2001; Wilson & Quintana 2004). This is especially true after the point where oxygen stores are exhausted ('aerobic dive limit'), because metabolizing lactate during the postdive interval is time-consuming. Thus, increasing

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foraging time at depth can result in long surface pauses and therefore reduce foraging time as a proportion of total time in the dive cycle (Thompson & Fedak 2001; Gaston 2004; Wilson & Quintana 2004). There have been several attempts to model how diving birds manage the trade-off between extending foraging time and reducing surface pauses to maximize net energy gain or efficiency (Kramer 1988; Ydenberg & Clark 1989; Mori 1998a, b, 1999).

Early attempts to model dive behaviour focused on trying to explain why some dives were exceptionally long (Kramer 1988). These models showed that using anaerobic metabolism, despite its associated longer surface intervals, could be a beneficial strategy if prey densities were rich, if prey were unlikely to be encountered after a patch was left, or if travel time to patches was long (Ydenberg & Clark 1989; Houston & Carbone 1992; Mori 1998a, b). Furthermore, diving for the maximum time possible depleted oxygen reserves entirely and therefore maximized oxygen uptake rates (Kramer 1988). Later researchers noted that very few dives actually exceed the aerobic dive limit (Kooyman & Ponganis 1998; Thompson & Fedak 2001). Thus, later models attempted to explain why few dives are as long as the maximum duration possible. Explanations included the benefits of giving up early in a dive when no prey is located (Thompson & Fedak 2001) and maintenance of excess oxygen reserves to enhance survival when rare events, such as the appearance of predators or prey requiring extended handling time, occur (Wilson & Quintana 2004).

Oxygen consumption rate is one of the variables that determine the trade-off between foraging time and surface pause duration (Carbone & Houston 1996; Carbone et al. 1996). Higher oxygen consumption rates during diving increase surface pauses for a given dive duration. Application of the marginal value theorem showed that, on theoretical grounds, divers should spend less time foraging if the energetic costs of foraging increase, while surface duration should not change (Houston & Carbone 1992). Houston & Carbone's (1992) model assumes that the curve of oxygen gain with surface duration is fixed and, therefore, that a diver balances its oxygen gains and losses over a dive cycle, for a given time at the surface. Consequently, an increase in the energy costs of foraging forces a decrease in time spent at the foraging site. Experimental manipulations, primarily in the laboratory, have shown that dive duration decreases in response to increased energetic costs (Carbone & Houston 1994; Webb et al. 1998; Cornick & Horning 2003), although Halsey et al. (2003) found that captive tufted ducks, *Aythya fuligula*, increase dive duration. In two studies, surface pauses did not change (Carbone & Houston 1994; Halsey et al. 2003).

A potential complication when testing this hypothesis in an experimental setting is that diving metabolic rate may change through the dive bout. Green et al. (2003, 2005a, b) noted that a drop in core body temperature (e.g. Bevan et al. 1997; Handrich et al. 1997) reduces metabolic rate. As a dive bout progresses and core body temperature decreases, metabolic rate may decrease and, thus, dive duration may increase. This observation suggests that dive depth and duration might increase during the dive bout. However, Green et al. (2003) found that

dive duration did not increase during dive bouts of macaroni penguins, *Eudyptes chrysolophus*. These authors suggested that this effect may be more likely in species that exceed their aerobic dive limit regularly. Brünnich's guillemots, *Uria lomvia*, may be a good candidate species to test the hypothesis that dive duration and depth increase during a dive bout, because individuals regularly exceed their aerobic dive limit (Croll et al. 1992). However, Niizuma et al. (2007) found that guillemots reduce their peripheral temperature but increase their core body temperature during dive bouts. Nevertheless, guillemots may use other mechanisms (e.g. reduced blood flow to metabolically expensive organs) to reduce diving metabolic rate progressively through dive bouts.

A second complication is that Houston & Carbone (1992) assumed that the oxygen uptake rate decreases smoothly with time spent on the surface (Kramer 1988). Walton et al. (1998) noted that, for birds, the dive-to-surface ratio peaks at an intermediate value. They suggested that this is because oxygen uptake in birds is biphasic; there is a rapid increase in oxygen uptake upon surfacing as oxygen enters the respiratory track followed by a slower increase in oxygen uptake (representing oxygen recovery in haemoglobin and myoglobin) after the respiratory track is completely replenished. Walton et al. (1998) showed that a biphasic oxygen uptake curve necessarily results in a peak in the dive-to-surface ratio at the value representing the 'kink' in the oxygen uptake curve.

The relation between time allocation during the dive cycle and energy expenditure has seldom been examined on free-living, pursuit-diving birds. Currently available information deals mainly with species feeding on sessile prey and hence knowing exactly where their prey is at the start of each dive (Carbone & Houston 1994, 1996; Parkes et al. 2002; Halsey et al. 2003; Heath et al. 2007). To address this issue, we attached blocks, equivalent to 2.6 and 5.3% of the body cross-section, to the backs of free-living guillemots, and compared time allocation for the same individuals with and without these handicaps. We tested the following hypotheses: (1) handicapped individuals will reduce dive duration but will not alter surface pause duration; and (2) dive duration will increase as the dive bout increases.

METHODS

Our observations were made at the Brünnich's guillemot colony at Coats Island ('Q Plot'; 62°57'N, 82°00'W), Nunavut, Canada (Gaston et al. 2003, 2005a, b) during chick-rearing season in 2004, 2005 and 2006 ($N = 23$ in 2004; $N = 33$ in 2005; $N = 57$ in 2006). We equipped adult guillemots with cylindrical Lotek 1100LTD Time–Depth–Temperature Recorders (TDRs; Lotek Marine Technology, St John's, Newfoundland, Canada; mass = 4.5 g; diameter = 1 cm; length = 3.3 cm; sampling interval = 3 s) attached to the leg bands. Deployment methodology was approved under the guidelines of the Canadian Committee for Animal Care (Protocol No. F04-030). Whereas back-mounted TDRs are known to impact guillemot provisioning rates (Watanuki et al. 2001; Hamel et al. 2004; Paredes et al. 2005), number of foraging trips (Tremblay et al. 2003; Hamel et al. 2004; Paredes et al. 2005), adult

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